

Biogeography of body size in Pacific island birds

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Many insular vertebrates have undergone rapid and dramatic changes in body size compared to their mainland counterparts. Here we explore the relationship between two well known patterns of island body size – the tendency for large-bodied species to dwarf and small-bodied species to get larger on islands, known as the “island rule”, and the scaling of maximum and minimum body size of island assemblages with island area. Drawing on both fossil and modern data, we examined the relationship between body size and island area in Pacific island birds, both within clades and at the island assemblage level. We found that the size of the smallest bird on each island decreased with island area while the maximum body size increased with island area. Similarly, within clades the body size of small-bodied groups decreased and large-bodied groups increased from small to large islands, consistent with the island rule. However, the magnitude of size change within clades was not sufficient to explain the overall scaling of maximum size with island area. Instead, the pattern was driven primarily by the evolution of very large, flightless birds on large islands. Human-mediated extinctions on islands over the past few millennia severely impacted large, flightless birds, to the effect that this macroecological pattern has been virtually erased. After controlling for effects of biogeographic region and island area, we found island productivity to be the best predictor of maximum size in flightless birds. This result, and the striking similarities in maximum body size between flightless birds and island mammals, suggests a common energetic mechanism linking body size and landmass area in both the island rule and the scaling of island body size extremes.

The body sizes of insular vertebrates often differ dramatically from those of their mainland counterparts. Body size is a fundamental ecological parameter that reflects many other ecological characteristics associated with resource requirements, life-history, and ecological interactions (Heaney 1978, Damuth 1981, Lomolino 1985, Brown 1995, McNab 2002) across species and assemblages. Mammal and bird body size on islands often follows a predictable pattern, known as the “island rule”, where species that are large on the mainland tend to decrease in size on islands and small species increase in size (Clegg and Owens 2002, Lomolino 2005, Raia and Meiri 2006; see also Meiri et al. 2008). In a related pattern, the maximum body size of vertebrates on islands and other landmasses appears to increase with island area while minimum body size decreases, producing a divergent scaling of body mass extremes over island area referred to here as “area-scaling of body size extremes” (Marquet and Taper 1998, Burness et al. 2001, Okie and Brown 2009).

The island rule is based on a species-focal, evolutionary perspective, where body size changes result from differential selection on body size in the island environment. In contrast, studies of body size extremes involve attributes of a whole assemblage and causal mechanisms may involve both species-level evolutionary processes as well as community-level processes. In a key study linking the island rule with

island area, Filin and Ziv (2004) found the degree of body mass change in island birds and mammals to be inversely related to island area, where both insular dwarfing of large-bodied forms and gigantism in small-bodied forms were more pronounced on the smallest islands. These findings suggest that island rule-like body size changes could produce a scaling relationship between island area and maximum and minimum size in island assemblages. Alternatively, it is also conceivable that the scaling of size extremes occurs without the island rule and is driven by very large or small single-island endemics. Given these direct connections and likely causal overlap, a joint assessment is likely to integrate and advance our understanding of the structure of island communities.

We hypothesize that area-scaling of size extremes may arise from an interaction between how island area and body size affect immigration, survival (emigration and extinction), or in situ evolution. However, size-area scaling could also be a simple result of sampling effects. Following well-established empirical and theoretical evidence in island biogeography (MacArthur and Wilson 1967, Rosenzweig 1995, Kalmar and Currie 2007, Kreft et al. 2008, Whittaker et al. 2008), larger islands are expected to harbor higher species richness. Even with just slight body size variance in the regional pool, species-rich assemblages on large islands should show larger body size

maxima and smaller minima than assemblages of fewer species on small islands. In this case a simple null model that simulates random colonization from the regional pool (following Simberloff 1978) should be sufficient to explain the area-extremes pattern. However, we expect variation above and beyond this sampling effect (see Marquet and Taper 1998) and we explore several other hypotheses for area-scaling that make additional, directional predictions.

Area-scaling of body size extremes could arise in the absence of evolutionary processes through size-neutral (or potentially size-selective) immigration. Island biogeography theory and empirical studies have shown that colonization rate declines as a function of isolation (Heaney 1986, Whittaker and Fernández-Palacios 2007). Under the “target effect”, larger islands may receive more immigrants than smaller islands of similar isolation (Whitehead and Jones 1969, Lomolino 1990), but no straightforward body size trends are obvious. While some larger-bodied species tend to disperse longer distances (e.g. birds: Sutherland et al. 2000; mammals: Van Vuren 1998), possible interactions between body size and island area are unknown. If immigration has played an important role in area-scaling of body size extremes, we would expect an effect of island isolation where less isolated islands have larger body size maxima and smaller minima than similar-sized, more isolated islands.

Body size and island characteristics such as area should have clear ramifications on body size extremes by influencing the persistence of species. Extinction probabilities are strongly negatively associated with population size (Lande 1993, IUCN 2001) and limited land area may necessarily limit population size on islands. Population size per unit area (density) is constrained by body size such that small-bodied species may attain high or low densities but large species usually exhibit lower density (Damuth 1981, Silva et al. 1997, Jetz et al. 2004a). Assuming species of different body sizes require similar minimum viable population sizes (Traill et al. 2007), this means that on small islands large-bodied species may be more prone to extinction and less likely to persist than small-bodied species. Population densities are additionally affected by environmental conditions. More productive areas are expected to facilitate larger energy flux through consumers and support a larger number of individuals and populations (Wright 1983, Evans et al. 2006, Hurlbert and Jetz 2010), and strong positive relationships between energy availability and population density have been demonstrated in, among other groups, ants, birds, and lizards (Evans et al. 2005, Meehan 2006, Buckley and Jetz 2007). Higher environmental temperature and precipitation are associated with higher environmental productivity (Woodward et al. 1995). We therefore predict, above and beyond sampling and area effects, wider body mass extremes on islands with increasing temperature and precipitation.

