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IS ISLAND LIFE TURNING BIRDS INTO GIANTS? AN ASSESSMENT OF FOSTER'S RULE ACROSS ALL BIRDS

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IS ISLAND LIFE TURNING BIRDS INTO GIANTS? AN ASSESSMENT OF FOSTER'S RULE ACROSS ALL BIRDS.

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ABSTRACT

The differences in the body sizes observed in island birds versus their closest mainland relatives have puzzled biologists for decades. First noted in other vertebrate groups by Dr. Bristol Foster, the general trend is usually summarized as small mainland species evolving larger bodies on islands, while typically large mainland species shift towards dwarfism. With many examples in both living and extinct fauna, the overall phenomenon became known as Foster's rule. Herein, we examine Foster's rule as it applies to class Aves (the group that contains all modern birds). We analyzed the body mass (n=9,316), body length (n=7,260) and wingspan (n=708) of avian species from around the world. To account for phylogeny, we employed the use of multiple independent phylogenetic generalized least squares analyses (PGLS). We first analyzed class Aves as a whole and then looked at each individual order separately. We found support for Foster's rule in class Aves overall, island species heavier and longer than mainland species. Wingspan did not vary between island and mainland species for the class as a whole. Looking at each order, we found that body size varied between islands and mainland in Anseriformes, Accipitriformes, Charadriiformes, Galliformes, Piciformes, Pelecaniformes, and Strigiformes. Whereas body mass in Galliformes and Piciformes increased on islands, Anseriformes decreased. Similarly, body length in Piciformes and Pelecaniformes increased, while Anseriformes and Strigiformes length decreased. Wingspan increased in both Accipitriformes and Charadriiformes. Although we found support for Foster's rule, the direction of effects varied by order, and by body size metric, indicating that the biogeographical pattern is not generalized across class Aves as has been previously suggested, and underscores the idea that body size evolution may be driven by a combination of stochastic and deterministic forces specific to bird orders.

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INTRODUCTION

An intriguing biological change occurs in island populations in which the body sizes of animals tend to differ markedly from their mainland counterparts. Dr. J. Bristol Foster first noted that island mammals often exhibit differing body sizes compared to their closest mainland relatives. The Island rule, also known as Foster's rule, describes the phenomenon of large-bodied mainland species becoming smaller (insular dwarfism) and small-bodied mainland species demonstrating the reverse (insular gigantism) (Van Valen 1973). Beyond its initial application to terrestrial mammalian clades, the influence of island biogeography on body size has been expanded to include other vertebrate groups like bats (Krzanowski 1967), squamates (snakes and lizards) (Itescu et al. 2018), and even non-avian dinosaurs (Benton et al., 2010). Foster's rule has also been tested in birds multiple times, yet only with a limited subset of species (Grant 1965; Grant 1966; Case 1978; Gaston and Blackburn 1995; Clegg and Owens 2002). To our knowledge, no comprehensive study of Foster's rule for the entire class Aves has been done to date despite the data being available (but see Olson et al. 2009 assessment of Bergmann's rule in birds).

The causes of insular dwarfism or gigantism are controversial and vary depending on the species and the selective pressures they face. These include food availability, energy use, predation risk, intraspecific and interspecific competition, and heat regulation (Clegg and Owens 2002; Lomolino 2005). For bird species, food availability has been proposed as the driving factor behind changes in body morphology when moving from mainland environments to islands (Keast 1968; Mayr 1963; Abbott 1980; Grant 1998; Blondel 2000). Large-bodied species are thought to have reduced fitness on islands where they encounter increased population densities and intraspecific competition, leading to selection favouring decreases in overall body size as smaller individuals. require less food and therefore less energy to survive and reproduce (Lomolino 2005). Island

environments are also typically species poor when compared to mainland ecosystems and often lack the mammalian predators and interspecific resource competitors found on the mainland (McNab 2002; Lomolino 2005). While being the largest member in a group of conspecifics may serve as protection against predation in mainland habitats, islands without large mammalian predators make this adaptation an energetic liability (McNab 1994; Lomolino 2005). With reduced predation pressure, we would expect to see the largest directional change in body mass occurring in species with the largest bodies, and therefore the highest energetic demands overall (Lomolino 2005). In addition to energy requirements, it should also be noted that Clegg and Owens (2002) observed that body mass decline in larger birds intensified as they neared the equator. They suggested that this was possibly an adaptation to increase heat dissipation but could not be specific as to the exact mechanism.

