

**Morphological divergence in the House Wren (*Troglodytes aedon*) species complex:
A study of island populations with a focus on the Grenada House Wren (*T. a. grenadensis*)**

by

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ABSTRACT

House Wrens (*Troglodytes aedon*) are common throughout North, Central and South America; however, there is a knowledge gap regarding the morphology of certain populations, particularly those residing on islands, which may have adapted to the unique geographic pressures compared to the conditions House Wrens face on the mainland. I examined three questions to understand the morphology of insular house wrens, by using both museum samples and live-captured male House Wrens and other closely related species within the genus *Troglodytes* ($n = 1,189$). I analyzed six morphological characteristics: wing chord, tarsus length, bill length, bill width and bill depth. First, I examined whether island House Wrens were morphologically different from mainland House Wrens as well as different among each island population. Insular birds were larger than mainland birds in all morphological measurements. I found morphological features were unique to each island, suggesting there are different factors on each island influencing morphology. I then used linear regression to examine the influence of island proximity and island size on House Wren morphology of thirteen island populations. House Wrens on smaller islands had shorter tails and tarsi, and smaller bill depth and width. Islands that were further from the mainland had House Wrens with longer tails and smaller bills. Lastly, I examined whether House Wrens on Grenada, the southern-most Caribbean island, are morphologically distinct within the House Wren complex, based on seven morphological characteristics. When the Grenada House Wren was compared to 26 other subspecies and closely related species within the genus *Troglodytes*, morphology of Grenada House Wrens was different in 81% of morphological comparisons, and of these, was bigger in 88% of comparisons. These findings on insular House Wren morphology allows for a deeper understanding of the debated taxonomy of these House Wrens while also filling a data gap for the understudied island populations.

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1. INTRODUCTION

1.1 Background on Island Ecosystems

The natural environment can influence the adaptation and evolution of species, and compared to mainland ecosystems, islands provide unique ecological and environmental conditions for evolution to occur. Islands often have relatively low species richness, unusually high or low predation pressure, relatively low habitat diversity, increased intra-specific competition, and reduced gene flow (MacArthur, 1972). The combination of these conditions can lead to unique evolutionary pathways that impact and significantly alter the morphology of island populations.

Islands are naturally isolated landscapes, as over-water dispersal creates a significant barrier, and thus reduces colonization and gene flow. This may promote divergence within a species that also occurs the mainland (Ricklefs and Bermingham, 2008). Island populations may develop significantly different traits from their mainland conspecifics due to the unique insular conditions and, in some cases, lead to island populations that are reproductively isolated and genetically unique (e.g., Campagna et al., 2012). Many insular bird populations, such as those on Lesser Antillean islands, have yet to be thoroughly studied. The extent of their divergence is generally unknown as there is a significant lack of basic natural history. The need for this natural history is prevalent as these island populations may provide opportunity to understand adaptation to local conditions and evolutionary trends. This is especially true for species that have large populations ranges and inhabit various island and mainland regions.

1.2 Background on House Wrens (Troglodytes aedon)

The House Wren (*Troglodytes aedon*) is a species that has a large and diverse geographical range; their range is the largest of any native songbird in the western hemisphere (del Hoyo et al., 2005; Kaluthota et al., 2016). They are found from north-central Canada, south to Argentina and east into the Lesser Antillean islands. House Wrens currently are found on four islands within the Lesser Antillean range: Dominica, Saint Lucia, Saint Vincent and the Grenadines, and Grenada. Historical records also reported subspecies on Guadeloupe and Martinique, but they are believed to be currently extirpated from these islands (Bond, 1960; eBird, 2012).

Morphology of House Wrens differs throughout their range, but some general trends have been noted. Sosa-López and Mennill (2014a) found that latitude impacted morphological traits; tarsus length and bill size were largest at the equator and decreased with increasing latitude. They also determined that wing and tail length were greatest in the north and gradually decreased through to the southern populations. This may be due to the migratory behavior of northern House Wrens as migratory subspecies tend to have larger wings for long, sustained flight (Nowakowski et al., 2014; O'Hara et al., 2006). Although this study examined a large proportion of House Wren subspecies, Lesser Antillean House Wrens were not well represented with only nine adult male House Wrens from Dominica included (Sosa-López and Mennill, 2014a). Furthermore, another study on the Cozumel Wren (*Troglodytes beani*), a House Wren subspecies found on the Mexican island of Cozumel, showed results consistent with the hypothesis of insular ecological release with Cozumel Wrens having bigger bills and longer wings and tails than mainland subspecies (Sosa-López and Mennill, 2014b). It is therefore possible that other insular populations may experience the same morphological trend.

1.3 Problem Statement

House Wrens on Lesser Antillean islands have not been well studied and the natural history of these populations still needs to be comprehensively described. Although large-scale morphology studies have been conducted on mainland House Wrens (e.g., Sosa-López and Mennill, 2014a), very few insular House Wren subspecies have been included; this is likely due to the complicated logistics of researching multiple island populations and a lack of available museum specimens. My research aims to fill this knowledge gap and gain a clearer understanding of the morphology of insular House Wrens and the mechanisms leading to their unique morphology.

1.4 Objectives

The objective of this study was to examine the morphology of insular House Wrens, with a particular focus on House Wrens on the island of Grenada, a small Lesser Antillean island at the south end of the Caribbean chain. This objective was broken down into several smaller goals:

1. To determine whether insular House Wrens had different morphological characteristics than their mainland counterparts and whether they follow the predicted morphological trends for island birds.
2. To determine whether island geographical conditions influence the trends in morphology for insular House Wrens.
3. To assess whether House Wrens in Grenada are significantly different morphologically from other subspecies or closely related species.

1.5 Organization of Thesis

This thesis has been organized into four chapters and written as a “sandwich thesis”. The first chapter provides an introduction of the thesis topic and includes the objectives for the study. Chapter two contains the methods, results, and discussion on the research done comparing mainland and island House Wren morphology, differences in morphology among insular House Wrens, and insight into geographical factors that may influence island morphology. Chapter three focuses on the morphology of Grenada House Wrens and attempts to identify whether they are morphologically unique within the House Wren species complex. The final chapter takes into consideration the results of this research in examining management implications for the conservation of House Wrens on Grenada and the potential taxonomic upgrading of this resident population.

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2. INSULAR MORPHOLOGY TRENDS WITHIN HOUSE WRENS (*Troglodytes aedon*)

Abstract

Islands generally have low species and habitat diversity and are geographically isolated, leading to unique evolutionary pressures and potential morphological divergence among island populations. I examined morphological trends of male insular House Wrens (*Troglodytes aedon*) as they are an ideal species to study morphological trends due to their wide geographic range across the Americas and on many isolated islands. I analyzed wing chord, tarsus length, tail length, and bill depth, width, and length of museum specimens from the mainland and sixteen island populations ($n=1,189$), along with live-captured male House Wrens from Grenada ($n=25$) and Mexico ($n=56$). Insular House Wrens showed patterns consistent with the island rule, which states islands have increased intra-specific and decreased inter-specific competition due to low species diversity, which leads to larger and more generalist morphology of island birds. When comparing among islands, geographically closer House Wren populations had more similar wing chord, tail length, and tarsus length, while bill morphology was independent of geographic proximity. When examining island geography, House Wrens on larger islands tended to be smaller, which may reflect the fact that to larger islands have more heterogenous habitat and increased intensity of inter-specific competition. House Wrens on islands further from the mainland had longer tails, which may be a trait passed down from founding populations that had longer tails that facilitated mobility. These results fill an important knowledge gap regarding understudied insular House Wrens and provides insight on how morphology of insular House Wrens vary with the geography of the island.

2.1 Introduction

Island biogeography suggests that islands close to the mainland and islands with larger land area tend to have greater species diversity (MacArthur and Wilson, 1967). Distance to the mainland and distance from other islands can both influence community composition. Islands closer to the mainland have higher colonization rates due to the shorter over-water barrier to dispersal (MacArthur and Wilson, 1967). As a result, different island populations experience different environmental and ecological pressures, and thus adaptation to these unique conditions is predicted to occur differently among islands. Islands that are close to one another may have more similar species and populations (Morand, 2000), and nearby populations tend to be more genetically similar (e.g., Le Roux et al., 2014) as colonization and dispersal of a species is more likely over smaller geographic distances (MacArthur and Wilson, 1967).

In addition to the geographic position of the island, island size can also contribute to the environmental conditions faced by insular populations. Compared to the mainland, most islands are species-depauperate (Cox and Ricklefs, 1977), and smaller islands, particularly those furthest from the mainland, tend to have the lowest species richness (e.g., MacArthur, 1972; Williams, 1964; Abbott 1980). Attempts to understand this relationship, though, have brought forth questions of other factors that vary with island size and that may also influence species richness. Islands that have more diverse habitats generally have more resources and thus higher species diversity (Ricklefs and Lovette, 1999); island size is correlated with habitat diversity and thus these two factors are likely related. Lower species diversity can lead to niche expansion within species because the lack of inter-specific competition allows for species to expand their use of resources and habitat, and allows for species to adapt (e.g., behaviorally, morphologically) to local conditions (MacArthur and Wilson, 1967).

Due to these patterns, island populations tend to show specific patterns in morphology. When compared to mainland conspecifics, smaller bodied animals tend to evolve towards gigantism whereas larger bodied animals tend to evolve towards dwarfism (Foster, 1964; Lomolino, 2005). This trend was first recognized in mammals and was named “Foster’s rule” or the “island rule” (Foster, 1964). The island rule has since been generalized to include morphological patterns of bats, passerine birds, snakes, and turtles (Lomolino, 2005). The island rule in passerines has been linked to geographic conditions unique to the island, including island size and isolation; passerines on smaller and more isolated islands exhibit the largest body sizes (Lomolino, 2005).

Mechanisms for this trend towards larger body sizes on islands include ecological release and increased intensity of intra-specific competition than on the mainland (Lomolino, 2005). Ecological release is the expansion of a species’ niche within landscapes that exhibit habitat and resources different from the original environment where its founding population resided (Cox and Ricklefs, 1977). Many studies have shown that this is common in island communities (e.g., Crowell, 1962; Cox and Ricklefs, 1977; Lomolino, 2005). Ecological release is strongest on islands with low species richness, which can be linked to islands that are isolated, small, and have low habitat diversity. On islands, selection tends to favor generalism and birds have adapted to ecological pressures by increasing body size, such as longer tarsi, and increasing both size and variability of their bill (Grant, 1965; Clegg and Owens, 2002; Lomolino, 2005; Vázquez and Stevens, 2004). Increased bill size allows for a wider variety of prey as well as ability to consume prey at higher trophic levels (Hsu et al., 2014), thus giving the species an advantage over other species with more specialized or smaller bills. Variability in bill size within a species allows for reduced intraspecific competition for resources (Van Valen, 1965; Hsu et al., 2014). In

some species the variation in bill size has led to sexual dimorphism in bill morphology (Luther and Greenberg, 2014) as a result of high intra-specific competition. The combination of decreased inter-specific competition and decreased predation pressures can result in high intra-specific competition (MacArthur, 1972), which can lead to birds with larger body sizes on islands compared to mainland conspecifics.

Given that each island has a unique combination of geographical conditions, islands provide a perfect opportunity to study the way these variables influence morphology. The purpose of this study was to determine: (1) if House Wrens show differences in morphology between mainland and island populations, (2) examine differences in morphology among island populations, (3) determine whether morphology of House Wrens is more similar on geographically proximate islands, and (4) evaluate the potential impacts of geographical conditions (distance to mainland and island size) on morphological characteristics of House Wrens.

2.2 Methods

This research was conducted under University of Manitoba animal care protocol F15-026/1 with permission of the Government of Grenada and private landowners.

2.2.1 Museum Sampling

It was beyond the scope of my research to collect live samples from all House Wren populations. Museum specimens were, therefore, sampled to provide a wide variety of House Wren subspecies and a few closely related species within the same genus of *Troglodytes* (*T. beani*, *T. sissonii*, and *T. tanneri*) for morphology comparisons. I measured specimens from four different museum collections: the Smithsonian National Museum of Natural History (Washington, D.C.), the Harvard University Museum of Comparative Zoology (Boston,

Massachusetts), The Manitoba Museum (Winnipeg, Manitoba) and The University of Manitoba Zoology Museum (Winnipeg, Manitoba). To further add to the sample size, a database of morphology measurements collected by Sosa-Lopez and Mennill (2014) was included. These samples came from specimens at the American Museum of Natural History (New York), the Field Museum of Natural History (Chicago), Museo de Zoología “Alfonso L. Herrera” (Mexico City), and from live House Wrens captured on the islands of Cozumel and Socorro in Mexico.