Evolutionary change in body size on islands is a third possible mechanism for between-island variation in body mass extremes. Immigrant species may undergo in situ evolutionary changes in body size after establishment on an island, consistent with the island rule (Anderson and Handley 2002, McNab 2002). If island rule-like body size changes produce the area-scaling of maximum and minimum size in island assemblages, we would expect to see

strong effects of island area on the body sizes of closely-related species on different islands. Fourth, in situ diversification could produce area-scaling of size extremes because larger islands may support more speciose adaptive radiations (Kisel and Barraclough 2010), resulting in more species, and wider body mass extremes. This expectation would be partly captured by the null model based on species richness, or at least the same variables associated with higher species richness (area and productivity as above) may also promote diversification. In both evolutionary hypotheses we would expect to observe wider size extremes on older islands, relative to similarly-sized young islands, due to a longer period for in situ evolution.

In summary, we predict an increase of body mass maxima and decrease of minima with island area, beyond the effect expected under random colonization. If mass- and area-selective immigration govern body size distributions then we expect size extremes to vary with island isolation. If energetic constraints on population densities and body sizes are important we predict higher temperature and precipitation to be associated with wider size extremes. Strong positive effects of island age on body size extremes would indicate in situ evolutionary processes generating the area-scaling pattern. Finally, if island rule type body size changes contribute to the area-scaling of maximum and minimum size in island assemblages, we would expect to see a strong association of body size and island area within lineages.

Although island body size patterns have been studied primarily in mammals, birds colonized and thrived on many oceanic islands, and island birds provide an independent opportunity to examine the constraints on body size evolution. Abundant zooarchaeological and fossil remains of birds from Pacific islands reveal a wide ecological and taxonomic diversity of birds that once dominated terrestrial vertebrate communities on oceanic islands (Worthy and Holdaway 2002, Steadman 2006). Fossil evidence shows that flightlessness on islands evolved in at least eight orders of birds (Dinornithiformes, Anseriformes, Psittaciformes, Strigiformes, Columbiformes, Gruiformes, Ciconiiformes, and Passeriformes), and rails, geese, ducks, pigeons, and ibises repeatedly evolved the flightless condition after colonization of numerous isolated islands (McNab 1994b, Slikas et al. 2002, Steadman 2006). On islands lacking mammalian predators, reduction of flight ability may have been selected for because of the associated decrease in individual metabolic requirements (McNab 2002), and a corresponding increase in population size (McNab 1994a). While this pattern is not strictly consistent with the island rule, it does appear to be energetically driven (Lomolino 2005). Island birds show several predictable patterns in response to island living, including the classical island rule (Clegg and Owens 2002), lower metabolic rates compared to mainland populations (McNab 1994b), niche expansion (Scott et al. 2003) and density compensation (MacArthur et al. 1972, Wright 1980). In addition, McNab (1994b) presented data suggesting a loose relationship between island area and body size in island birds.

Here we use species-occurrence and body size data from fossil and extant assemblages to reconstruct the biogeography of body size in Pacific island birds. We examine the scaling of minimum and maximum body size with island area in both prehuman and modern avifaunas and test for

the additional effects of island age, isolation, environment and other island attributes on body size extremes. We also examine patterns of body size variation with island area within lineages in an effort to determine the relationship between the island rule and area-scaling of body size extremes.

Methods

We gathered species occurrence and body size data for all known land birds from 48 Pacific islands, incorporating both fossil and modern data. Only islands with at least 10 fossil specimens were included in the dataset, as a lower-bound on fossil sampling effort. The data set spanned the tropical Pacific including Melanesia (10 islands), western Polynesia (14 islands), eastern Polynesia (9 islands), the Marianas (5 islands), New Zealand (4 islands), and the Hawaiian Islands (6 islands). Today, these islands range in size from 5 km² to almost 146 000 km² and cover a total area of 317 200 km².

On these islands, birds were the dominant terrestrial vertebrates due to the limited over-water dispersal abilities of non-volant mammals. We focused on the terrestrial environment, so all seabirds and shorebirds were excluded from analysis. Species lists of breeding birds for each island were primarily gathered from Worthy and Holdaway (2002) for the New Zealand region, Olson and James (1991) for the Hawaiian islands, and Steadman (2006) for other islands, but were supplemented by information from a variety of published sources (Supplementary material Appendix S1). Invasive species were excluded. The total historic and extant breeding avifauna across the study islands consists of 583 species. Physical attributes of each island, including land area (km²), maximum elevation (m), geology, distance from nearest continent (km) and isolation index (a composite measure incorporating distance from the nearest continent, island group, and island) were gathered from the United Nations Environment Program Islands Directory (1998). Mean annual temperature (°C) and mean annual precipitation (mm) for each island were extracted from WorldClim climatic layers (Hijmans et al. 2005).

Body size estimates

Available body size data for Pacific island species were gathered from the literature (Supplementary material Appendix S1). However, few body size estimates for Pacific island endemics, especially extinct species, have been published. For these species, we developed body mass estimates based on the allometry of hind limb skeletal measurements in over 600 avian skeletal specimens (277 species from 13 orders of birds and 21 Passerine families) following the methods of Campbell and Marcus (1992). Only specimens with associated live-masses were measured and females and left leg were used preferentially. Specimens were selected to include a broad range of body sizes and an effort was made to include as many Pacific island genera as possible.