McNab (1994, 2002) suggested that when small bodied species experience reduced predation pressure on islands, they become larger and occupy similar niches to intermediate sized herbivores on the mainland. In times of resource scarcity, individuals with larger body sizes can dominate food sources (Lomolino 2005). As competition intensifies within species groups and between similar species, dietary divergence through niche expansion and speciation may result; this has been hypothesized to be the main evolutionary force behind insular gigantism in vertebrates (Runemark et al. 2015). For species capable of high dispersal (such as birds), islands represent an opportunity to fill terrestrial niches that are already occupied in older, mainland environments. Consistent with Foster's rule, body sizes in birds appear to increase following island colonization, suggesting that larger body size is, at least in part, adaptive in island conditions (Owen and Clegg 2002; Oslon et al. 2009). Boyer and Jetz (2010) examined the predictors of body size in insular

bird species and found that body size is positively correlated with island size, i.e., larger birds are found on larger islands.

On a macroevolutionary scale, body size may also, in part, be due to ancestry. In relation to Bergmann's rule, Olson et al. (2009) suggested that phylogenetic history may constrain body size. They note that all penguins are relatively large in size and occupy similar niches as a result of shared ancestry. We thus need to be cautious in assuming that ecological factors are the major influences on body size. Observed differences between island and mainland species may be deeply rooted in phylogeny rather than ecology. Therefore, evolutionary relationships must be accounted for when testing broadly related taxa such as class Aves. One such approach is to use a phylogenetic generalized least squares analysis, as outlined later on in our methods.

The generalizability of Foster's rule in birds has previously been called into question and thus been the focus of multiple studies (e.g., Grant 1965; Grant 1966; Case 1978; Gaston and Blackburn 1995; Clegg and Owens 2002; Olson et al. 2009; Wright and Steadman 2012). Early (e.g., Grant 1966; Carlquist 1974; Case 1978; Gaston and Blackburn 1995) failed to find support for larger body sizes in birds using mass as a metric, instead noting potential trends towards increased tarsal and beak length compared to mainland species (Grant 1965). In contrast, more recent studies have found explicit support for Foster's rule in birds based on body mass (Clegg and Owens 2002; Olson et al. 2009). One of the first attempts at a broad-scale study of the island rule in birds was conducted by Clegg and Owens (2002) and included 110 pairs of island species and their closest-related mainland counterparts. The most inclusive study to date was conducted by Olson et al. in 2009), in which sthey analyzed the body masses of 8270 species from across a wide geographic range. Although they did include an island/mainland body mass analysis, the primary focus of Olson et al. (2009) was a test of Bergmann's rule (in which body size increases with

higher latitudes) in birds. They found that median body masses in island birds were higher than expected by latitude alone (Olson et al. 2009). Our study expands Olson et al. (2009) by including more than one body size variables and asking whether Foster's rule is generalizable l avian orders.

Here, we tested the application of the Foster's rule to class Aves (all modern birds), specifically using body mass, body length, and wingspan as metrics of body size in the comparison of island versus mainland endemic taxa. We hypothesize that birds will follow the island rule in general terms as outlined by Van Valen (1973): small-bodied taxa will be typical of mainland environments and large-bodied taxa will be endemic to islands, as one would expect if niche expansion and dietary divergence on islands drives gigantism in the absence of predators and interspecific competition, as previously hypothesized.

METHODS

Data Collection

To test for differences in body size between island and mainland birds, we collected body mass, length, and wingspan data from Wilman et al. (2014) and from the Handbook of Birds of the World (2020). We categorized species as either mainland or island, based on the range maps provided by the IUCN Redlist (2020). Specifically, we classified each species as being island (n=2,056), mainland (n=7,260) intermediate between these (n=544), or oceanic (n= 133). We described species as discretely island or mainland if at least 70% of its range was occupied by the respective land type. Species with more ambiguous ranges of 50-60% were termed intermediate. Lastly, species with vast ocean ranges (roughly 70% open water, often connecting islands to mainland

shores) were considered as oceanic. We included Greenland as our upper limit to island size (2,130,800 km²). Continental Australia (not including Tasmania) was considered as a mainland environment. Birds noted as being intermediate or oceanic were subsequently excluded from the analyses. Only extant resident and breeding ranges were used except in unique cases, such as species that are only recently extinct in the wild (e.g., *Corvus hawaiiensis*) or are believed to be extinct but have not been confirmed to be so (e.g., *Campephilus principalis*); in these cases, the historical ranges were used. We excluded introduced, migratory, and non-breeding ranges from consideration. General body size in an order was determined using methods similar to those of Clegg and Owens (2002) where large-bodied birds were those above the mainland mean and smallbodied were below. We classified mainland taxa as either being large or small depending on whether they were larger or smaller than the calculated median body mass for mainland birds as a whole (Table 1). Finally, in all figures we present logarithmic transformed data to help with interpretation.