Measurements from museum specimens were conducted using the same techniques as in the field to maintain consistency among samples. Some specimens exhibited wear from use in the museums (e.g., broken bills); measurements from these specimens were only used if the wear did not impact the characteristic being measured.

2.2.2 Field Methods in Grenada

Nine study sites were used for field research across Grenada, a small (348.5 km²) southern Caribbean island (12.135212, -61.685795). Grenada is a tri-island state, but all field research was conducted on the main island of Grenada as there have been very few House Wrens documented on the smaller islands (eBird, 2012; Williams, 2020). Eight of the sites were on private property and one was on publicly accessible government property. Study sites were chosen to encompass a large geographical range on Grenada, both inland and coastal, while also covering a wide range of habitat types (Figure 1). Most sites were in highly human-altered habitats as most of low- to mid-elevation areas of Grenada consist of agricultural land or low-density residential areas with patchy semi-deciduous forests (Helmer et al., 2008). One location was mid-elevation, mature lowland forest in a large (approximately 200 acre) undeveloped lot; most House Wrens at this location were caught on the perimeter of this property, near human

infrastructure. Five sites were located in private property consisting of human-created garden habitat near residences or out-buildings (all < 1 acre). Another site in the south-east was a higher elevation cocoa plantation and private gardens (approximately 2 acres). One site was in a 300-acre, diverse, working agroforest property that consisted of mixed plant species such as citrus, soursop, mango, cocoa, and nutmeg. Lastly, the southernmost site was in a 1-acre, coastal dry-forest habitat of secondary scrub located on government property.



Figure 1: Map showing the location of my nine banding sites that were used in 2018 to 2019 across the main island of Grenada.

House Wrens ($n = 73$) were caught in Grenada between 2015 and 2019. Both passive mist-netting without song lure and targeted mist-netting with song lure were used to capture House Wrens. All House Wrens were banded using numbered aluminum bands on their right tarsus (size 1 or 1B) and, to visually distinguish among individuals, most House Wrens were also banded with a unique combination of two plastic colour bands on the left tarsus. Several

measurements were taken as per Pyle (1997). Wing chord length was taken from a non-flattened wing and to the nearest millimeter. Tail was measured from base of rectrices to tip of the longest rectrix and to the nearest millimeter. Tarsus was measured using calipers and to the nearest 0.1mm. Bills were measured to the nearest 0.1mm in three different dimensions from the distal end of the nares opening: (1) bill length from nares to tip, (2) width at nares, and (3) depth at nares.

All birds were aged using the Wolfe-Ryder-Pyle (WRP) system; this is the ideal system for tropical passerines as it uses plumage stages for aging and disregards the calendar year (Wolfe et al., 2010). For analysis, I used the WRP age to then categorize House Wrens as either “adult” or “juvenile” with juvenile birds classified as still showing juvenal body feathers. House Wrens are sexually monomorphic (Pyle, 1997), so breeding characteristics (e.g., cloacal protuberance, brood patch) were the only way to accurately sex them in the field. Since the timing of breeding is unknown for House Wrens on Grenada, several birds that we expected to be males (e.g., long wing chord, singing actively, interacting with a known female) could not be sexed by cloacal protuberance; however, we were able to sex twenty-five of the captured Grenada House Wrens as male using the presence of a swollen cloacal protuberance.

2.2.3 Data Management

House Wrens were categorized as an “island resident” if that island had a distinct subspecies or the population had been upgraded to species status. Therefore, any bird that was not labelled as an island resident was either (1) from a continental location and was maintained in a “mainland” category, or (2) was an island individual from a subspecies that was considered the same as a mainland population and thus may interbreed. An example of this was two House

Wrens from Cristobal Island in Panama. The taxonomy of these House Wrens indicate they are the same subspecies as found throughout the rest of Panama (*T. a. inquietus*); this may mean that wrens can interbreed with individuals from the mainland and thus are not a distinct, resident island population. Another example includes one sample from the island of Trinidad was removed from the dataset as, even though it was collected on an island, it was labelled as a migratory subspecies (*T. a. aedon*) and thus was not a true island resident.

Only adult, male House Wrens were used in analyses. Sexes can show significant morphological differences in northern, migratory populations (Pyle, 1997); using only males reduces any potential sex-related biases. For live-captured House Wrens, only individuals showing a swollen cloacal protuberance were sexed as male. For museum specimens, most samples had sex information included on the specimen tag that had been collected by examining the gonads during taxidermy. Only House Wrens that no longer showed juvenal characteristics (e.g., juvenal body feathers, gape in bill, all flight feathers still in sheath) were used. This means that all House Wrens had to have reached or exceeded their first pre-formative molt to be used in these analyses and thus considered an “adult”.

2.2.4 Geographical Factors

We collected data on two geographical factors (island area and island proximity) for thirteen islands with historical and/or current resident House Wrens. This included Grenada, Guadeloupe, Martinique, St. Lucia, St. Vincent and the Grenadines, Dominica, Clarion Island (Mexico), Cozumel Island (Mexico), Coiba Island (Panama), Kidney Island (Argentina), Cristobal Island (Panama), Tobago, and Socorro Island (Mexico). Island distance to mainland was calculated as the distance from the island to the nearest mainland point and was done using Google Earth mapping tools. Island area was collected from a report of the Caribbean Island

Commonwealth (Federal Research Division of the Library of Congress, 1987) or, for smaller islands, was calculated using Google Earth polygon mapping.

2.2.5 Statistical Analyses

Statistical analyses were completed in R Statistical Software, Version 3.5.1 and 3.6.3 (R Core Team, 2018). There were several banders ($n = 10$) over several years ($n = 5$) that collected data on live Grenada House Wrens using two different methods (passive and targeted capture). I examined to see whether year, bander or method had an effect on morphology. I examined year to rule out influence of annual differences in food availability due to weather and I examined bander to rule out influence of different measuring techniques. When examining bander, I only looked at the two banders that collected data on more than five house wrens each; the two banders measured $n = 20$ and $n = 33$ Grenada House Wrens. Linear models ($p > 0.05$) for each morphological measurement were done. I detected no significant effect of bander or year on morphology (Table 1). Therefore, no subsequent models included year or bander as a random effect variable.

Table 1: Linear regression results, including estimate, standard error (SE) and p value, examining the effect of bander or year on six different morphological measurements taken on live-captured male Grenada House Wrens. No significant effect was found for either bander or year on any morphological measurements.

	<i>Bander</i>			<i>Year</i>		
Measurement	Estimate	SE	p	Estimate	SE	p
Wing chord	0.58	0.67	0.39	-0.58	0.93	0.54
Tail length	0.88	0.63	0.17	0.28	0.87	0.75
Tarsus	-0.12	0.15	0.44	0.02	0.25	0.93
Bill length	-0.24	0.30	0.43	0.04	0.31	0.90
Bill depth	-0.06	0.06	0.28	0.14	0.08	0.07
Bill width	-0.14	0.07	0.06	-0.02	0.14	0.86

The first analysis examined morphological differences between island and mainland House Wrens. I grouped all House Wrens designated as island residents, as pre-defined, into an “Island” category and all mainland House Wrens into a “Mainland” category. I used ANOVA with a post-hoc Tukey HSD test to determine whether there was a significant difference in morphological traits. Assumptions of residual normality were evaluated using QQ plots and a Shapiro-Wilk test and normality was met.

I then used ANOVA with multiple pairwise comparisons using post-hoc Tukey HSD Tests to examine whether House Wren morphology differed among different islands. I chose *a priori* to include only populations with more than five samples per island, as this allowed for some variation in morphology within the population. Ten islands were included for this analysis, including Carion Island (Mexico), Coiba Island (Panama), Cozumel Island (Mexico), Dominica, Grenada, Guadeloupe, Kidney island (Argentina), Socorro Island (Mexico), St Lucia, and St Vincent and the Grenadines. Assumptions of normality were tested on residuals using QQ plots and a Shapiro-Wilk test and normality was met.

To examine whether geographical proximity of islands influenced morphology among island populations, I used a Mantel’s test. The Mantel’s test is a non-parametric test used to examine spatial autocorrelation within data using a general regression of matrices (Mantel, 1967; Quinn and Keough, 2002). Mantel’s test helps determine if there is a significant pattern in traits based on distance matrices, with one matrix being geographical distance based off latitude and longitude values (Legendre et al., 2005). For this study, a distance matrix was created for each morphological measurement (providing average difference in size) as well as a distance matrix was created for geographic location (providing geographic proximity). For each morphological characteristic, the morphology matrix was tested against the geographical matrix using

“mantel.rtest” in R package “ade4” with a Monte Carlo set at 999 repetitions (Dray and Dufour, 2007; Bougeard and Dray, 2018; Chessel et al., 2004; Dray et al., 2007). The simulated p -value every time the test is run; therefore, the p -value was categorized as either “Yes” if it was consistently below the 0.05 value and “No” if it was consistently above the 0.05 value when the test was run ten times.

Lastly, I used linear regressions to examine whether geographical factors (island size and distance to mainland) influenced each morphological trait on island populations. Thirteen islands were included in the analysis. I first conducted linear mixed effect models to determine whether random variables related to island (whether specimens on the same island were independent of one another) and year (whether year collected influenced morphology) were necessarily to include in the base models. I used AIC to assess model fit and none of the models with a random variable increased model fit so linear regression was used for further analyses.

I tested for collinearity among the two geographical variables by conducting a Pearson’s correlation test. Island size and distance to mainland showed no association ($R = 0.046$, $p = 0.55$) between the variables and thus both were included in the models (Figure 2). QQ Plots were then used to assess normality of the residuals and normality was met for all models.

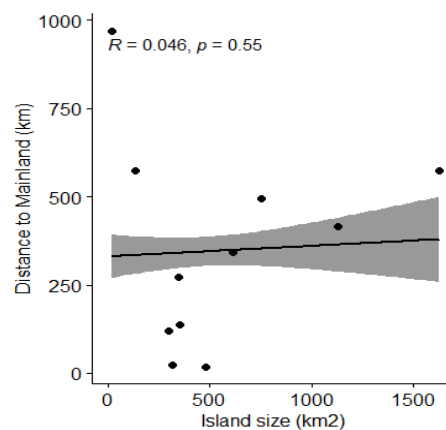


Figure 2: Results of Pearson correlation test that examined the correlation between the geographical factors of island size and distance to mainland ($n = 13$).

Although multiple, simultaneous hypothesis tests were done with a p value < 0.05 (Table 2), I was not concerned about having to make corrections (e.g., Bonferroni correction) to my data. It is known that as the number of tests increase, the chances of incurring a Type 1 error also increase (Rice, 1989). Each question was designed to answer a biologically meaningful question about insular House Wren morphology and this information has not previously been researched; therefore, it was not necessary to conduct a correction for multiple comparisons although the potential of a Type I error was considered in interpreting the results.

Table 2: Overview of statistical tests I conducted in this chapter to answer four questions regarding House Wren morphology in island populations. “Morphology” as a response variable include six different analyses using different characteristics: wing chord (mm), tail length (mm), tarsus length (0.1 mm), bill length (0.1 mm), bill width (0.1 mm) and bill depth (0.1 mm).

Question	Analysis	Response Factor	Fixed Factor
Is there a difference in morphology between mainland and island House Wrens?	ANOVA	Morphology	Island/Mainland (categorical)
Do House Wrens on different islands all have similar morphology?	ANOVA	Morphology	Island Name (categorical)
Are House wrens more similar morphologically when more geographically proximate?	Mantel Test*		
Do geographical characteristics of an island influence House Wren morphology?	Linear Regression	Morphology	Island Size (km ²) + Distance to Mainland (km)

* Mantel’s test does not use fixed or response variables but instead correlates a morphology matrix with a geographic location matrix.

2.3 Results

2.3.1 Morphology on Islands versus Mainland

A total of 1,189 adult male House Wrens from 49 taxonomically distinct groups were included in this analysis. These samples were from the continental mainland of North and South America ($n = 999$) and from 16 different islands ($n=190$). Most morphological traits differed significantly between island and mainland populations (Table 3); tail length was the only trait that did not show a significant difference ($F(1,1165) = 3.02, p = 0.094$). House Wrens on islands had significantly larger wing chord, tarsus and bill measurements compared to mainland populations (Figure 3).