We examined the scaling of mass with hindlimb diameter using linear regression of natural log-transformed

bone diameter (mm) on natural log-transformed mass (g). Body mass (M) was predictable from femur diameter ($\ln(M) = 2.44 \times \ln(\text{femur}) + 2.50$, $R^2 = 0.95$, $n = 580$), tibiotarsus diameter ($\ln(M) = 2.41 \times \ln(\text{tib.}) + 2.72$, $R^2 = 0.96$, $n = 561$), and tarsometatarsus diameter ($\ln(M) = 2.30 \times \ln(\text{tars.}) + 2.97$, $R^2 = 0.93$, $n = 547$). Allometry of femur and tibiotarsus diameters did not differ between flightless and volant birds, although flightless birds showed a slightly steeper scaling of tarsometatarsus diameter (t -tests, femur: $t = 0.19$, $DF = 576$, $p = 0.85$; tibiotarsus: $t = 1.92$, $DF = 557$, $p = 0.05$; tarsometatarsus: $t = 5.56$, $DF = 543$, $p < 0.001$). We calculated the average prediction error (APE) of the regression equations using independent measurements of 33 specimens of disparate sizes and taxonomy. APE reflects the mean percent difference between the mass estimate and the actual mass for each specimen. We found an APE of 5.96% for estimates based on the tibiotarsus, a value well within the range acceptable for studies utilizing body size estimates (Damuth and MacFadden 1990).

To estimate body size of extinct species, we measured the hindlimb of 591 fossil specimens of 155 Pacific island species, and obtained measurements from the literature for 77 more taxa. We applied the formulas listed above, using the tibiotarsus preferentially over the other bones, to obtain mass estimates. Although a multivariate model incorporating all three hindlimb elements may have been preferred, this was not an option for the majority of fossil specimens due to the lack of associated skeletal material. One mass estimate was made for each specimen, and population-level size estimates were based on the mean of specimens of each species from each island.

Analyses

We examined the relationship between island area and the mass of the largest and smallest species on each island with least-squares linear regression. Although the fossil record for many islands is far from complete, we were confident in characterizing maximum body sizes on each island for the following reasons: 1) large-bodied birds have a much higher likelihood of being preserved as fossils than small-bodied birds (Duncan et al. 2002, Boyer 2010), 2) large-bodied birds and non-passerine taxa are often discovered and described early in paleontological study of an island (Steadman 2006), and 3) the discovery of a larger species on one or a few islands would be unlikely to change our results since strong area-size relationships have been observed for both the largest and the second-largest species in island mammals (Okie and Brown 2009). For minimum size on each island, all volant species identified as smallest are extant and their size estimates were not based on fossils. Minimum size of flightless species was based primarily on fossil evidence, and the future discovery of smaller flightless species could alter our results for this group.

To facilitate interpretation, for area-scaling analyses, we excluded all predatory birds, such as owls, hawks, and herons, due to the substantially different population densities of carnivorous vertebrates (Juanes 1986, Jetz et al. 2004a), and because size evolution in different trophic levels of island mammals has been shown to result

from different underlying mechanisms and result in different body size patterns (Raia and Meiri 2006). Insectivores were included in the analysis; they comprised the majority (37 of 46) body size minima, but no body size maxima were insectivorous. Body mass (g) and area (km²) were log₁₀-transformed prior to analysis. Because flightless birds, which in most cases evolved in situ on each island, might be expected to reflect a stronger relationship between island area and size than volant (flying) species, we analyzed flightless and volant species separately. We repeated the analysis including only those species still living today (extant species).

Because large islands and landmasses support both higher species richness and also a greater total resource supply, it is important to determine the influence of sampling effects on size-area scaling. We developed a simple null model to evaluate whether the scaling of body size extremes with island area is simply a result of the greater species richness on larger islands given the regional species pool. Ideally the species pool should reflect the potential source pool of species that are capable of dispersing to, establishing on, and/or evolving on Pacific islands. Understanding of the potential source pools for Pacific island birds is severely hampered by the lack of phylogenetic studies of island birds (Steadman 2006). Without clear, defensible source pools for each island or island group, it is unclear whether localized (based on biogeographic regions) or extensive source pools (including source areas from which colonists originated in the past – Australia, New Guinea, Asia, and North America) would represent the most accurate source pool for our null model. As an intermediate solution, we used the total species list from across the 48 islands in our dataset (502 species) as the regional source pool. For each of the islands we drew from the species pool at random without replacement the number of species known from that island and recorded their masses. In separate model runs, body masses were drawn from the Pacific-wide list of species either 1) unweighted, and 2) weighted by the number of island occurrences (Gotelli and Graves 1996, Jetz et al. 2004b). Expected null values for the size-area scaling relationship were estimated by fitting regressions to the simulated maximum and minimum body size over empirical island area. This procedure was repeated 1000 times to produce a distribution of expected slopes for the null model. Null models were run for the full pre-human avifauna, the extant avifauna, as well as for pre-human flightless and volant species. We compared empirical slopes to the distribution of null model slopes using one-tailed t-tests.

We compared the effect of area on maximum body size in birds to that of other environmental factors on each island in a generalized linear modeling framework (function `glm` in R v2.8.1; R Foundation for Statistical Computing 2008). Categorical predictors of maximum body size for each island included biogeographic region (eastern Polynesia, Hawaii, Melanesia, Marianas, New Zealand, and western Polynesia) and geological type (continental, coralline, volcanic-coral mix, and volcanic, see also Kreft et al. 2008). Continuous environmental predictors were mean annual temperature (°C), annual precipitation (mm), maximum island elevation (m), species richness, island area (km²), an estimate of island age or time since last emergence

(millions of years), distance to nearest continent (km), and isolation (UNEP Island Directory Isolation Index). All continuous predictors were log₁₀-transformed before analysis, except isolation, which was normally distributed. Predictor variables were mostly weakly correlated, but 5 out of 28 variable combinations had Pearson correlations of 0.70 or greater (Supplementary material Table S1). We ran single-predictor and multi-predictor generalized linear models (GLM) to test the influence of predictors on maximum body size (M_{\max}) in flightless and volant island birds. To control for the effect of species richness, null model predictions of body size maxima were included as a covariate in “richness-controlled” glm models. Because biogeographic region showed a strong and significant effect on M_{\max} in pairwise models, we also developed multi-predictor mixed-effects models where biogeographic region (Region LME) was treated as a random effect. Goodness of fit of each model was measured by Akaike information criterion (AIC; Burnham and Anderson 2002) where smaller AIC values indicate a better model fit.

