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ORIGINAL RESEARCH

Assessing the relative influence of island climatic and geographical factors on body size in an endangered iguana species of the French Caribbean

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Abstract

Body size is an important organismal trait on which many physiological and behavioral factors depend, and can be used to study how animals adapt to insular environments. In this regard, reptiles on islands exhibit remarkable size extremes, ranging from giants to some of the smallest vertebrate species in the world. In addition, the dependence of ectotherms on external temperature makes them particularly sensitive to climatic conditions. We tested the hypotheses that adult body size in Lesser Antillean iguanas (*Iguana delicatissima*) would increase with island area and isolation, as well as with increasing annual rainfall and ambient temperature. We used a database of 6878 individuals collected on seven islands in the French West Indies from 2009 to 2021. We measured individual size by the snout-vent length. GLMM analyses showed that iguana body size increased with island size, and that iguanas on the islands located closer to the mainland were larger compared to those on islands located the furthest from the mainland. Regarding climatic conditions, we found that annual rainfall and ambient temperature had no significant effect on iguana body size. These findings indicate that geographical conditions have a greater influence on iguana size compared to climatic conditions. The lack of influence of climatic conditions may be related to the fact that iguanas are critically endangered, meaning that their populations consist of limited numbers of individuals far from the carrying capacity of their habitat. If ecological resources are not currently a limiting factor for Lesser Antillean iguanas, then conservation efforts could successfully promote the growth of their populations.

Introduction

The evolutionary process can result in morphological divergences between island and mainland populations of a given species. In particular, island mammal populations tend to exhibit different body sizes compared to their mainland counterparts (e.g., rodents, marsupials and artiodactyls: Benítez-López et al., 2021; Brown & Maurer, 1989; Itescu et al., 2014; Leisler & Winkler, 2015; Meiri, 2007; Meiri & Dayan, 2003). Morphological traits such as size and weight are major characteristics on which various physiological and behavioral factors depend (Peters, 1983; Schmidt-Nielsen, 1984; Wikelski, 2005). Such traits are useful for tracing population adaptation to the specific environmental characteristics of islands (Harvey & Purvis, 1999). The "island rule" states that variation in body size and weight on islands is predictable and consistent across taxa, with small species evolving to large and large species evolving to small on islands relative to their mainland counterparts. (Benítez-López et al., 2021; Kohler et al., 2008; Lomolino, 2005). It has been shown that the effects of the 'island rule' are widespread in reptiles, although they range remarkably widely in size, from giants to some of the smallest vertebrate species in the world (Benítez-López et al., 2021). Other descriptive rules have been proposed, such as Bergmann's rule, which predicts that the size of endotherms increases with increasing latitude, while Cope's rule suggests that animal species generally evolve toward larger body sizes (Brown & Maurer, 1989; Meiri & Dayan, 2003).

The accuracy of the aforementioned rules remains a matter of contention (Blackburn et al., 1999; Watt et al., 2010). They are often criticized for oversimplifying evolutionary processes and failing to be universally applicable to all organisms or evolutionary contexts. Bergmann's rule, for instance, is widely observed in endotherms (e.g., mammals; Ashton et al., 2000; Meiri et al., 2004). However, its applicability to ectotherms is less consistent. While a study has found evidence for Bergmann's rule in *Liolaemus* lizards (Cruz et al., 2005), others report conflicting results in other lizards (sceloporines and squamates: Angilletta et al., 2004; Ashton & Feldman, 2003). Similarly, Cope's rule has been substantiated in vertebrates such as mammals, albeit with numerous exceptions (Alroy, 1998; McShea, 2000). Presently, the extent to which these rules are accurate in reptiles is currently known only for some lizard species, and no information is available for iguanas.

In view of the uncertainty surrounding the validity of these rules, it appears necessary to evaluate the underlying mechanisms driving variations in body size. Several factors contribute to these variations. The first element is the total surface area of an island (Burness et al., 2001). The number of predators decreases with the size of the island, and smaller species on smaller islands therefore tend to use their energetic resources to adapt to their environment by growing larger, whereas larger species often decrease in size (Lomolino, 2005). Large size can become a disadvantage on small islands due to increased energy and resource demands, leading to high population densities and intense intraspecific competition. This phenomenon, known as Island dwarfism, is frequently observed among vertebrates that originate from larger mainland populations (Lomolino, 2005).

A relationship between body size and island area has been found in mammals (Meiri et al., 2005, 2006), snakes (Boback, 2003) and lizards (Meiri, 2007). Heaney (1978) predicted that the body size of small mammals would decrease with an increase in surface area, whereas that of large mammals would increase. This prediction was supported by Melton (1982) and Marquet and Taper (1998). However, Meiri et al. (2005) found no support for Heaney's prediction (Heaney, 1978) and reported no linear response of body size to island area. Another factor that may affect body size is isolation, whether spatial or temporal. Spatial isolation, typically quantified as the distance between the island and the nearest mainland (Anderson & Handley, 2002; Meik et al., 2010), is known to reduce immigration rates and thus gene flow and *in situ* adaptation (Heaney, 2000). The effect of spatial isolation on body size may be indirect, reflecting factors such as predation and competition pressure (Arnold, 1979; Heaney, 1978). Anderson and Handley (2002) proposed that, in the absence of overland dispersal, body sizes on nearby and distant islands do not differ.