Table 3: ANOVA results, with mean and SD, comparing seven different morphological characteristics between mainland (North and South America) and island ($n = 16$) male House Wrens for seven different morphological characteristics. A total of 1,189 adult male House Wrens were used in analysis with 999 specimens from the mainland and 190 specimens from islands.

Measurement	<i>Mainland</i>		<i>Island</i>		<i>ANOVA</i>		
	Mean	SD	Mean	SD	F	df	p
Wing chord	51.8	2.7	53.8	3.7	76.85	1 1182	<0.001
Tail length	39.5	4.2	40.1	4.2	2.81	1 1165	0.094
Tarsus	18.1	1.7	19.4	1.4	110.4	1 1168	<0.001
Bill length	9.4	1.3	11.5	1.4	401.7	1 1145	<0.001
Bill depth	3.1	0.3	3.4	0.4	142.8	1 1112	<0.001
Bill width	2.9	0.3	3.3	0.4	224.4	1 1169	<0.001

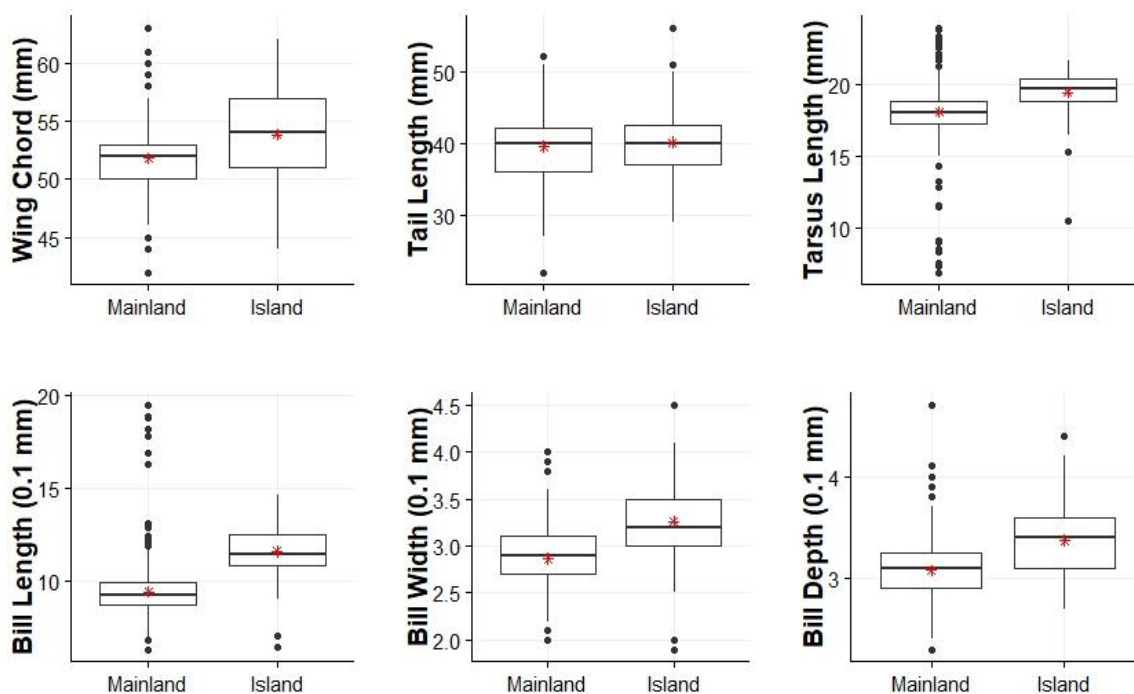


Figure 3: Boxplots comparing mainland and island House Wrens for six different morphological characteristics. Mean value indicated in red asterisk (*). Only tail length was similar for both mainland and island House Wrens; in all other morphologies, island House Wrens were larger. There was also more variation in island House Wrens morphology except in tail and tarsus lengths.

2.3.2 Are the island populations different morphologically from each other?

I included 175 adult male House Wrens from 10 different islands to compare whether each island exhibited different morphology from one another (Appendix A). Tail length varied the most among islands (27 of 46 comparisons: 60%). Wing chord was significantly different in 26 of the 45 comparisons (57%). Tarsus length was significantly different in 24 of the 45 comparisons (52%). Bill length and bill depth were significantly different in 19 of the 45 comparisons (42%). Bill width varied the least amongst islands with only significant differences found in 16 of the 45 comparisons (35%).

2.3.3 Is morphology more similar among geographically closer island populations?

Ten different islands were assessed for whether geographical proximity influenced morphological similarity. Wing chord, tail length and tarsus showed significant similarity among geographically closer populations, whereas all bill dimensions showed no geographical relationship (Table 4).

Table 4: Results of Mantel tests done for each morphological characteristic comparing for 13 different island populations. Samples for each morphology ranged from 169 to 183. The results show the correlation between geography and morphology (R) with significance. All relationships were positive.

Measurement	<i>n</i>	R	<i>p</i> < 0.05
Wing Chord	181	0.1129	Yes
Tail Length	179	0.2591	Yes
Tarsus	183	0.1967	Yes
Bill Length	171	0.0563	No
Bill Width	178	0.0390	No
Bill Depth	169	0.0398	No

2.3.4 Geographical Factors Influencing House Wren Morphology

The relationship between island geography and House Wren morphology (*n*=175) was calculated for thirteen different islands. Islands ranged from 17 – 970 km from the mainland and ranged from 0.3 – 1628 km² in size. House Wrens on smaller islands had shorter tails, tarsi, bill depth and bill width. No significant relationship with wing chord, bill length and exposed culmen was determined between House Wrens and island size. House Wrens that were on islands further away had longer tail lengths but had smaller overall bill morphology (Table 5).

Table 5: Linear regression results and significance for the influence of geographical factors (island size and distance to mainland) on morphology for 13 different island populations of House Wren ($n = 174$). Significant results are bolded.

Measurements	Island Size			Distance to Mainland		
	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>
Wing Chord	-0.001	0.001	0.15	-0.001	0.001	0.28
Tail	-0.005	0.0006	<0.001	0.007	0.001	<0.001
Tarsus	-0.002	0.0002	<0.001	0.0001	0.0003	0.74
Bill Length	-0.0002	0.0002	0.44	-0.002	0.0004	<0.001
Bill Depth	-0.0003	0.00007	<0.001	-0.0004	0.0001	<0.001
Bill Width	-0.0001	0.00007	0.038	-0.0003	0.0001	0.007

2.4 Discussion

2.4.1 Island versus Mainland Morphology

Island House Wrens were larger than mainland House Wrens in most morphological characteristics. The trend towards insular gigantism, as observed in other small-bodied species such as the Tropical Parula (*Parula pitiayumi*), Red-breasted Chat (*Granatellus venustris*) and Happy Wren (*Thryothorus felix*) (Grant, 1965), was also apparent in House Wrens. Ecological release, as predicted by the low inter-specific competition and low predation pressures on islands (Lomolino, 2005), may have led to larger features within insular House Wrens. The larger bill dimensions of island House Wrens could be a result of more generalist feeding behavior (Grant, 1965) as a result of increased intra-specific competition for the potentially limited resources on islands. These results are consistent with niche expansion within House Wrens residing on islands.

Tail length did not vary significantly between island and mainland House Wrens. Advantages of long tails are linked to aerial maneuverability and agility (Fitzpatrick, 1999), both of which are likely relatively unimportant for House Wrens after island colonization, due to this species' affinity for low, dense vegetation (del Hoyo et al., 2005). There is also evidence that tail

length is also linked to migratory behavior, with migratory species having longer tail lengths (Fitzpatrick, 1999). Most House Wren populations, both on the mainland and on islands, appear to be territorial residents that do not migrate long distances; the exception to this are two neotropical migrant populations *T. a. aedon* and *T. a. parkmanii*. These populations breed in the northern United States and the boreal forests of Canada and then winter in southern United States and north/central Mexico (Cornell Lab of Ornithology, 2019). As the migratory subspecies made up only a small proportion of the mainland data, the results appear to support the idea that tail length should be similar among island and mainland populations as all these populations were mainly resident.

2.4.2 Morphological differences among island populations

Long distance over-water dispersal is difficult for small passerines and, therefore, islands that are closer together will more likely have dispersal between the islands (Le Roux et al., 2014). This leads to a level of genetic relatedness amongst closer islands, so more proximate islands may have more similar morphologies (Le Roux et al., 2014). An unpublished study on House Wren genetics showed that closer islands had more genetically similar House Wrens, but this trend did not follow through the entire Lesser Antillean islands (J. Klicka, unpublished data). There appears to have been two founder populations: one that originated from the western South America (e.g., Peru, Bolivia) and colonized Dominica, and another that originated from the eastern South America (e.g., Venezuela, Trinidad) and colonized St. Vincent and the Grenadines and Grenada (J. Klicka, unpublished data). Unfortunately, the full genetic analysis of all island populations has not yet been completed, thus questions on the genetic relatedness among all Lesser Antillean islands are still present; however, it is possible that the genetic similarities

among closer islands could explain why closer populations have more similar wing chord, tail, and tarsus lengths. One study on the Hihi (*Notiomystis cincta*) of New Zealand showed tarsus length can be a strongly heritable trait (Duntsch et al., 2020). In another study, genetics explained a high proportion of variance in wing, tarsus, and bill length, and bill depth in House Sparrows (*Passer domesticus*) on islands off Norway (Silva et al., 2017). This supports the concept that geographically closer islands may have more similar morphology due to initial dispersal patterns and the genetic heritability of traits these traits.

Bills showed the fewest differences among the island populations, with bill width having the fewest significant comparisons (Appendix A). Bill morphology is correlated with food type; however, in one study, diet proved to only account for 12% of bill variation (Navalon et al., 2018). House Wrens tend to eat a high proportion of invertebrates (del Hoyo et al., 2005). There is a mechanical advantage to having a “tweezer-like” bill for invertebrate consumption (Navalon et al., 2018). Wide bills may therefore not be a selective advantage for House Wrens, which could be why they did not differ significantly across island populations. Bill dimensions were independent of geographic proximity of islands, suggesting that adaptations to local environmental conditions might influence bill morphology more strongly than genetic relatedness.

2.4.3 Island Geography Influences Morphology

A majority of the islands included in this study are volcanic in origin, and birds likely all colonized by over-water dispersal (Ricklefs and Bermingham, 2008). Low avian diversity on these islands reflects the likely limited colonization opportunities due to the significant geographic barriers between islands and the mainland (Ricklefs and Bermingham, 2001). House

Wrens that lived on islands further from the mainland exhibited longer tail length. There is an aerodynamic advantage of longer tails and this may have played a role in which individual House Wrens founded the initial colonization on islands (Thomas and Balmford, 1995). In contrast, one study noted that there is also a selective advantage to having shorter tails for birds with especially long migrations as shorter tails have less drag (Fitzpatrick, 1999); however, annual migration is a very different behavior compared to colonization and thus the founding individuals may have experienced an advantage of longer tails, which allowed for better aerial maneuverability (Thomas and Balmford, 1995).

House Wrens on larger islands had thinner bills, shorter tails, and shorter tarsi perhaps because larger islands have more habitat and species diversity, and thus are most similar to the mainland. This means that larger islands would also have smaller House Wrens that are similar to the size of mainland House Wrens. This would likely be due to weakened ecological release and thus less generalist behavior. Larger islands also may have a higher rate of initial colonization, which leads to higher diversity, based on the “target effect” that states larger land masses provide a larger target for birds flying over-water (Whitehead and Jones, 1969). Islands with low species diversity and low numbers of individuals per species also have higher probabilities of extinction (Lande, 1993), further reducing inter-specific competition and leading to increased ecological release and niche expansion. Therefore, smaller islands with low species diversity may have House Wrens with a large ecological niche and thus a reason for the larger and more generalist morphological features.

Although island biogeography has long been linked to trends in morphology, other factors can also influence morphological characteristics and should be considered in future studies. Environmental factors have been shown to have a strong influence on morphology. For

example, higher average temperatures have been linked to larger bill size for better heat dissipation (Greenberg and Danner, 2013). Precipitation can also influence morphology indirectly through local productivity; more precipitation and higher temperatures leads to higher productivity and thus higher resource availability, which reduces inter-specific competition intensity (Ricklefs and Bermingham, 1999; Lomolino, 2005; Cox and Ricklefs, 1977). Beyond natural environmental factors, human influence on the ecosystem can also have a significant impact on morphology. A study of the Medium Ground Finch (*Geospiza fortis*) found that in populations with only minor human influence, there was strong associations between environment (diet), beak size and bite force, whereas in areas with strong human influence, the associations began to fail (De Leon et al., 2011). The size and shape of available, natural foods put pressure on finches to attain a certain beak size and bite force, but foods introduced to the environment by humans (i.e., feeders) reduces this pressure and thus beak size undergoes a different adaptation processs (De Leon et al., 2011). Caribbean islands with House Wrens all experience relatively heavy human influence (e.g., Helmer et al., 2008), thus this could be a potential pressure altering the adaptation and evolution of House Wren morphology. Further studies in insular House Wren morphology should try and understand the connections among these factors and to understand the differences in size morphology among different Caribbean islands.