Table 1. Mainland median body masses (g) depicting which orders were considered large-bodied and which were small relative to overall median value.

order	mainland	body	order	mainland	body
	med. (g)	size	continued	med. (g)	size
All orders	32.30	-	Cuculiformes	80.70	large
Accipitriformes	754.37	large	Falconiformes	261.00	large
Anseriformes	922.19	large	Galliformes	549.39	large
Apodiformes	5.20	small	Gruiformes	159.09	large
Bucerotiformes	292.00	large	Passeriformes	20.54	small
Caprimulgoformes	57.84	large	Pelecaniformes	846.00	large
Charadriiformes	158.00	large	Piciformes	54.51	large
Columbiformes	169.00	large	Psittaciformes	122.43	large
Coraciiformes	52.96	large	Strigiformes	191.00	large

Phylogeny

To generate our core phylogeny, we downloaded 1000 trees from BirdTree.org (Jetz et al. 2012) in the "HackettStage2_1001_2000" subset. We then used the package *ape* (Paradis and Schliep 2018) in R (Rstudio Team 2016) to read the trees. We created maximum clade credibility trees with 1% burn-in state and mean node height based on the remaining species within each dataset using TreeAnnotator V.1.10.4 (Rambaut and Drummond 2018).

PGLS Analyses

To test the evolutionary associations between body size and island occupancy, we generated three phylogenetic generalized least squares models (PGLS) for the body mass (n=9,316), body length (n=7,584), and wingspan (n=708) datasets. PGLS analyses were generated using the R

packages *ape* (Paradis and Schliep 2018) and *nlme* (Pinheiro, Bates, DebRoy, Sarkar, and R core team 2019). We first analyzed for differences in body size using all birds; in each model, land status (island or mainland) served as a main effect, with body size measures serving as response variables. All models included Brownian correlation and maximum likelihood methods. We used the *phytools* package (Revel 2012) to isolate species by order and remove any species with insufficient data. Only orders containing twenty or more species with at least five island and five mainland species were included in the within-order analysis. Once these restrictions were applied, our analysis was reduced to 19 orders for body mass, 18 for body length, and 3 for wingspan. Because within orders, species vary in their biology and ecology, we treated each order as a separate hypothesis, so we did not correct the P value for multiple hypothesis testing (i.e., setting the stringency of our alpha from 0.05 to 0.0025 to avoid increased chances of making a Type II error). In total, we performed 43 separate PGLS analyses.

RESULTS

Body Mass

Overall, birds on islands were larger, with a median body mass 16.8g heavier than their mainland counterparts (Table 2, Figure 1 (A), df = 9314, Z = 1109.14, p < 0.01), a finding consistent with Foster's rule. For the order analyses, as predicted, the characteristically larger-bodied Anseriformes (ducks, geese, swans and kin) showed a decrease in median body mass of ~ 91.2g on islands indicating a shift to dwarfism (Table 2, Figure 2 (B; E), df = 148, Z = 179.01, p < 0.01). In contrast, Galliformes (chickens, pheasants and kin) were ~ 65g heavier on islands versus mainland (Table 2, Figure 2 (C; F), df = 270, Z = 16.90, p = 0.01). Accipitriformes (hawks, eagles,

vultures, and kites) also trended towards smaller body sizes on islands; however, this difference was marginal with island species being lighter by 179.4g (Table 2, df = 134, Z = 12.68, p = 0.10). On the other hand, the smaller Piciformes (woodpeckers and kin) were ~ 27g heavier on islands compared to mainland (Table 2, Figure 2 (A; E), df = 378, Z = 17.62, p = 0.01). We found no differences in body size between island and mainland species in the remaining orders (15/19).



Figure 1. Boxplots showing differences in the log_{10} median body mass (**A**) and the log_{10} body length (**B**) between island and mainland species for class Aves overall. Both body mass and body length had a significant increase in island birds versus their mainland counterparts.