To test for within-clade patterns of body size evolution, we explored the relationship between log₁₀ body mass and log₁₀ island area within avian genera and families in a nested linear mixed-effects model. Separate models were constructed for small- and large-bodied birds, with the cutoff point at 60 g corresponding roughly to the mode of the global body size distribution of birds (Blackburn and Gaston 1994, Maurer 1998). Scaling intercept was allowed to vary between clades as a random effect of family nested within order. This mixed effects model was compared to a cross-species, GLM model of body size over area where all data points were equally weighted.

In an additional analysis we compared the scaling of maximum size in flightless island birds to that observed in island mammals. We gathered data from the literature (sources given in Supplementary material Appendix S1) on the largest mammal species found on seven Caribbean islands, New Guinea, Madagascar, and five continental landmasses during the late-Pleistocene. We compared our results to the area-scaling relationship observed by Okie and Brown (2009) for mammals on islands of the Sunda shelf.

Results

The maximum size of birds in the pre-human avifauna of Pacific islands was geographically structured (Fig. 1). The large islands of New Zealand in particular, but also New Caledonia and the Hawaiian islands emerge as harboring particularly large-bodied species, while small, isolated islands in the Marquesas and Henderson island had much smaller species. Before human impacts, maximum body size (M_{\max}) of birds strongly increased with island area (Table 1, Fig. 2a). After severe extinctions of Pacific island birds over the past few millennia, the modern avifauna shows a much weaker but still statistically significant area-scaling of maximum size (Table 1, Fig. 2b). In the pre-human avifauna, the scaling of M_{\max} appeared somewhat nonlinear, with a steeper slope above 10² km². The structure of this increase was further enlightened when flightless and volant species were considered separately (Fig. 2c and d). Flightless species showed a much steeper scaling of M_{\max} with area

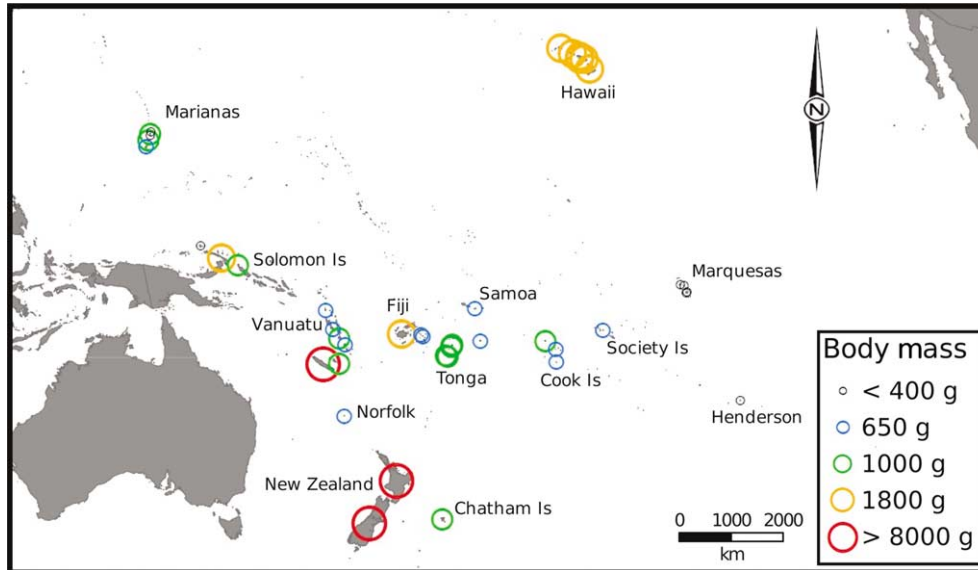


Figure 1. Map of Pacific islands showing the maximum body size of birds before human colonization on each island.

than did volant species (Table 1). Minimum body size decreased with island area, with similar slopes observed in pre-human, modern, flightless, and volant birds (Table 1, Fig. 2).

Size extremes in island birds were correlated with species richness (Supplementary material Table S2, Fig. S1), but the overall observed scaling of maximum and minimum avian body size with island area was not a simple sampling artifact of greater numbers of species on large islands (Table 1, Supplementary material Fig. S1) – regardless of whether the species pool was weighted by number of island occurrences – and was steeper than expected from such a null model (Fig. 2a). Observed size maxima were significantly lower than that predicted based on species richness for flightless species (paired t-test, $DF = 28$, $t = 4.42$, $p < 0.001$; Supplementary material Fig. S2) but not in volant species (paired t-test, $DF = 39$, $t = 1.49$, $p = 0.14$; Supplementary material Fig. S2). For flightless species, area-scaling of M_{max} was significantly steeper than expected, but the scaling of minimum size was not significantly different than that expected under random sampling (Table 1). The scaling of maximum size in extant and volant species did not differ from the null model, but for minimum size in

extant and volant species the observed slope was steeper than the null expectation (Table 1, Fig. 2b, d).