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3. GRENADA HOUSE WREN (*Troglodytes aedon grenadensis*) MORPHOLOGY

Abstract

Although House Wrens have been studied throughout the mainland of the Americas, the populations on Caribbean islands have been relatively overlooked and little is known about their morphology. Incidental reports have indicated that these populations look quite different from mainland populations; this is especially true for House Wrens on Grenada, which are large and darkly coloured compared to all other distinct populations. The objective of this study was to quantify the morphological differences between Grenada House Wrens and other subspecies of House Wrens and other closely related species within the genus *Troglodytes*. Data came from both live House Wrens in Grenada that were captured between 2015-2019 and from museum specimens of House Wrens from across North, Central, and South American and Lesser Antillean islands. I analyzed seven morphological characteristics, which consisted of wing chord, tarsus, tail length, bill length, bill width, bill depth, and exposed culmen. Grenada House Wrens were larger compared to most other populations; however, Grenada House Wrens were found to have shorter tails than most other House Wrens. Grenada House Wrens were most morphologically similar to House Wrens on St. Vincent and the Grenadines, which is closest geographical island population. Overall, Grenada House Wrens showed more similarities with other island populations to than mainland populations, indicating that island morphological trends are likely different from mainland morphological trends. The low species richness and resulting ecological release on Grenada may be providing conditions that allow the Grenada House Wren to adapt larger morphology than other populations.

3. 1 Introduction

3.1.1 Grenada

Grenada is the southernmost island country in the Lesser Antillean chain and consists of the main island of Grenada plus several smaller surrounding islands. Grenada is of volcanic origin. It is likely to be remnants of a larger island called the Grenada Bank and is less than 10 million years old (Newton, 2003; Ricklefs and Bermingham, 2008; Groome, 1970). This means that Grenadian islands were likely once connected to each other by a shallow land bridge (Groome, 1970); however, deep oceanic trenches surround the country, indicating Grenada was never connected to any continent nor to the neighbouring island countries (Groome, 1970). Grenada is located approximately 140 km north-east of mainland South America. The isolated nature of Grenada, and other Lesser Antillean islands, likely inhibited avian dispersal, limiting the colonization of many species (Ricklefs and Lovette, 1999).

Fauna found on Grenada must have originated from the mainland or other surrounding islands. One hypothesis stated that most avian species in Grenada likely originated from tropical North American lineages and dispersed south throughout the Greater and Lesser Antilles (Groome, 1970; Bond, 1979). More recently, genetic evidence points to a nearly equal rate of colonization from both South America and the Greater Antilles (Ricklefs, 2010). A genetic analysis of House Wrens in Grenada found that birds in this population are most closely related to wrens in Trinidad and Venezuela (J. Klicka, unpublished data), indicating that they likely did not colonize from the north as originally suspected (e.g., Bond, 1948). Understanding where the founding population of Grenada came from may help understand the morphological links among the extant populations.

The ecology of Grenada is unique when compared with other island countries in the Lesser Antilles. It has the smallest landmass of the countries and the lowest avian diversity ($n=150$ and $n = 161$; Government of Grenada, 2014; eBird, 2012, respectively). Many of the species found in Grenada are migrating shorebirds ($n = 29$), seabirds ($n = 25$) and other waterbirds ($n = 30$) (eBird, 2012), with only 35 species being resident landbirds. There are also very few records of Neotropical migrants on Grenada compared to other Lesser Antillean islands (eBird, 2012). Trade winds cross the Lesser Antillean chain just north of Grenada and likely force migrating passerines across the Caribbean Ocean towards South America (La Sorte et al., 2017), and as such, may be causing most neotropical migrants to by-pass Grenada, leading to the low records of migrants. This lack of neotropical migrants may result in relatively low resource competition within the avian community; in contrast, islands with neotropical migrants will experience spikes of inter-specific competition during the winter months as migrants recuperate from the fall migration and prepare for spring migration north (Morganti et al., 2017).

With both low avian diversity and lack of neotropical migrants, Grenada birds may face especially low inter-specific competition pressures and thus, perhaps, a unique evolutionary pathway and stronger ecological release than other Lesser Antillean islands (Ricklefs and Lovette, 1999). Birds on islands with low species richness, and thus low inter-specific and high intra-specific competition, experience the strongest ecological release (Ricklefs and Bermingham, 1999; Lomolino, 2005; Cox and Ricklefs, 1977). This leads to generalist morphology in passerines, including larger body size and larger and more variable bill size (Grant, 1965; Clegg and Owens, 2002). Smaller islands tend to have overall lower species richness than larger islands (e.g., MacArthur, 1972; Williams, 1964; Abbott 1980) and this is likely linked to low habitat diversity (Ricklefs and Lovette, 1999), high and localized extinction

rates (Ricklefs and Lovette, 1999) and fewer island predators (MacArthur and Wilson, 1967). Therefore, compared to more species-rich islands, birds on Grenada may have unique morphology as a result of adaptations to the strong ecological release.

3.1.3 House Wren Taxonomy

Species delineations for species found across large geographical ranges are challenging. Even simply defining the term “species” is controversial, since at least twenty-five different species concepts exist, each with unique distinguishing criteria of what defines a species (Mayden, 1999; Baker and Bradley, 2006). Currently, the biological species concept (BSC), which states that species are unique only if they cannot interbreed successfully, is the dominant concept in decision making under the American Ornithological Society (Agapow et al., 2004). Defining species gets further complicated when species are broken down into “subspecies”; this defines unique units within a species that do not meet the formal requirements for species status (Zink, 2004). Although the concept of “subspecies” has been used within taxonomy for a long time, the meaning has changed throughout history depending on which species concept was in the forefront of decision making at that time. Under the BSC, “subspecies” are defined as a stage in the process of speciation due to adaptive response to the specific local environment (Mayr, 1982). The term subspecies can encompass morphologically different populations that also could successfully hybridize (Mayr, 1982). Allopatric populations, such as those on isolated islands, are particularly hard to delineate under the BSC as the geographical barrier of over-water dispersal makes determining successful hybridization nearly impossible.

The taxonomic status of House Wrens on Caribbean islands has been criticized and a definitive taxonomic placement has not been produced. Very little natural history has been

studied on these populations, so they have consistently been placed as a race of House Wrens (Avibase, 2020); however, it has been suggested that House Wrens across the Caribbean should be, at minimum, their own species (*T. martinicensis*) (Bond, 1979).

To date, some island populations of House Wrens have undergone quantitative research and have since had their taxonomic status clarified and upgraded. One House Wren population that underwent taxonomic upgrading is the Cobb's Wren (*Troglodytes cobbi*). This island population is found on the Malvinas – Falkland Islands located off the coast of Patagonia. Research was conducted on the natural history of Cobb's Wren and it was determined to be an independent evolutionary lineage. This led to the population gaining species status and the IUCN subsequently up listed its status from “Least Concern” to “Vulnerable” (BirdLife International, 2017) as the population had been devastated by introduced predators such as rats and mice (Hall et al., 2002). The change of IUCN status prompted an increase in rat eradication programs, which have been successful in decreasing predation pressure on the Cobb's Wren (BirdLife International, 2017). In 2017, the IUCN was able to down-list the species back to “Least Concern” due to successful conservation practices (BirdLife International, 2017). Conservation resources and attention were directed at the Cobb's Wren only after species status was obtained.

A similar process occurred for both the Clarion Wren (*Troglodytes tanneri*) and Cozumel Wren (*Troglodytes beani*). Both these wren populations occur on islands off the coast of Mexico. Clarion's Wren underwent the same path as the Cobb's Wren. Once the Clarion Wren was taxonomically upgraded, the IUCN status changed from “Least Concern” to “Vulnerable”, and further protection against mammal predators on the island was promptly enacted (BirdLife International, 2016). The Cozumel Wren went through a similar taxonomic process, but they maintained their status of “Least Concern” since their population is stable (BirdLife

International, 2017). These examples of other isolated, island House Wren populations being upgraded to species status sets a strong precedent that the House Wrens on Caribbean islands, such as Grenada, may also undergo the same process.

3.1.2 Grenada House Wren

Grenada House Wrens are common residents on the main island of Grenada. On the smaller islands within the country of Grenada, particularly Carriacou and Petite Martinique, there are no reports of House Wrens on eBird (2012). A recent study conducting bird surveys found only one House Wren on Carriacou and none on Petite Martinique (Williams, 2020). This implies there is no substantial population of House Wrens on the smaller island of Grenada.

Grenada House Wrens appear to be associated strongly with human infrastructure and occur in low densities in unbroken forest, much like other House Wren populations (del Hoyo et al., 2005; Williams, 2020). Their strong association with human infrastructure could be related to their nesting behavior. House Wrens mainly nest in cavities. Other House Wren populations rely on nest boxes or artificial nesting sites, such as cavities in human infrastructure (del Hoyo et al., 2005). Similarly, several House Wrens on Grenada were found nesting in building crevices (K. Wetten, pers. obs.). In 2018, nest boxes built for House Wrens were deployed at several locations throughout the country, but it is unknown whether House Wrens have begun using the boxes for nesting as this is the first House Wren nest box project in Grenada (K. Wetten, pers. obs.).

Males and females exhibit monomorphic plumage. House Wrens on Grenada are overall dark brown with an orange hue to their body feathers. Unlike other House Wren populations, most Grenada House Wrens do not have light-coloured feathers on their underside and instead

have a consistent dark, orange hue over the entire body (K. Wetten, pers. obs.). Grenada House Wrens exhibit the typical dark barring on their wings and tail.

House Wrens on Grenada also appear to have unique song structure compared to other House Wren subspecies (K. Wetten, unpublished data). A recent study indicated that song structure differed between urban and rural House Wrens on Grenada with birds in urban areas singing faster trills, lower frequency notes, and shorter duration songs (Cyr et al., 2020). To date, this is the only study examining House Wren song on Grenada.

The diet of House Wrens on Grenada has also not been described. Observations of Grenada House Wrens in the field suggest that they eat a variety of insects (C. De Ruyck, pers. comm.), but their diet may vary depending on season and resource availability. A recent study on passerine diet on Grenada found House Wrens consumed mostly arthropods and most were various moth species (De Ruyck, unpublished data); some plant matter from crop species (e.g., mango, wheat, guava) and other arthropods (e.g., a cricket, a beetle) were also identified in the House Wren's feces.

Taxonomy of the Grenada House Wrens is highly debated. Depending on the taxonomic authority, the Grenada House Wren is listed as either a race or a subspecies. If they are listed as a subspecies, Grenada populations are placed under species *aedon* (e.g., Clements et al., 2019), *martinicensis* (e.g., Avibase, 2020) or *musculus* (e.g., del Hoyo et al., 2005) depending on the governing body. This conflicting taxonomy is a result of differences in taxonomic principles guiding the organizations and thus allows for a remarkably high level of subjectivity in taxonomy. Some researchers believe that each of the Lesser Antillean populations should be upgraded to full species status (e.g., del Hoyo et al., 2005; Sosa-Lopez and Mennill, 2014); however, more clarity on their natural history is needed prior to making any changes to

taxonomy. Therefore, the objective of this study was to provide evidence for morphological divergence of the Grenada House Wren compared to other House Wren subspecies.

3.2 Methods

This research was conducted under University of Manitoba animal care protocol F15-026/1 and with permission of the Government of Grenada.

3.2.1 Grenada House Wren Samples

Morphological data were collected from Grenada House Wrens in the form of museum samples ($n = 21$) and live-captured House Wrens ($n = 73$). I measured museum specimens of Grenada House Wrens at two different museums: the Smithsonian National Museum of Natural History (Washington, D.C.) and the Harvard University Museum of Comparative Zoology (Boston, Massachusetts) ($n = 6$ and 8 , respectively). A database of House Wren morphology from Sosa-Lopez and Mennill (2014) included data for seven Grenada House Wrens which came from the American Museum of Natural History (New York) and the Field Museum of Natural History (Chicago) ($n = 1$ and 6 , respectively).