Figure 2. Top: (**A**) A phylogeny of 380 species (39 island and 341 mainland) examined belonging to the order Piciformes. (**B**) A phylogeny of the 150 species (16 island and 134 mainland) examined belonging to the order Anseriformes. (**C**) A phylogeny of the 272 species (49 island and 223 mainland) examined belonging to the order Galliformes. Island species are visually represented by black, while red corresponds to mainland. Bar length denotes mean body mass (g) for the species. Bottom: Boxplots showing significant differences in the log₁₀ median body mass between island and mainland species of (**D**) Piciformes versus (**E**) Anseriformes and (**F**) Galliformes.

Table 2. PGLS results for all bird orders together, then separated by order. Median body mass (g) values for both island and mainland groups provided. Statistically significant results have been bolded. Marginally significant results have been italicized.

order	n (island/mainland)	df	Z (test stat)	Р	island median (g)	mainland median (g)
Accipitriformes	236(49/187)	234	12.68	0.10	575.00	754.37
Anseriformes	150(16/134)	148	179.01	<0.01	831.02	922.19
Apodiformes	409(52/357)	407	10.00	0.98	11.90	5.20
Bucerotiformes	60(21/39)	58	11.85	0.18	1086.00	292.00
Caprimulgoformes	102(23/79)	100	10.06	0.80	70.30	57.84
Charadriiformes	345(48/297	343	10.08	0.77	142.50	158.00
Columbiformes	298(172/126)	296	10.08	0.77	205.65	169.00
Coraciiformes	144(63/81)	142	10.04	0.84	60.97	52.96
Cuculiformes	129(54/74)	127	10.23	0.63	160.00	80.70
Falconiformes	61(10/51)	59	10.56	0.46	145.40	261.00
Galliformes	272(49/223)	270	16.90	0.01	614.75	549.39
Gruiformes	149(37/111)	147	11.59	0.21	205.92	159.09
Passeriformes	5701(1187/4514)	5699	10.00	0.97	22.80	20.54
Pelecaniformes	100(7/93)	98	12.25	0.14	802.00	846.00
Piciformes	380(39/341)	378	17.62	0.01	81.91	54.51
Psittaciformes	339(129/210)	337	11.03	0.31	112.00	122.43
Strigiformes	184(61/123)	182	10.12	0.73	151.00	191.00
Suliformes	41(9/32)	39	11.23	0.27	2072.67	1517.55
Trogoniformes	38(9/29)	36	12.10	0.16	72.82	80.29
All orders	9316(2056/7260)	9314	1109.14	<0.01	49.10	32.30

Body length

Across the class Aves, species on islands had median body lengths ~2.5cm longer than birds on the mainland (Table 3, Figure 1(B), df = 7584, Z = 1106.43, p < 0.01), which again is consistent with Foster's rule given the small overall median value for mainland birds. Anseriformes on islands were also smaller, however, this is not reflected in the median lengths overall (both were 53cm) (Table 3, Figure 3 (B; F), df = 125, Z = 147.05, p < 0.01). Here we chose to include the mean body length and the standard deviation to provide context. Island Piciformes were larger than their mainland counterparts by roughly 8.3cm (Table 3, Figure 3 (A; E), df = 317, Z = 136.19, p < 0.01). Strigiformes species (owls) are also consistent with Foster's rule being ~ 0.75cm smaller on islands (Table 3, Figure 3 (C; G), df = 164, Z = 110.96, p < 0.01). Island Pelecaniformes increased in size by ~1.5cm (Table 3, Figure (D; H) df = 94, Z = 14.24, p = 0.04). All remaining orders (14/18) did not meet the threshold of significance.



Figure 3. Top: (A) A phylogeny of 319 species (24 island and 295 mainland) examined belonging to the order Piciformes. (B) A phylogeny of the 127 species (16 island and 111 mainland) examined belonging to the order Anseriformes. (C) A phylogeny of the 162 species (57 island and 109 mainland) examined belonging to the order Strigiformes. (D) A phylogeny of the 96 species (7 island and 89 mainland) examined belonging to the order Pelecaniformes. Island species are visually represented by black, while red corresponds to mainland. Bar length denotes median body

length (cm) for the species. Bottom: Boxplots showing significant differences in the log_{10} median body length between island and mainland species of (E) Anseriformes versus (F) Piciformes and (G) Strigiformes (H) Pelecaniformes.