Maximum body size in flightless island birds was positively correlated with species richness, area, and elevation, and was negatively related to temperature and distance from mainland (Supplementary material Table S2). Biogeographic regions Hawaii, Melanesia, and New Zealand harbored significantly larger flightless birds, as did continental islands in comparison to other geologic types. After controlling for richness, these effects remained significant (Table 2). In volant birds, maximum body size was related to species richness, area, temperature and distance (Supplementary material Table S2). Eastern Polynesia and the Marianas had smaller volant birds than other biogeographic regions. After correcting for richness, none of these effects remained significant (Table 2). After correcting for richness using the null model, a multi-predictor model incorporating area, temperature and precipitation provided the best fit to maximum size of flightless birds, explaining 89% of variation in M_{max} (Table 3). This model remained the best fit within mixed-effects models incorporating biogeographic region. In volant birds, maximum size was best explained by area alone, but models including island

Table 1. Scaling of \log_{10} maximum and minimum body mass with \log_{10} island area in non-predatory Pacific island birds. Linear regression statistics (from Fig. 2) and null model slopes (above: species pool unweighted, below: species pool weighted by number of occurrences) are provided. No unweighted null model was run for flightless species due to very high levels of endemism. p_{null} was measured by one-tailed t-tests between empirical and null model slopes.

	Maximum body size						Minimum body size					
	Int.	Slope (SE)	p	R ²	Null slope (SE)	p_{null}	Int.	Slope (SE)	p	R ²	Null slope (SE)	p_{null}
Pre-human (n = 46)	2.17	0.44 (0.05)	***	0.61	0.24 (0.09)	*	1.25	-0.11 (0.03)	***	0.29	-0.04 (0.01)	*
					0.23 (0.10)	*					-0.03 (0.01)	*
Extant (n = 46)	2.49	0.13 (0.05)	*	0.15	0.10 (0.03)	ns	1.5	-0.16 (0.06)	**	0.19	-0.03 (0.01)	*
					0.08 (0.03)	ns					-0.03 (0.01)	*
Flightless (n = 32)	1.2	0.69 (0.09)	***	0.68	0.31 (0.14)	*	2.37	-0.09 (0.09)	ns	0.04	-0.03 (0.11)	ns
Volant (n = 46)	2.7	0.14 (0.04)	***	0.29	0.11 (0.06)	ns	1.25	-0.11 (0.03)	***	0.29	-0.04 (0.02)	*
					0.08 (0.04)	ns					-0.04 (0.02)	*

Significance of p-values: ns > 0.10, * < 0.05, ** < 0.01, *** < 0.001.

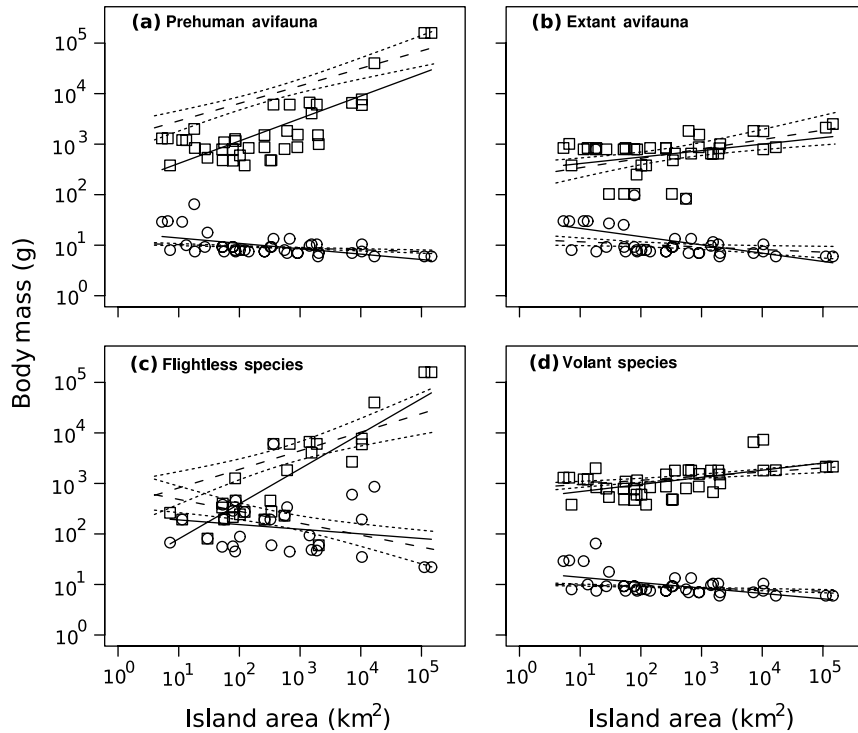


Figure 2. Scaling of body size extremes with island area for non-predatory birds on 48 Pacific islands. Solid lines show linear regression fits to the maximum (squares) and minimum (circles) body mass of (a) the pre-human avifauna, (b) extant birds, (c) flightless, and (d) volant species on each island. Null model predictions based on sampling (unweighted species pool) are shown with dashed lines (with confidence intervals given by dotted lines). Regression statistics are given in Table 1.

age, elevation, precipitation, and distance were also well-supported (Table 3).

We found considerable support for island rule type body size patterns within genera and families of Pacific island birds (Fig. 3). Several small-bodied groups showed a negative relationship between island area and body size, where large islands supported smaller species than small

islands, and for large-bodied groups the trend was the opposite. Accounting for different intercepts among clades, mixed effects models showed a trend reminiscent of the island rule: large-bodied groups decreased in size on smaller islands and small-bodied groups increased in size (Table 4). We tested the effect of biogeographic region in the within-clade analysis by including it (as a categorical fixed effect) in

Table 2. Relationships between environmental predictors and \log_{10} maximum body size (M_{\max}) in Pacific island birds, while controlling for effects of species richness (see Supplementary material Table S2 for regressions on raw data). Regression statistics are given for each predictor; smaller AIC values indicate better fit. Sample sizes: flightless $n=32$ and volant $n=46$. In the two categorical variables Geology and Region, each level was related to the baseline category (Continental and E. Polynesia, respectively). All continuous predictors, except isolation, were \log_{10} -transformed before analysis.