House Wrens were caught on the island of Grenada between 2015 and 2019. Most ($n = 38$) were caught during my field season (2018 - 2019), but additional House Wrens ($n = 35$) were caught by other banders in previous years (2015 - 2019). All birds were caught on the main island of Grenada at a total of nine sites across the country (See Chapter 2: Figure 1 and Section 2.2.2). Both passive and targeted mist-netting (with song lure) were used to capture House Wrens in Grenada. All House Wrens caught prior to 2018 were caught using passive capture (i.e., no song lure). Mist-nets were either 6- or 12-m long with 30 mm mesh, which is standard

for songbird capture. Generally, two to six nets were active at a time in an House Wren's territory. For targeted capture, song lure consisted of using one or two Bluetooth JBL Charge speakers that played recordings of either Grenadian (recorded locally by us) or North American House Wren songs and calls (Sibley Birds V2 app). Song lures were played for a maximum of 1 hour. Mist-netting was done primarily early morning and late evening and in non-adverse weather conditions. All House Wrens were banded with aluminum bands; in addition, most were banded with two colour bands on the opposite leg. Most Grenada House Wrens took a size 1 band with two individuals requiring a 1B band size; all birds were leg gauged prior to band application.

3.2.2 Comparison House Wren Population Samples

To compare Grenada House Wrens with a wide variety of other House Wren populations, I measured specimens of 26 different subspecies from four different museum collections (Table 6). The museums visited were the Smithsonian National Museum of Natural History (Washington, D.C.), the Harvard University Museum of Comparative Zoology (Boston, Massachusetts), the Manitoba Museum (Winnipeg, Manitoba) and the University of Manitoba Zoology Museum (Winnipeg, Manitoba). To further add to the sample size, a database of morphology measurements collected by Sosa-Lopez and Mennill (2014) was included. These samples came from specimens at the American Museum of Natural History (New York), the Field Museum of Natural History (Chicago) and Museo de Zoología “Alfonso L. Herrera” (Mexico City); this database also included data from House Wrens captured during field research on Cozumel and Socorro island in Mexico.

Table 6: List of twenty-six species and subspecies latin names with the countries where the museum specimens or live-captured birds were collected from. (Sub)species names in bold indicate these are a resident island population.

(Sub)species	Sample Size	Locations/Countries where Samples Collected
<i>T. a. aedon</i>	89	Canada, USA
<i>T. a. albicans</i>	54	Brazil, Columbia, Ecuador, Guyana, Peru, Suriname, Trinidad and Tobago, Venezuela
<i>T. a. atopus</i>	16	Colombia
<i>T. beani</i>	22	Cozumel Island (Mexico)
<i>T. a. bonariae</i>	21	Argentina, Brazil, Uruguay
<i>T. a. brunneicollis</i>	39	Mexico
<i>T. a. cahooni</i>	82	Mexico, USA
<i>T. a. carychrous</i>	12	Panama
<i>T. a. chilensis</i>	27	Argentina, Chile
<i>T. a. columbae</i>	18	Colombia
<i>T. a. compositus</i>	24	Mexico
<i>T. a. duidae</i>	14	Venezuela
<i>T. a. guadeloupensis</i>	16	Guadeloupe
<i>T. a. inquietus</i>	44	Belize, Colombia, Panama
<i>T. a. intermedius</i>	89	Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua
<i>T. a. musculus</i>	12	Argentina, Brazil, Paraguay
<i>T. a. musicus</i>	13	St. Vincent and the Grenadines
<i>T. a. parkmanii</i>	66	Canada, USA
<i>T. a. rehni</i>	10	El Salvador, Guatemala, Honduras
<i>T. a. rex</i>	10	Argentina, Bolivia, Paraguay
<i>T. a. rufescens</i>	14	Dominica
<i>T. a. rufulus</i>	18	Guiana, Venezuela
<i>T. sissonii</i>	33	Socorro Island (Mexico)
<i>T. solititalis</i>	46	Ecuador, Peru
<i>T. a. striatulus</i>	22	Colombia
<i>T. tanneri</i>	17	Clarion Island (Mexico)

3.2.3 Morphological Measurements

All measurements were taken as per Pyle (1997) and included wing chord (mm), tarsus length (0.1mm), bill length (0.1mm), exposed culmen (0.1mm), bill width (0.1mm), and bill depth (0.1mm). Measurements from museum specimens were conducted using the same techniques in Pyle (1997) to maintain consistency across samples. Some specimens exhibited wear from use in the museums (e.g., broken tips of bills) so measurements from these specimens were only used if the wear did not directly impact the measurement. All measurements of

museum specimens were taken twice to double check for accuracy, but only one final measurement was recorded.

3.2.4 Data Management

Only adult, male House Wrens were used in analyses since sexes in some House Wren populations can show significant morphological differences (Pyle, 1997); using only males reduces sex-related biases in the analyses. House Wrens are monomorphic, so breeding characteristics were used to determine sex. In live-captured House Wrens, a bird that exhibited a swollen cloaca that is indicative of active breeding was concluded to be male, as per Pyle (1997). In museum samples, sex of the specimen was often provided on the information card as the gonads were examined during the taxidermy process. If sex information was not provided, then the specimen remained “unknown” sex. Only adult House Wrens were included in analyses as juvenile birds may still be growing, and thus could bias morphology results. House Wrens showing juvenile characteristics (e.g., juvenal body feathers, gape in bill, all flight feathers still in sheath) were removed from the database prior to analysis. This means that all House Wrens had to have reached or exceeded their first pre-formative molt to be used in these analyses. Lastly, I decided a priori to only include subspecies and closely related taxa within the genus *Troglodytes* that I had a minimum of ten adult male samples (range $n = 10$ to 89).

3.2.5 Statistical Analyses

All analyses were conducted in R version 3.5.1 (R Core Team, 2018). I conducted ANOVA for each morphological measurement comparing all House Wren populations. All data met the assumption of normality using QQ Plots. I then used a Dunnett Test's (package

DescTools (Signorell et al., 2020)) using Grenada House Wren as the reference dataset to allow for comparison of all populations against the Grenada population (Dunnett, 1955).

3.3 Results

A total of 1,233 adult male House Wrens were measured across most of their geographic range. This included 34 adult male House Wrens from Grenada, of which 21 were live-captured birds and 13 were museum specimens. Grenada House Wrens were compared with 26 distinct populations of House Wren (Table 7, Appendix B), which included 18 mainland subspecies, 3 island species, 3 island subspecies, and 2 migratory subspecies.

Morphological traits differed significantly in a majority (80.8%) of comparisons among Grenada House Wrens and other House Wren populations. Most comparisons (88.4%) indicated Grenada House Wrens were larger. The Grenada House Wren had the longest and deepest bills of all House Wren populations measured. Grenada House Wrens had longer wings compared to 20 (sub)species and had shorter average wings compared to *T. tanneri*, which is a recently taxonomically upgraded species found on Clarion Island (Mexico) (Figure 4). Grenada House Wrens had shorter tails than most subspecies (15 groups) and had longer tails than 3 subspecies (Figure 5). Grenada House Wrens had longer tarsi than 17 other groups and shorter tarsi than *T. a. duidae*, which are found in Venezuela (Figure 6). For all bill measurements (Figure 7 to 10), Grenada House Wrens were bigger than all other groups except six different taxa: *T. beani* (bill width, bill depth, exposed culmen), *T. a. carychrous* (bill width, bill depth), *T. a. musicus* (all bill measurements), *T. a. duidae* (bill width), *T. a. rufulus* (bill width), and *T. tanneri* (bill width, bill depth). Overall, Grenada House Wrens were most similar morphologically to *T. a. musicus* (St. Vincent and the Grenadines), which is the geographically closest insular population.

Table 7: Results of the ANOVA and Dunnett's test comparing Grenada House Wren ($n = 34$) to 26 other species. "+" in orange cells mean that Grenada House Wren was bigger, and "-" in blue cells mean that the Grenada House Wren was smaller. Blanks indicate no significant difference in morphology ($p > 0.05$). See Appendix B for mean (SD) for these results. Besides tail length, Grenada House Wrens are generally larger morphologically than other House Wren populations.

Group	(Sub)species	Sample Size	Wing Chord	Tarsus	Tail	Bill Length	Exposed Culmen	Bill Width	Bill Depth
Island Subspecies	<i>T. a. rufescens</i>	14	+	+		+	+		+
	<i>T. a. musicus</i>	13			-				
	<i>T. a. guadeloupensis</i>	16	+	+		+	+	+	+
Island Species	<i>T. tanneri</i>	17	-		-	+	+		
	<i>T. sissonii</i>	33	+		-	+	+	+	+
	<i>T. beani</i>	22	+		-	+			
Migratory Subspecies	<i>T. a. aedon</i>	89	+	+	-	+	+	+	+
	<i>T. a. parkmanii</i>	66	+	+	-	+	+	+	+
Mainland Subspecies	<i>T. a. albicans</i>	54	+	+		+	+	+	+
	<i>T. a. atopus</i>	16	+	+		+	+	+	+
	<i>T. a. bonariae</i>	21	+	+	-	+	+	+	+
	<i>T. a. brunneicollis</i>	39	+	+	-	+	+	+	+
	<i>T. a. cahooni</i>	82	+	+	-	+	+	+	+
	<i>T. a. carychrous</i>	12	+			+	+		
	<i>T. a. chilensis</i>	27	+	+	-	+	+	+	+
	<i>T. a. columbae</i>	18			-	+	+	+	+
	<i>T. a. compositus</i>	24	+	+	-	+	+	+	+
	<i>T. a. duidae</i>	14		-		+	+		+
	<i>T. a. inquietus</i>	44	+	+		+	+	+	+
	<i>T. a. intermedius</i>	89	+	+	+	+	+	+	+
	<i>T. a. musculus</i>	12	+	+	-	+	+	+	+
	<i>T. a. rehni</i>	10	+	+	+	+	+	+	+
	<i>T. a. rex</i>	10	+	+	-	+	+	+	+
	<i>T. a. rufulus</i>	18				+	+		+
	<i>T. a. solitialis</i>	46	+	+	+	+	+	+	+
	<i>T. a. striatulus</i>	22			-	+	+	+	+

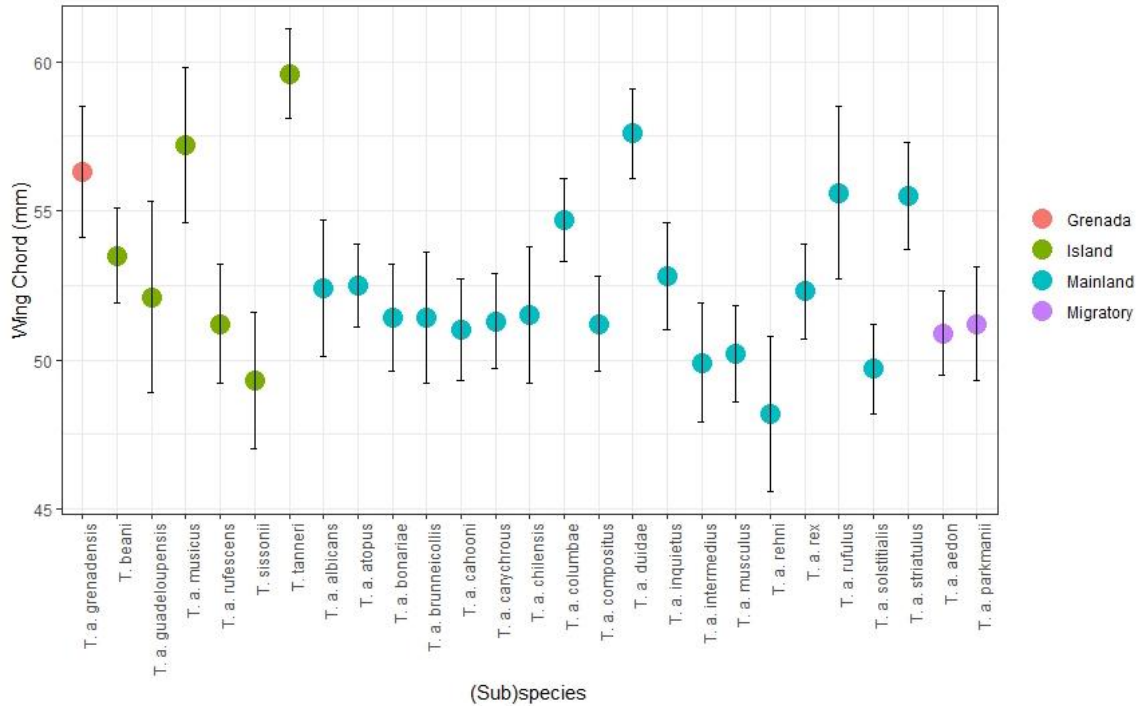


Figure 4: Mean and SD of Grenada House Wren wing chord compared to 26 other subspecies of House Wren and closely related *Troglodytes* species. Data is grouped by whether they are an island resident (green), a mainland resident (blue) or a migratory subspecies (purple).