Table 3. PGLS analyses conducted using the body length data set, separated by order, along with the median value (cm). Significant results have been bolded. * Island and mainland medians were equal for Anseriformes, but the means with standard deviations were 53.72 ± 10.72 cm for islands and 58.41 ± 23.12 cm for mainland. *

order	n (i-ld/i-ld)	df	Z (test stat)	Р	island	mainland
	(Island/mainland)				med. (cm)	med.(cm)
Accipitriformes	212(49/163)	210	12.41	0.12	47.50	52.00
Anseriformes	127(16/111)	125	147.05	<0.01	53.00	53.00
Apodiformes	349(36/313)	347	10.41	0.52	11.75	11.00
Bucerotiformes	41(12/29)	210	12.41	0.12	52.50	50.00
Caprimulgiformes	78(19/59)	76	10.26	0.61	25.00	23.50
Charadriiformes	302(42/260)	299	10.04	0.83	28.75	28.00
Columbiformes	263(149/114)	261	10.48	0.49	33.50	28.31
Coraciiformes	124(48/76)	122	10.04	0.85	23.50	25.25
Cuculiformes	108(43/65)	106	10.03	0.92	43.50	33.00
Falconiformes	59(9/50)	57	10.03	0.86	47.00	35.25
Galliformes	194(34/160)	192	10.14	0.71	34.00	40.50
Gruiformes	100(19/81)	98	10.63	0.43	29.00	28.00
Passeriformes	4519(941/3578)	4517	12.18	0.27	15.50	15.00
Pelecaniformes	96(7/89)	94	14.24	0.04	68.00	67.50
Piciformes	319(24/295)	317	136.19	<0.01	27.75	19.50
Psittaciformes	314(125/189)	312	10.68	0.41	25.00	26.00
Strigiformes	166(57/109)	164	110.96	<0.01	24.00	24.75
Trogoniformes	36(8/28)	34	12.40	0.13	29.75	29.00
All orders	7584(1660/5924)	7582	1106.43	<0.01	20.00	17.50

Wingspan

For wingspan, we did not detect a difference between island and mainland species for the class Aves overall. However, diurnal raptor species (Accipitriformes) on islands had roughly ~27cm shorter median wingspans than those on the mainland (Table 4, df = 201, Z = 19.15, p < 0.01). Similarly, in Charadriiformes (shore birds, gulls, and auks) island species had wingspans that were ~ 3.5cm shorter than those on the mainland (Table 4, df = 197, Z = 14.24, p = 0.04). The remaining orders did not exhibit differences in wingspan between island and mainland orders.



Figure 4. Mainland bird species are indicated by red bars; island birds indicated by black bars. (A) A phylogeny of 203 species (49 island and 154 mainland) examined belonging to the order Accipitriformes. (B) A phylogeny of the 199 species (21 island and 178 mainland) examined

belonging to the order Charadriiformes. Island species are visually represented by black, while red corresponds to mainland. Bar length denotes mean body mass (g) for the species. Boxplots showing significant differences in the log_{10} median body mass between island and mainland species of (C) Accipitriformes versus (D) Charadriiformes.

Table 4. PGLS analyses conducted using the wingspan data set, separated by order, along with the median value (cm). Significant differences are bolded.

order	n (island/mainland)	df	Z (test stat)	Р	island media n (cm)	mainland median (cm)
Accipitriformes	203(49/154)	201	19.15	<0.01	95.50	122.50
Anseriformes	66(5/61)	64	11.71	0.20	84.00	82.50
Charadriiformes	199(21/178)	197	14.24	0.04	60.50	64.00
Falconiformes	57(9/48)	55	10.14	0.71	56.00	76.25
All orders	709(98/611)	707	12.15	0.14	75.00	85.00