Predictor	Category	Flightless M_{\max}				Volant M_{\max}			
		Int.	Slope (SE)	p	AIC	Int.	Slope (SE)	p	AIC
Island area		-0.61	0.43 (0.10)	***	37.55	0.08	0.07 (0.04)	ns	0.2
Island age		-1.23	0.16 (0.17)	ns	52.56	-0.70	0.01 (0.07)	ns	2.88
Island elevation		-1.59	0.46 (0.21)	*	48.51	-0.73	0.01 (0.06)	ns	5.05
Precipitation		2.35	-1.15 (0.83)	ns	51.43	-0.92	0.06 (0.32)	ns	2.87
Temperature		4.16	-2.98 (1.21)	*	38.52	0.95	-0.52 (0.45)	ns	3.15
Distance		2.33	-0.96 (0.44)	*	48.56	-0.24	-0.07 (0.22)	ns	2.79
Isolation		-1.33	0.00 (0.004)	ns	53.5	-1.09	0.00 (0.001)	ns	2.48
Geology	Continental	1.92	-	-	45.6	-0.44	-	-	4.72
	Coralline	-	-1.69 (0.49)	**	-	-	-0.11 (0.17)	ns	-
	Volc. and coral	-	-1.54 (0.49)	**	-	-	-0.16 (0.17)	ns	-
	Volcanic	-	-1.13 (0.38)	**	-	-	-0.04 (0.15)	ns	-
Region	E. Polynesia	-0.39	-	-	38.51	1.19	-	-	2.44
	Hawaii	-	1.06 (0.24)	***	-	-	0.23 (0.15)	ns	-
	Melanesia	-	0.72 (0.26)	*	-	-	0.22 (0.20)	ns	-
	Marianas	-	0.27 (0.24)	ns	-	-	-0.14 (0.13)	ns	-
	New Zealand	-	1.58 (0.43)	**	-	-	0.32 (0.23)	ns	-
	W. Polynesia	-	0.56 (0.25)	*	-	-	0.19 (0.14)	ns	-

Significance of p-values: ns > 0.10, * < 0.05, ** < 0.01, *** < 0.001.

Table 3. Multi-predictor models of \log_{10} maximum body size (M_{\max}) in the pre-human avifaunas of Pacific islands. AIC values are given for both general linear models (GLM) and linear mixed-effect models incorporating random effects of biogeographic region (Region LME); R^2 values are given for GLM models. The combined model includes: Area + Age + Elev. + Dist. + Precip. + Temp. + Geology. All models control for the effects of species richness by including the species richness null model (unweighted species pool) as a fixed effect. All continuous predictors were \log_{10} -transformed before analysis. Models with AIC values within 2 AIC of the lowest for each model type are shown in bold.

Model	Flightless M_{\max}			Volant M_{\max}		
	GLM		Region LME	GLM		Region LME
	AIC	R^2		AIC	R^2	
Intercept	51.50	–	51.19	0.91	–	8.54
Area	37.55	0.80	46.05	0.20	0.41	11.16
Area + Age	39.46	0.80	49.53	2.15	0.41	15.47
Area + Elev.	39.54	0.80	49.21	1.10	0.46	15.80
Area + Age + Elev.	41.46	0.80	52.62	2.71	0.47	20.70
Area + Precip.	34.13	0.84	41.15	2.04	0.41	13.13
Area + Temp.	33.58	0.82	41.41	2.65	0.35	10.78
Area + Temp. + Precip.	22.80	0.89	31.85	4.52	0.35	12.91
Area + Dist.	39.44	0.80	47.27	2.15	0.41	13.12
Area + Geology	38.85	0.83	45.34	3.82	0.45	23.18
Combined	28.60	0.92	40.87	7.20	0.54	30.83

the nested taxonomic model. The addition of region to the model improved fit for both large-bodied (Area: AIC 541 vs Area + Region: AIC 494) and small-bodied species (Area: AIC –281 vs Area + Region: AIC –294). We conclude that region has a significant effect on the within-clade scaling of body size with island area. However, within-clade evolution did not appear sufficient to account for the scaling of M_{\max} with area in the prehuman avifauna, as the slope within clades of large-bodied species was more shallow than the slope in the cross-species model (Table 4). The upper boundary on body size appeared to increase with the accumulation of additional clades and singleton taxa on larger islands (Fig. 3c, d).

In mammals, maximum body size exhibits a strong scaling with landmass area on Caribbean islands and continental landmasses (linear regression, $n = 14$, slope = 0.66, SE = 0.05, $p < 0.001$; Fig. 4), and the slope is statistically indistinguishable from the observed scaling in Pacific island flightless birds (slope = 0.69; t-test, DF = 39, $p = 0.36$). The area-scaling of M_{\max} in flightless birds is also consistent with the size-area scaling exponents of 0.56 and 0.62 observed for the largest and second largest mammal species on islands of the Sunda shelf (t-tests, DF = 39 and 39, $p = 0.17$ and 0.29; Okie and Brown 2009), and the size-area scaling exponent of 0.52 observed for top endothermic herbivores of landmasses around the world (t-test, $p = 0.11$; Burness et al. 2001).