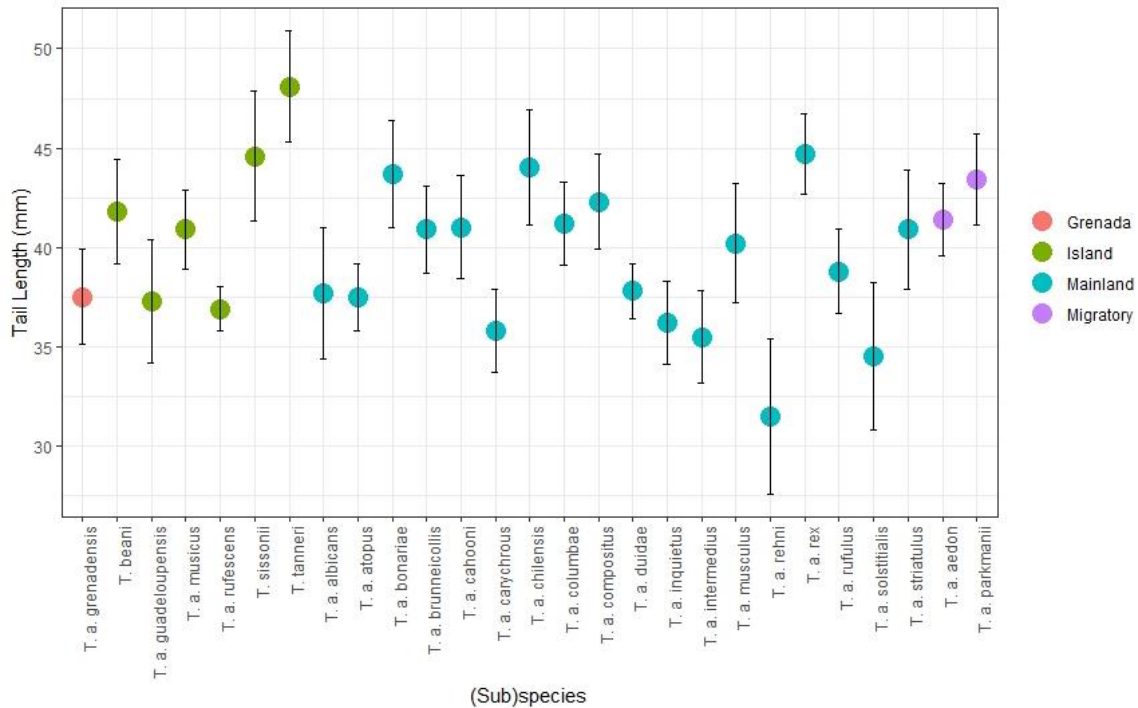


Figure 5: Mean and SD of Grenada House Wren tail length compared to 26 other subspecies of House Wren and closely related *Troglodytes* species. Data is grouped by whether they are an island resident (green), a mainland resident (blue) or a migratory subspecies (purple).

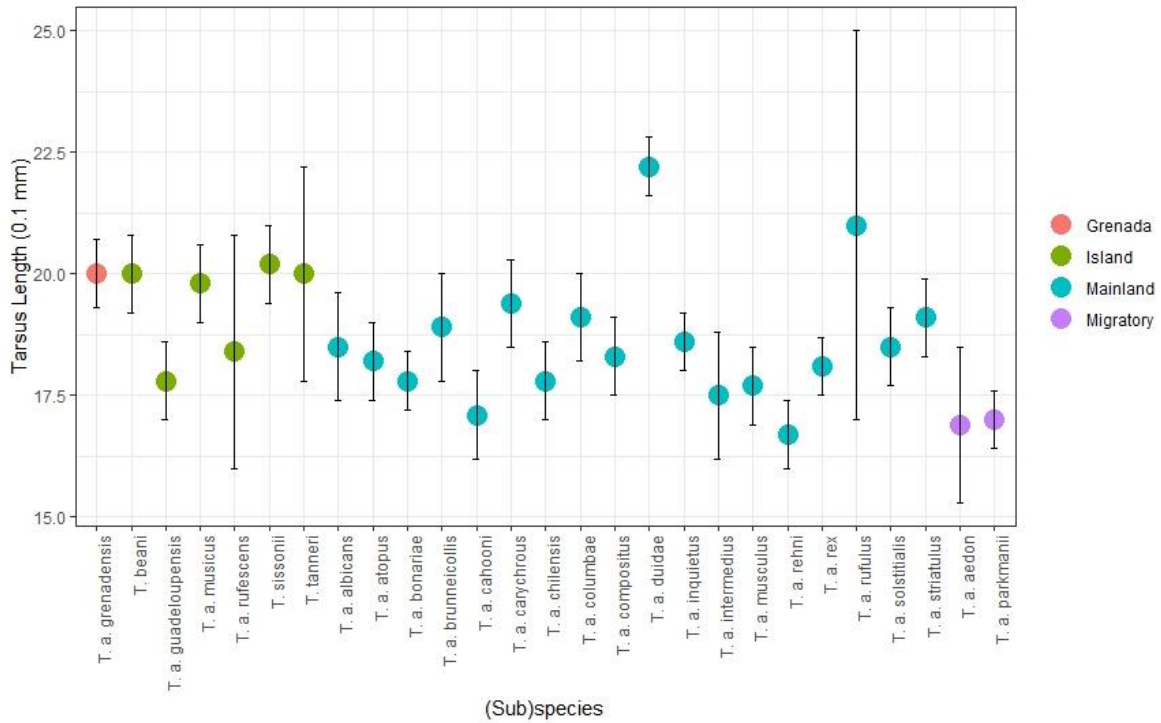


Figure 6: Mean and SD of Grenada House Wren tarsus length compared to 26 other subspecies of House Wren and closely related *Troglodytes* species. Data is grouped by whether they are an island resident (green), a mainland resident (blue) or a migratory subspecies (purple).

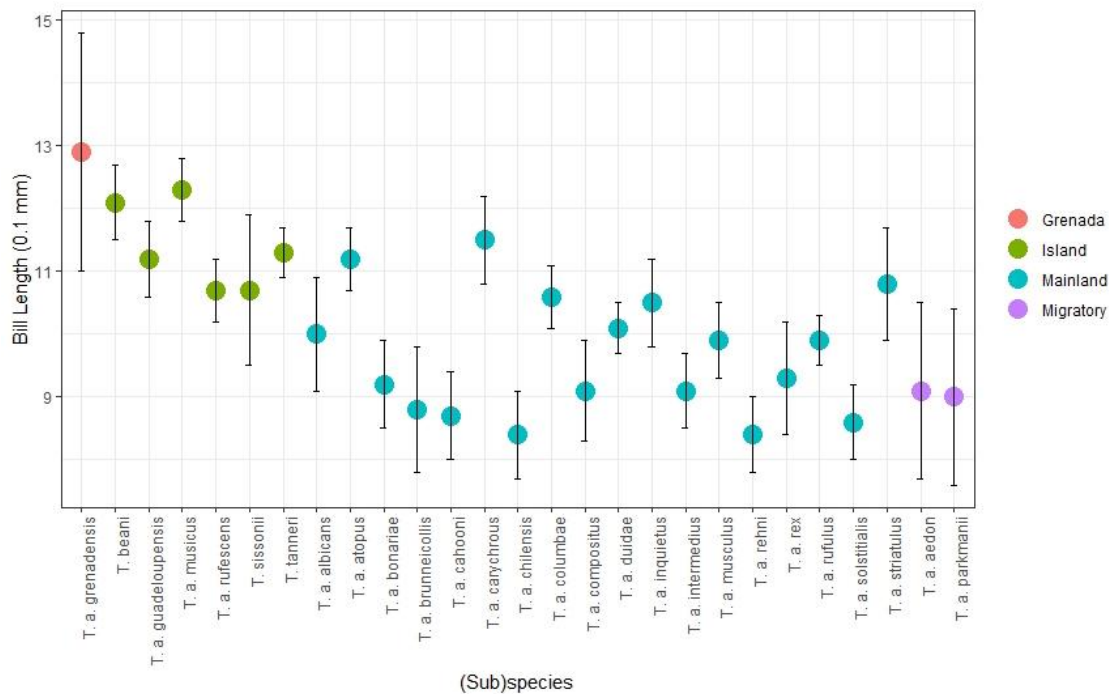


Figure 7: Mean and SD of Grenada House Wren bill length compared to 26 other subspecies of House Wren and closely related *Troglodytes* species. Data is grouped by whether they are an island resident (green), a mainland resident (blue) or a migratory subspecies (purple).

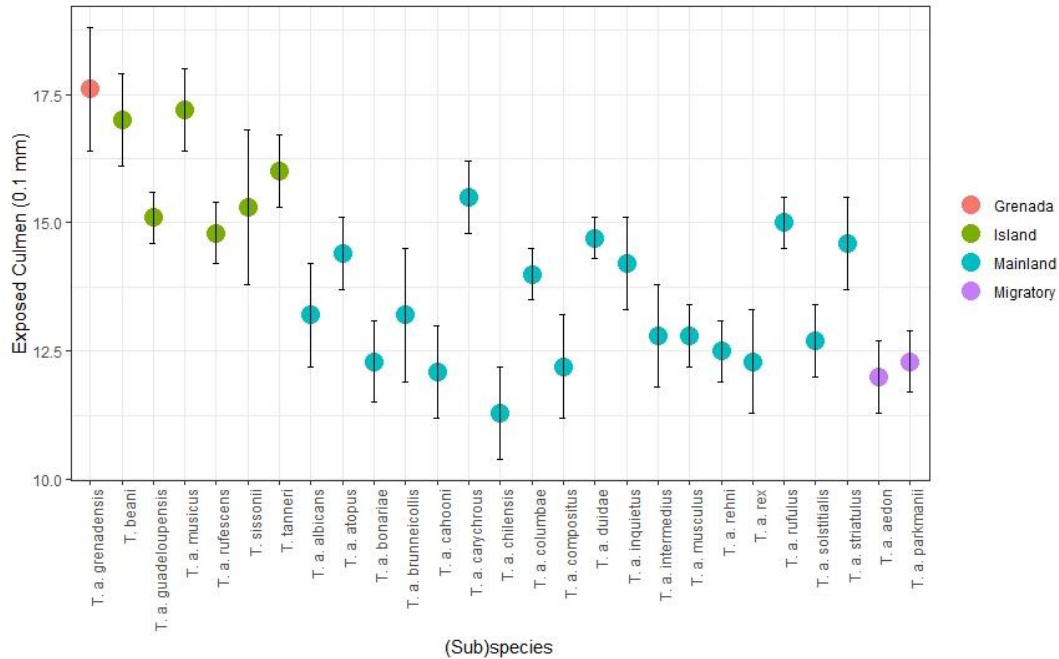


Figure 8: Mean and SD of Grenada House Wren exposed culmen compared to 26 other subspecies of House Wren and closely related *Troglodytes* species. Data is grouped by whether they are an island resident (green), a mainland resident (blue) or a migratory subspecies (purple).