DISCUSSION

Based on our analyses, we found support for Foster's rule across class Aves, with an overall increase in the small mainland median values (as measured by body mass and body length (Figure 1, A and B)) compared to island species; however, this pattern was largely dependent on order. In orders of larger birds (e.g., Anseriformes and Accipitriformes), island species were usually smaller than those on the mainland. The general support for Foster's rule across class Aves, with larger species more likely to be found on islands, supports the results of previous studies done by Clegg and Owens (2002), Boyer and Jetz (2010), and Olson et al. (2009). Of the approximately 10,000 bird species, over half belong to the order Passeriformes (perching birds) which have

characteristically small body sizes (Clegg and Owens 2002). In pioneering studies, such as Grant's 1965 analysis, the disproportionately high numbers of small-bodied species in their datasets were thought to have masked support for Foster's rule among the class Aves (see Clegg and Owens 2002). No small-bodied groups appeared overrepresented in our dataset compared to what they should be in the phylogenetic tree created by Jetz et al. (2012) containing all known modern bird species (at the time of their publication). We addressed overrepresentation by mirroring the proportions of bird orders as naturally represented in class Aves. For example, of the 9,316 species tested in our mass dataset, 5,701 were passerines (~61%). The next largest order by species was another small-bodied taxon, Apodiformes (Hummingbirds, swifts and kin), at 409 (~7%). Supporting earlier work by Grant (1965), wingspan did not differ between island and mainland species across class Aves. Only in Accipitriformes and Charadriiformes did we detect differences in wingspan, with both orders showing a reduction in median wingspan. It should also be noted that wingspan is typically only used as a metric of body size when mass is unavailable (Hamilton 1961). Additionally, our wingspan dataset was fairly small, including fewer than 10% of all bird species (708 compared to 9,316 for body mass and 7,584 for body length). As such, we note that these results do not necessarily have the same statistical power as our other two response variables.

The support for Foster's rule in all birds creates an apparent contradiction when broken down by order. Except for taxa listed in the above results (Tables 1,2, and 3) the majority (15/19) displayed no differences in body mass between island and mainland species—a finding consistent with Olson et al. (2009). Similarly, we found no differences in body length between island and mainland species for a majority (14/18) of orders. As noted earlier, body size gradients may be at least partly adaptive (Olson et al. 2009) and could be a response to processes occurring at the assemblage level (i.e., inter and intraspecies interactions unique to the animal life of each island probably have a significant role) (Gaston et al. 2008). Bird body size has also been shown to change after island colonization as a response to dietary expansion, competition, energetic costs, and heat regulation (Clegg and Owens 2002) but different orders are likely to have varying degrees of response to at least some of these factors based on differing physiologies. For example, predatory birds such as Accipitriformes have differences in population densities compared to herbivorous species (Juanes 1986) and therefore would experience intraspecific competition differently as a result. With limited prey on species-poor islands, niche expansion may not be a driving force in this case. It is likely too simplistic to say groups that are ecologically different, such as Accipitriformes and Anseriformes, are predictable solely because they are large-bodied forms and should therefore follow Foster's rule without deviation. Additionally, factors like competition and niche expansion depend on what species are present on which islands. Therefore, aspects of island ecology are likely to play significant roles in size trends overall.

An alternate explanation may come down to stochastic events. Lomolino (2005) notes that relatively poor flyers may become stranded, especially on remote islands, invoking a Darwinian metaphor of a shipwrecked crew clinging to their wreck. Those that can travel back to their mainland habitats may do so leaving a smaller population of weak flyers behind. One mechanism could be through the founder effect, which has been shown to account for morphological and genotypic variation in some island bird species (Clegg et al. 2002; Estoup and Clegg 2003; Spurgin et al. 2014). In other words, changes in body size may arise from pure chance related to which individuals get stranded and the genetic contributions they bring to the population. The influence of genetic drift should also not be overlooked. Non-adaptive selection may partially explain why so many orders contain species, genera, and likely even families that exhibit dwarfism or gigantism, yet fail to demonstrate a clear trend across orders.

We have only scratched the surface when it comes to the exploring island biogeography. Islands are exceptionally diverse, both in terms of geography and ecology. Wright and Steadman (2012) noted that factors like island size and geographical region can also impact the physical traits of the birds living on them. A study by Filin and Ziv (2004) appeared to show that the degree of change in body size from the mainland species was inversely related to the size of the island area. The complex associations within and among avian taxa are complicated by both living and nonliving components of their island environments, all of which may affect the evolution of bird morphology. To summarize, our study has found that birds as whole had higher median masses and body lengths on islands compared to mainland environments indicating a move towards gigantism. On the level of order, this pattern begins to breakdown for the exception of only a handful of groups. There was no significant difference in wingspan overall, except for two isolated orders. Why and how body size changes on islands have been partly addressed, but more work is required to reveal the nuances and specific mechanisms. When analyzed closely at higher taxonomic power (i.e., family and genus), the causes of insular dwarfism and gigantism are likely to be as unique and variable as the bird species they influence.

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