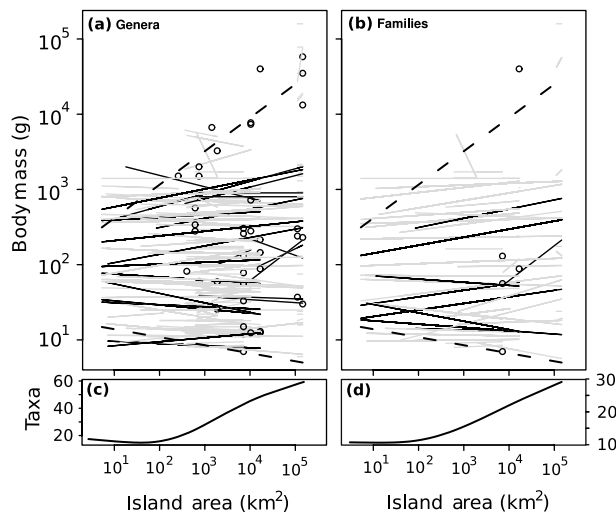


Figure 3. Scaling of body size with island area within (a) genera and (b) families of Pacific island birds. Regression lines for significant ($p < 0.10$; black lines) and non-significant (gray lines) are shown without species data points for purposes of clarity. Singleton genera and families are shown with open circles. Heavy dashed lines indicate the overall area-size scaling for maximum and minimum size in the pre-human avifauna (from Fig. 2a). Number of (c) genera and (d) families on each island increases with area (cubic spline fits).

Discussion

The body size of Pacific island birds before human arrival was strongly structured by island area and geography. We found a strong increase in body size maxima and a decrease in size minima with increasing island area in Pacific island birds (Fig. 2) and the striking similarity of this relationship to that in mammals suggests a common mechanism. Interspecific patterns reminiscent of the island rule (intra-specific in its original form) were present in Pacific island bird clades (Fig. 3), and these patterns matched the overall area-scaling of minimum size, but within-clade patterns were not sufficient to account for the steep area-scaling of maximum size. Area-scaling of maximum body size on Pacific islands was driven by the pattern within flightless species, as 12 of 46 largest species were flightless and these flightless species were found on larger islands. Although area was the best single predictor of maximum size in flightless birds, Region also had a strong effect (Table 2), reflecting the complex biogeographic histories of Pacific islands.

Area-scaling of maximum size in flightless birds is not a sampling artifact, where large islands would be expected to support larger-bodied species as a result of greater species richness. On the contrary, flightless birds have a very high degree of endemism, having primarily evolved their body

Table 4. Results of cross-species and nested mixed-effects models on the scaling of body size with island area in pre-human Pacific island birds. Sample sizes (n), slopes, standard error of slopes (SE), and p -values are given for each model. In the nested taxonomic model, scaling intercept was allowed to vary between clades as a random effect of Family nested within Order. Cutoff between large- and small-bodied species was 60 g. Significance of p -values: ns > 0.10, * < 0.05, ** < 0.01, *** < 0.001.

	Cross-species model			Nested taxonomic model		
	Slope	SE	p	Slope	SE	p
All species ($n = 1197$)	0.015	0.017	ns	0.003	0.004	ns
Large-bodied species ($n = 668$)	0.104	0.016	***	0.033	0.011	**
Small-bodied species ($n = 529$)	-0.010	0.010	ns	-0.031	0.007	***

size in situ on each island, and thus their body size is tightly linked to local conditions. Under these circumstances, one might expect a strong signal of island age on the maximum size of flightless birds. However, age did not account for much variation in size, neither in single-predictor models (Table 2) nor in multi-predictor models incorporating effects of area and biogeographic region (Table 3). Perhaps this should not be surprising given that loss of flight (Slikas et al. 2002) and dramatic changes in body size (Lister 1989, Keogh et al. 2005) are thought to occur very rapidly on islands. We found little effect of distance or island isolation on maximum size in flightless birds. It seems clear that flightless birds have very low dispersal capabilities. While the phylogenetic affinities of many flightless island birds are subjects of debate (Worthy 2001, Worthy and Holdaway 2002), it is thought that many flightless rails may have originated from multiple colonizations of one or a few widespread, volant rails (Slikas et al. 2002, Kirchman and Steadman 2006). In this case, there is little reason to expect a strong influence of isolation on size in flightless birds.

Islands are often likened to replicated “natural experiments” where evolutionary processes can be studied (MacArthur and Wilson 1967, Carlquist 1974, Williamson 1981, Whittaker and Fernández-Palacios 2007). Repeated on islands around the world, evolution of large body size in flightless birds is one such natural experiment. The scaling of M_{max} with island area in Pacific island flightless birds parallels that observed for island mammals, with empirical scaling exponents in the range 0.52–0.69. Might these exponents simply reflect a common effect of resource limitation in the evolution of island communities? Following allometric theory and empirical support from mammals,

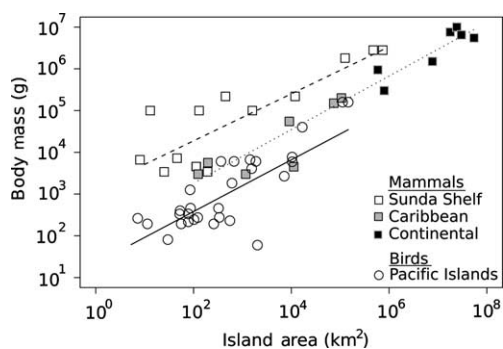


Figure 4. Scaling of maximum body size with island area in birds (circles) and mammals (squares). Area scaling of maximum body size in flightless Pacific island birds (solid line), Sunda shelf mammals (dashed line; data from Okie and Brown 2009), and Caribbean and continental mammals (dotted line).

the body-mass scaling of area A required to support an individual I of mass M can be approximated as $A/I \propto M^b$ (Jetz et al. 2004a), where the exponent b represents the body mass scaling exponent or field of basal metabolic rate B , $B \propto M^b$. In mammals b varies around 0.75 (Savage et al. 2004, Anderson and Jetz 2005) although the exponent may be lower in some clades (White et al. 2009). In birds b is usually slightly smaller (Savage et al. 2004, Jetz et al. 2008) and the body mass dependence of area needs is weaker (Brown and Maurer 1987). Assuming that minimum viable number of individuals, I_{min} (minimum viable population size; Traill et al. 2007) as well as the proportion of habitable island area are invariant with regard to body size, then the area (i.e. the “minimum dynamic area”, sensu Pickett and Thompson 1978) necessary to accommodate the total minimum viable population size, I_{min} should be approximated by $A \propto I_{min} M^b$. Conversely, the maximum size M_{max} supported on an island of area A would scale as $M_{max} \propto A^{1/b}$. For both mammals and birds we might thus expect a maximum body size-island area scaling exponent, $1/b$, in the range of 1.25–1.50.