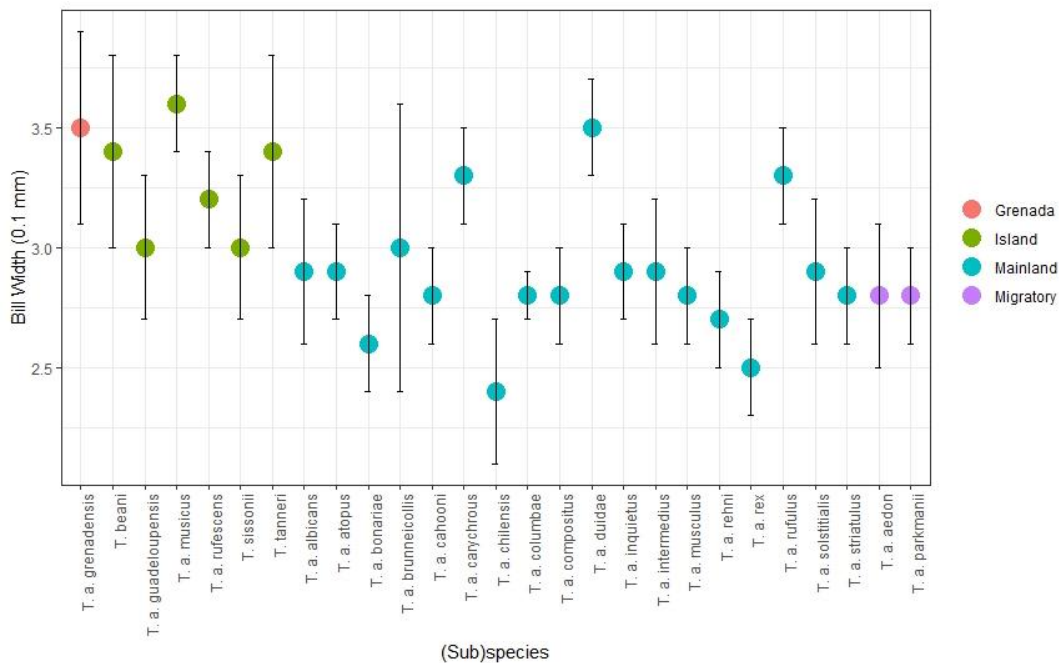


Figure 9: Mean and SD of Grenada House Wren bill width compared to 26 other subspecies of House Wren and closely related *Troglodytes* species. Data is grouped by whether they are an island resident (green), a mainland resident (blue) or a migratory subspecies (purple).

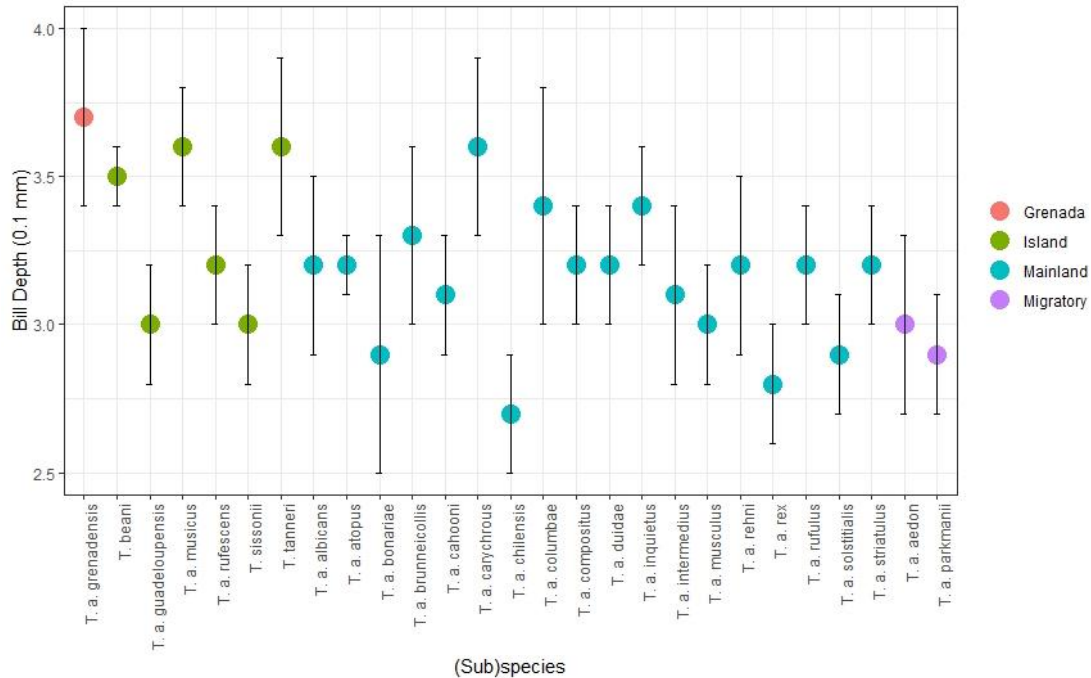


Figure 10: Mean and SD of Grenada House Wren bill depth compared to 26 other subspecies of House Wren and closely related *Troglodytes* species. Data is grouped by whether they are an island resident (green), a mainland resident (blue) or a migratory subspecies (purple).

3.4 Discussion

Grenada House Wrens were larger than most other House Wrens. As anticipated by the island rule, Grenada House Wrens were larger than individuals from mainland populations, consistent with the pattern that small birds evolve towards gigantism on islands compared to their mainland counterparts (Foster, 1964; Lomolino, 2005). This pattern may be because the realized niche of House Wrens is expanded compared to mainland birds as there is more opportunity and necessity for generalist foraging due to the decreased intensity of interspecific competition and increased intensity of intraspecific competition for resources (Hamilton, 1961).

Grenada House Wrens were also larger than individuals from most other island populations, particularly in bill dimensions. Of note, they showed the longest and deepest bills of all measured House Wrens. The island area of Grenada is relatively small and thus may have low habitat diversity (Ricklefs and Lovette, 1999; Wunderle, 1985). This could result in the relatively

low avian diversity found on Grenada (Government of Grenada, 2014). As they also face little competitive pressure from neotropical migrants, it is likely that that inter-specific competition is lower on Grenada than many other islands. Low inter-specific competition on islands has been linked with larger and more generalist morphology (Lomolino, 2005); under low competitive pressure, a species can increase its realized niche and use a wider variety of resources, thus morphology adapts to this by becoming bigger and more generalist.

Tarsus length of Grenada House Wrens was longer than in most other mainland populations, but similar to other island populations. Previous studies have shown that selection for larger body size (using wing as the metric) and longer tarsus length can be independent of one another (Grant, 1971). Our data supports this as, in several comparisons, Grenada House Wrens had longer wings, but tarsus lengths were either similar or smaller (Table 5). Therefore, tarsus length may not necessarily be explained in terms of other body measurements and instead could be a result of external environmental pressures. Longer tarsi can provide greater thrust on take-off (Earl, 2000; Berg and Biewner, 2010; Provini, 2012), thus allowing for quicker escape from predators. Longer tarsi can also allow for the use of a more diverse selection of perch sites (Grant, 1971). Due to the small size of the island of Grenada and the large amount of human infrastructure that may create diversity in perches, Grenada House Wrens may need to adapt to using many diverse perches to allow for a greater diversity of foraging strategies.

Tail length was the only measurement that was consistently smaller in Grenada House Wrens than other populations. Migratory birds tend to have longer tails than resident birds (Fitzpatrick, 1999) as tail shape influences aerodynamics of birds, including producing lift and agility (Thomas and Balmford, 1995). House Wrens tail lengths decrease from north to south (Sosa-Lopez and Mennill, 2014), perhaps as a result of varying migration behavior as the

northernmost samples of House Wrens are all migratory. This idea was supported by this study as the two migratory subspecies (*T. a. aedon* and *T. a. parkmanii*) had relatively long average tail length. The short tails of the Grenada House Wren may instead be strongly correlated with ecological factors; for instance, short tails allow for maneuverability in thick vegetation (Fitzpatrick, 1999; Fitzpatrick, 1997). The short tails of Grenada House Wrens may also reflect the lack of necessity for long flight distances (Fitzpatrick, 1997) as they are a resident population on a small island. Short tails may also reflect the need for high-speed flight to escape predators, such as the Indian mongoose (*Herpestes auropunctatus*), in thick vegetation found on Grenada (Thomas and Balmford, 1995).

Grenada House Wrens are most similar morphologically to House Wrens found on the island of St. Vincent and the Grenadines. This population is the closest geographically and most similar genetically to the Grenada population (J. Klicka, pers. comm.). House Wrens in both island countries are believed to be closely genetically related to House Wrens from Trinidad and Venezuela (J. Klicka, pers. comm.). Genetics may play a strong role in explaining these morphological patterns; however, geographically closer islands may additionally have more similar environmental conditions and thus environmental pressures may cause similar adaptive pathways. Nonetheless, House Wrens on St. Vincent and the Grenadines show a colour patterning that is quite different to those in Grenada; they have stark white underbellies whereas Grenada House Wrens have dark overall plumage (Appendix C). Gloger's rule indicates that darker coloured individuals should be found in warmer and more humid regions (Delhey, 2017). Pheo-melanins, the melanin pigmentation that create the buff, brown and rufous colours, are believed to be influenced by temperature and rainfall (Delhey, 2017). Therefore, the environment on Grenada may be influencing both the morphology and plumage characteristics of the local

population. The stark difference in colouration also suggests that there is isolation between Grenada and St. Vincent and the Grenadines populations, even though their structural morphology is similar.

One limitation of this study was the lack of data on the mass of House Wrens. Mass is often used as a way to standardize morphological data as it is used as a measurement of body size. By including body size, I could have indicated whether the larger morphologies seen in Grenada House Wrens were independent of or in relation to simply a bigger body size. Although mass was collected on live-captured birds from Grenada, museum specimens rarely had body mass measurements and therefore there was no data to compare Grenada House Wrens to. Future studies should aim to include a metric of body size in the morphological analysis to better parse the morphological differences among populations.

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4. SUMMARY AND KEY MANAGEMENT IMPLICATIONS

I determined that island House Wrens showed larger average morphology than mainland House Wrens, as predicted by the literature on strong ecological release experienced by island bird populations; however, my results showed that each island is unique in how the House Wrens have adapted morphologically to the local conditions. Tail length and wing chord varied the most among island populations and bill width varied the least. House Wrens on geographically closer islands had more similar wing chord, tail, and tarsus length, suggesting that dispersal and genetics may play a more important role on these characteristics, whereas environmental conditions may have a stronger influence on bill morphology.

In particular, I determined that the Grenada House Wrens have significantly different morphology than most other House Wren populations, on both the mainland and islands, and other closely related island species within the genus *Troglodytes*. This significant difference in morphology could be used as a line of support for consideration as their own species. The American Ornithological Society (AOS) requires a minimum of two lines of evidence before considering a population for a taxonomic change (American Ornithologists' Union, 1998); if the data from this study are used, this means only one other line of evidence is required. Some work has been done on Grenada House Wren genetics (J. Klicka, unpublished data) and on song structure (Cyr et al., 2020); by using these data, it is possible that the Grenada House Wren could have enough evidence to be taxonomically upgraded to its own endemic species.

The Grenada House Wren would be an important species to conserve. It is a recognizable species in Grenada as the average person can distinguish this species based on behavior and song. It is locally known as the “House Bird” or “Guard Bird” as it is often the first to alert birds to the presence of predators. Conserving birds that the most people can recognize can help foster appreciation and serve as a meaningful reminder to think about the environment and be aware of conservation (Brophy, 2018). Conservation based on human connection can lead to the species becoming an umbrella species and thus provide protection to many other species in Grenada. It is apparent that House Wrens on Caribbean islands are susceptible to severe population declines through predation by invasive species, such as the Indian mongoose (*Herpestes auropunctatus*), as House Wrens on Martinique and Guadeloupe have become extirpated since the introduction of mongoose (Bond, 1960; eBird, 2012). Although the Grenada population of House Wren appears common and stable throughout the main island, improving protection from mongoose could be a beneficial conservation action. By eradicating mongoose, we could both protect the Grenada House Wren while also reducing predation pressures and protecting other less common and more susceptible Grenadian bird populations.

Currently on Grenada there is one endemic species (Grenada Dove, *Heptotilla wellsi*) and one endemic subspecies (Grenada Hook-billed Kite, *Chondrohierax uncinatus murus*). If the House Wren on Grenada is considered its own species, it would add another endemic species to be monitored on the island. This would have management implications for Grenada. The first

step would be to understand the population dynamics and density of House Wrens. Although studies have indicated they are relatively abundant across the country (Williams, 2020), it is unclear whether there are small pockets of House Wrens on the smaller islands surrounding the main island of Grenada. Monitoring the population trends would be key to protecting House Wrens and maintaining their population. The conservation statuses of many avian species on Grenada are unknown, except recent studies have looked closely at the endemic bird species, including the Grenada Dove (Rusk, 2017) and the Grenada Hook-billed Kite (Campbell, 2019). Thus, taxonomic upgrading from subspecies to species status may promote researchers and/or authorities to gain a better understanding of the local, unique, and charismatic House Wren on Grenada.

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5.0 APPENDICES

Appendix A: Seven morphological pairwise comparisons among ten islands (arrange alphabetically) using ANOVA with Tukey HSD tests. Values indicate the difference (mm) between the means for the islands with negative values indicating that the leftmost column is smaller than the comparison island. The matrices indicate the correlation value between the morphological characteristic and each island population. Orange cells show comparisons with a p-value ≤ 0.05 and blue cells show comparisons with a p-value ≥ 0.05 .