The empirical values for area-scaling exponents we found are significantly lower than these predictions. There are several non-mutually exclusive explanations for this discrepancy (outlined in Okie and Brown 2009), including: 1) the proportion of each island that is occupied by a species is itself a function of body mass or island area (as may be expected from potential body mass-occupancy and scale-proportional occupancy relationships, Hartley et al. 2004, Hurlbert and White 2007), or 2) minimum viable population size (I_{min}) increases with body size (as suggested by Brook et al. 2006), or 3) individual area requirements scale much more steeply than $3/4$ (Okie and Brown 2009). While previous studies of size-area scaling in island mammals have been based on extinction-structured “relaxation” faunas (Marquet and Taper 1998, Okie and Brown 2009), the flightless Pacific island avifauna is derived from different historical biogeographic processes. While observed maximum size in flightless birds could be interpreted as an equilibrium at the largest sustainable maximum size for each island, it is unlikely that all islands supported a species at the maximum sustainable size due to biogeographic limitations and phylogenetic constraints on body plan and dietary plasticity.

Higher energy availability per unit area on highly productive (warm and wet) islands would be expected to decrease per individual area needs and thus facilitate the persistence of larger species. We found that, in addition to area, temperature and precipitation formed the best model of maximum size in flightless birds (Table 3). This

relationship appears to result from the interaction of temperature with precipitation. In richness-controlled, multi-predictor models including both temperature and precipitation (Table 3) the effect of temperature was positive. However, we found no significant pairwise effect of precipitation on M_{\max} in flightless or volant species. The average annual temperature on islands in our dataset ranges from 8.4 to 26.9°C and precipitation ranges from 71.5 to 417.7 cm yr⁻¹. We note that temperature and precipitation are only proxies for productivity, and that our dataset may not span enough variation in these variables for a significant signal. Future investigations will benefit from a careful assessment of the interaction between habitable area, occupancy, and estimates of island-wide net productivity which were not available for this study. The additional evaluation of higher trophic levels will also be critical, as energy and thus space needs can vary manifold between primary and tertiary consumers of the same body size (Damuth 1981, Jetz et al. 2004a, Nagy 2005).

The minimum size of volant birds on Pacific islands decreases with island area with an exponent steeper than predicted based on sampling alone (Table 1). There is little variation in minimum size across the range of island areas, with the majority (75%) of islands having a species in the range of 6–10 g. There could be problems in determining the smallest bird on each island because of incomplete sampling of small and inconspicuous birds both in modern surveys and the fossil record. However, the negative relationship between island area and body size within clades of small-bodied birds (Table 4) suggests that size in small-bodied birds does respond to island conditions. Similar patterns have been observed in small-bodied landbirds of New Zealand (Cassey and Blackburn 2004), islands off the coast of Australia (Scott et al. 2003), and in a sample of global islands (Clegg and Owens 2002) where size changes were thought to reflect release from interspecific competition on islands. Body size changes in large-bodied and small-bodied forms may be driven by different ecological factors (Heaney 1978, Clegg and Owens 2002, Cassey and Blackburn 2004). A reconciliation of the area-scaling of size extremes with the island rule will involve integrating information from both small- and large-bodied forms.

Extinction has substantially altered the biogeography of body size in island birds. The scaling of maximum size has become much weaker in the modern avifauna and today is only marginally different than expected under random sampling. Human colonization of islands is linked to severe extinction episodes on islands worldwide (Pimm et al. 1994, Steadman 1995, Burney 1997, Alcover et al. 1998, Biber 2002, Blackburn et al. 2004, Duncan and Blackburn 2004), and these extinctions were often strongly size-biased and removed many large-bodied and flightless bird species (Duncan et al. 2002, Roff and Roff 2003, Boyer 2008, 2010). The loss of island megafauna has potentially resulted in major changes in ecosystem function (Hansen and Galetti 2009). In New Zealand and the Hawaiian islands, two of the most well-studied island groups, coevolution of plants with now-extinct browsing birds has been documented (James and Burney 1997, Worthy and Holdaway 2002), and in Tonga extinction of large, frugivorous pigeons may have disrupted seed dispersal in several tree species (Meehan et al. 2002). Because today's Pacific island

avifauna has been through a severe extinction filter, we caution that basing biogeographic and macroecological theory on the modern island avifauna could be misleading.

In summary, we found that the increase of body mass maxima and decrease of minima with island area arise from a combination of evolutionary, ecological, and historical biogeographic processes. Area-scaling of maximum size in flightless island birds was not an artifact of the species–area relationship and sampling effects, and was not governed by size- or area-selective immigration or limited by island age. Within-clade, cross-species “island rule” type patterns were present, but only accounted for part of the variation. Instead, our results suggest that the effect of island area on maximum body size may reflect body size mediated constraints of energy availability on population survival. Further exploration of the energetic limitation of island populations will be necessary to elucidate the common mechanism linking body size and landmass area in both the island rule and the scaling of island body size extremes.

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