Figure 1: Wing Chord

	Clarion								
Coiba	-7.89	Coiba							
Cozumel	-5.89	2.00	Cozumel						
Dominica	-8.38	-0.50	-2.50	Dominica					
Grenada	-2.67	5.21	-1.23	5.71	Grenada				
Guadeloupe	-7.12	0.77	-1.23	1.27	-4.45	Guadeloupe			
Kidney	-3.42	4.47	2.47	4.97	-0.75	3.70	Kidney		
Socorro	-9.97	-2.08	-4.08	-1.59	-7.30	-2.85	-6.55	Socorro	
St. Lucia	-5.67	2.21	0.21	2.70	-3.01	1.44	-2.26	4.29	St. Lucia
St. Vincent	-2.17	5.71	3.71	6.20	0.49	4.94	1.24	7.79	3.50

Figure 2: Tail Length

	Clarion									
Coiba	-11.34	Coiba								
Cozumel	-5.43	5.91	Cozumel							
Dominica	-11.12	0.22	-5.68	Dominica						
Grenada	-9.52	1.82	-4.09	1.60	Grenada					
Guadeloupe	-9.92	1.42	-4.48	1.20	-0.40	Guadeloupe				
Kidney	-6.58	4.76	-1.15	4.53	2.94	3.33	Kidney			
Socorro	-2.70	8.64	2.73	8.42	6.82	7.22	3.88	Socorro		
St. Lucia	-10.67	0.66	-5.25	0.44	-1.16	-0.76	-4.10	-7.98	St. Lucia	
St. Vincent	-6.39	4.95	-0.96	4.72	3.13	3.52	0.19	-3.69	4.29	

Figure 3: Tarsus Length

	Clarion									
Coiba	-1.49	Coiba								
Cozumel	-0.74	0.75	Cozumel							
Dominica	-2.30	-0.81	-1.56	Dominica						
Grenada	-0.76	0.73	-0.02	1.54	Grenada					
Guadeloupe	-2.99	-1.50	-2.25	-0.69	-2.23	Guadeloupe				
Kidney	-4.22	-2.73	-3.48	-1.92	-3.46	-1.23	Kidney			
Socorro	-0.53	0.96	0.21	1.77	0.23	2.46	3.69	Socorro		
St. Lucia	-2.75	-1.26	-2.01	-0.45	-1.99	0.24	1.46	-2.22	St. Lucia	
St. Vincent	-1.00	0.49	-0.26	1.30	-0.23	2.00	3.22	-0.47	1.76	

Figure 4: Bill Length

	Clarion									
Coiba	-0.28	Coiba								
Cozumel	0.64	0.91	Cozumel							
Dominica	-0.94	-0.66	-1.58	Dominica						
Grenada	1.74	2.02	1.11	2.68	Grenada					
Guadeloupe	-0.21	0.07	-0.84	0.73	-1.95	Guadeloupe				
Kidney	-1.23	-0.95	-1.86	-0.29	-2.97	-1.02	Kidney			
Socorro	-0.69	-0.41	-1.33	0.25	-2.43	-0.48	0.54	Socorro		
St. Lucia	1.51	1.78	0.87	2.44	-0.24	1.72	2.74	2.20	St. Lucia	
St. Vincent	0.69	0.97	0.06	1.64	-1.05	0.90	1.92	1.38	-0.81	

Figure 5: Bill Width

	Clarion									
Coiba	-0.37	Coiba								
Cozumel	-0.14	0.22	Cozumel							
Dominica	-0.39	-0.03	-0.25	Dominica						
Grenada	-0.82	0.28	0.06	0.31	Grenada					
Guadeloupe	-0.55	-0.18	-0.40	-0.15	-0.46	Guadeloupe				
Kidney	-0.72	-0.35	-0.57	-0.33	-0.64	-0.17	Kidney			
Socorro	-0.59	-0.22	-0.44	-0.19	-0.50	-0.04	0.13	Socorro		
St. Lucia	-0.54	-0.18	-0.40	-0.15	-0.46	0.00	0.18	0.04	St. Lucia	
St. Vincent	0.02	0.39	0.16	0.41	0.10	0.57	0.74	0.61	0.56	

Figure 6: Bill depth

	Clarion								
Coiba	-0.19	Coiba							
Cozumel	-0.25	-0.06	Cozumel						
Dominica	-0.53	-0.34	-0.28	Dominica					
Grenada	-0.07	0.11	0.17	0.46	Grenada				
Guadeloupe	-0.76	-0.57	-0.51	-0.23	-0.68	Guadeloupe			
Kidney	-0.40	-0.21	-0.16	0.13	-0.33	0.36	Kidney		
Socorro	-0.71	-0.53	-0.47	-0.19	-0.64	0.04	-0.31	Socorro	
St. Lucia	-0.79	-0.60	-0.55	-0.26	-0.72	-0.03	-0.39	-0.08	St. Lucia
St. Vincent	-0.12	0.06	0.12	0.40	-0.05	0.63	0.28	0.59	0.67

Appendix B: Mean (sd) for each measurement type for all taxa included in analyses. **Bolded** results indicate that Grenada House Wren was larger, *Italics* indicate that Grenada House Wren was smaller, and regular font indicates an insignificant result. † indicates a migratory subspecies, * indicates an island subspecies and + indicates an island species.

(Sub)species	Sample Size	Wing Chord	Tarsus	Tail	Bill Length	Bill Width	Bill Depth	Exposed Culmen
<i>T. a. grenadensis</i>	34	56.3 (2.2)	20.0 (0.7)	37.5 (2.4)	12.9 (1.9)	3.5 (0.4)	3.7 (0.3)	17.6 (1.2)
<i>T. a. aedon</i> †	89	50.9 (1.4)	16.9 (1.6)	<i>41.4 (1.8)</i>	9.1 (1.4)	2.8 (0.3)	3.0 (0.3)	12.0 (0.7)
<i>T. a. albicans</i>	54	52.4 (2.3)	18.5 (1.1)	37.7 (3.3)	10.0 (0.9)	2.9 (0.3)	3.2 (0.3)	13.2 (1.0)
<i>T. a. atopus</i>	16	52.5 (1.4)	18.2 (0.8)	37.5 (1.7)	11.2 (0.5)	2.9 (0.2)	3.2 (0.1)	14.4 (0.7)
<i>T. beani</i> +	22	53.5 (1.6)	20.0 (0.8)	<i>41.8 (2.6)</i>	12.1 (0.6)	3.4 (0.4)	3.5 (0.1)	17.0 (0.9)
<i>T. a. bonariae</i>	21	51.4 (1.8)	17.8 (0.6)	<i>43.7 (2.7)</i>	9.2 (0.7)	2.6 (0.2)	2.9 (0.4)	12.3 (0.8)
<i>T. a. brunneicollis</i>	39	51.4 (2.2)	18.9 (1.1)	<i>40.9 (2.2)</i>	8.8 (1.0)	3.0 (0.6)	3.3 (0.3)	13.2 (1.3)
<i>T. a. cahooni</i>	82	51.0 (1.7)	17.1 (0.9)	<i>41.0 (2.6)</i>	8.7 (0.7)	2.8 (0.2)	3.1 (0.2)	12.1 (0.9)
<i>T. a. carychrous</i>	12	51.3 (1.6)	19.4 (0.9)	35.8 (2.1)	11.5 (0.7)	3.3 (0.2)	3.6 (0.3)	15.5 (0.7)
<i>T. a. chilensis</i>	27	51.5 (2.3)	17.8 (0.8)	<i>44.0 (2.9)</i>	8.4 (0.7)	2.4 (0.3)	2.7 (0.2)	11.3 (0.9)
<i>T. a. columbae</i>	18	54.7 (1.4)	19.1 (0.9)	<i>41.2 (2.1)</i>	10.6 (0.5)	2.8 (0.1)	3.4 (0.4)	14.0 (0.5)
<i>T. a. compositus</i>	24	51.2 (1.6)	18.3 (0.8)	<i>42.3 (2.4)</i>	9.1 (0.8)	2.8 (0.2)	3.2 (0.2)	12.2 (1.0)
<i>T. a. duidae</i>	14	57.6 (1.5)	22.2 (0.6)	37.8 (1.4)	10.1 (0.4)	3.5 (0.2)	3.2 (0.2)	14.7 (0.4)
<i>T. a. guadeloupensis</i> *	16	52.1 (3.2)	17.8 (0.8)	37.3 (3.1)	11.2 (0.6)	3.0 (0.3)	3.0 (0.2)	15.1 (0.5)
<i>T. a. inquietus</i>	44	52.8 (1.8)	18.6 (0.6)	36.2 (2.1)	10.5 (0.7)	2.9 (0.2)	3.4 (0.2)	14.2 (0.9)
<i>T. a. intermedius</i>	89	49.9 (2.0)	17.5 (1.3)	35.5 (2.3)	9.1 (0.6)	2.9 (0.3)	3.1 (0.3)	12.8 (1.0)
<i>T. a. musculus</i>	12	50.2 (1.6)	17.7 (0.8)	<i>40.2 (3.0)</i>	9.9 (0.6)	2.8 (0.2)	3.0 (0.2)	12.8 (0.6)
<i>T. a. musicus</i> *	13	57.2 (2.6)	19.8 (0.8)	<i>40.9 (2.0)</i>	12.3 (0.5)	3.6 (0.2)	3.6 (0.2)	17.2 (0.8)
<i>T. a. parkmanii</i> †	66	51.2 (1.9)	17.0 (0.6)	<i>43.4 (2.3)</i>	9.0 (1.4)	2.8 (0.2)	2.9 (0.2)	12.3 (0.6)
<i>T. a. rehni</i>	10	48.2 (2.6)	16.7 (0.7)	31.5 (3.9)	8.4 (0.6)	2.7 (0.2)	3.2 (0.3)	12.5 (0.6)
<i>T. a. rex</i>	10	52.3 (1.6)	18.1 (0.6)	<i>44.7 (2.0)</i>	9.3 (0.9)	2.5 (0.2)	2.8 (0.2)	12.3 (1.0)
<i>T. a. rufescens</i> *	14	51.2 (2.0)	18.4 (2.4)	36.9 (1.1)	10.7 (0.5)	3.2 (0.2)	3.2 (0.2)	14.8 (0.6)
<i>T. a. rufulus</i>	18	55.6 (2.9)	<i>21.0 (4.0)</i>	38.8 (2.1)	9.9 (0.4)	3.3 (0.2)	3.2 (0.2)	15.0 (0.5)
<i>T. sissonii</i> +	33	49.3 (2.3)	20.2 (0.8)	<i>44.6 (3.3)</i>	10.7 (1.2)	3.0 (0.3)	3.0 (0.2)	15.3 (1.5)
<i>T. a. solstitialis</i>	46	49.7 (1.5)	18.5 (0.8)	34.5 (3.7)	8.6 (0.6)	2.9 (0.3)	2.9 (0.2)	12.7 (0.7)
<i>T. a. striatulus</i>	22	55.5 (1.8)	19.1 (0.8)	<i>40.9 (3.0)</i>	10.8 (0.9)	2.8 (0.2)	3.2 (0.2)	14.6 (0.9)
<i>T. tanneri</i> +	17	<i>59.6 (1.5)</i>	20.0 (2.2)	<i>48.1 (2.8)</i>	11.3 (0.4)	3.4 (0.4)	3.6 (0.3)	16.0 (0.7)

Appendix C: Photos collected from museums showing visual morphological and colour differences among different House Wren populations. Figure 1 and 2 are photos taken of specimens at the Harvard University Museum of Comparative Zoology (Boston, Massachusetts). Figure 3 is photos of live capture Grenada House Wrens were taken during the 2018 field season.



Figure 1: Top: *T. a. grenadensis* (Grenada) and Bottom: *T. a. parkmanii* (USA). Note the differences in colour, bill shape and length, and overall body size.



Figure 2: From top to bottom: *T. a. rufescens* (Dominica), *T. a. mesoleucus* (St. Lucia), *T. a. musicus* (St. Vincent and the Grenadines), *T. a. grenadensis* (Grenada). Note the darker colouration of wrens on Dominica and Grenada.



Figure 3: Male Grenada House Wren caught in northern Grenada. Top photo shows entire body with dark colouration on underside and the long bill. Bottom left shows the rectrices and bottom right shows the wing patterning. All photos are from the same individual. Note the overall dark and rich rufous colouration over the entire body.