Another factor that may influence individual body size is the variation in environmental resources, which can differ across habitats (Case, 1976; Madsen & Shine, 1993). The variability and productivity of resources may affect body size, particularly if animals are not protected against sudden or long-term changes in productivity (Case, 1976). Furthermore, food availability poses a more significant challenge for large animals than for small ones and is considered the most important selection factor on small islands (Heaney, 1978). However, it is difficult to directly assess food availability for a given species. Indirect estimation is possible through the use of weather and climatic data (White, 2008). Increasing air temperatures and changes in precipitation patterns impact plant growth (DaMatta et al., 2010). Temperature is a major factor affecting the rate of plant development. The increase in temperatures that is expected with climate change, combined with more extreme temperature events, will impact plant productivity (Hatfield & Prueger, 2015). Furthermore, heavy precipitation influenced by climatic changes – linked to the El Niño phenomenon on groups of arid islands in the Gulf of Mexico in the 1990s – significantly increased the number of plants, leading to an immediate increase in the numbers of reptiles, mammals, and arthropods (Polis et al., 1997).

The impact of island size and isolation on the evolution of body size in reptiles has been a recurring question in the literature. Reptiles exhibit extremes in body size on islands, ranging from giant forms like giant tortoises (*Geochelone gigantea*) (Bourn & Coe, 1978) and Komodo dragons (*Varanus komodoensis*) (Purwandana et al., 2014), to the world's smallest lizards such as geckos (Hedges & Thomas, 2001; *Sphaerodactylus* spp.) and chameleons (Glaw et al., 2012; *Brookesia* spp.), as well as snakes such as thread snakes (Hedges, 2008; *Tetracheilostoma* spp.). The trend for reptile body size to either increase or decrease in animals on islands compared to those on the mainland appears to be specific to different clades (Boback & Guyer, 2003; Case, 1978; Itescu et al., 2014; Meiri, 2007, 2008). To date, studies on the evolution of body size in island reptiles have compared mainland and island species or populations (e.g., Boback & Guyer, 2003; Case, 1978; Itescu et al., 2014; Meiri, 2007), and have examined the effects of specific predictors on populations of single species (e.g., Meik et al., 2010; Soule, 1966) or genera (Dunham et al., 1978).

Ectotherms are particularly sensitive to climatic conditions because their performance hinges on body temperature, which is largely influenced by environmental temperatures (Halliday & Blouin-Demers, 2017). Body temperature significantly impacts physiological functions such as locomotion, reproduction, and growth (Adolph & Porter, 1993; Angilletta, 2009; Bestion et al., 2015; Kubisch et al., 2012), which operate optimally within specific temperature ranges (Angilletta et al., 2002). Therefore, the ability to maintain a relatively stable body temperature in a thermally variable environment directly affects survival and consequently fitness (Black et al., 2019). High temperatures can enhance the cardiovascular function and locomotor activity of iguanas during foraging, potentially improving access to both the quantity and quality of food resources. Locomotion and digestion incur energy costs and are closely linked to thermoregulation (Angilletta et al., 2002; van Marken Lichtenbelt et al., 1997). The efficiency of thermoregulation in ectotherms is strongly influenced by body size, with larger reptiles having a greater ability to regulate their temperature through greater thermal inertia, resulting in slower rates of heating and cooling (Dzialowski & O'Connor, 1999). In general, higher temperatures tend to favor larger body sizes in ectotherms because temperature facilitates more effective thermoregulation (Angilletta et al., 2002).

In this context, Lesser Antillean iguanas (*Iguana delicatissima*) are a valuable model for investigating how specific island characteristics, such as spatial isolation or environmental factors, contribute to body size variation. The diversity of the Lesser Antilles islands makes them an ideal study area. They vary significantly in size, spatial isolation, and floristic composition, and host different populations of the same iguana species. The colonization of the islands by iguanas appears to be recent, although it remains undocumented. The most plausible hypothesis posits a continental origin followed by island-to-island dispersal by sea, possibly with human assistance (Martin et al., 2015). We studied the populations of Lesser Antillean iguanas inhabiting several islands, including Anguilla, Saint-Barthélemy, Saint Eustatius, Guadeloupe, Dominica, and Martinique. Unfortunately, the species has been extirpated from many islands, such as Antigua and Barbuda, Saint Kitts and Nevis, and Saint Martin (van den Burg, Breuil, et al., 2018).

Lesser Antillean iguanas occupy a variety of environments ranging from xeric scrub and dry scrub forests to coastal and riverine forests, forest and mangroves, as well as low to mid-elevation transitional rainforests (van den Burg, Breuil, et al., 2018). These reptiles are generalist herbivores, feeding on leaves, flowers, and fruits from a wide range of shrubs and trees (van den Burg, Breuil, et al., 2018). Over the past 30 to 40 years, the population of Lesser Antillean iguanas has experienced a significant decline, leading to their classification as a critically endangered species by the IUCN (van den Burg, Breuil, et al., 2018). The ongoing threats contributing to this decline include predation, habitat loss, and fragmentation caused by agricultural and tourism development (van den Burg, Breuil, et al., 2018), and the severe impacts of droughts and hurricanes, which have hit the populations of iguanas (Breuil, 2001, 2002).

Our study aimed to assess the relative influence of climatic factors and island geography on the body size of Lesser Antillean iguanas. To investigate these influences, we analyzed a dataset of body size measures collected over 13 years by conservation managers across several islands. Specifically, we focused on populations inhabiting Saint-Barthélemy, Guadeloupe (including Basse-Terre, Petite-Terre and Désirade islands) and Martinique (including the main island and Chancel island), thus encompassing a diverse range of environments within the French islands. We tested two hypotheses regarding the body size of the Lesser Antillean iguanas in relation to island colonization and climatic variations: Firstly, there exists a positive correlation between body size and the size and degree of spatial isolation of the islands. Secondly, there exists a positive correlation between body size and annual rainfall and ambient temperature.

Materials and methods

Study sites and populations

We conducted a study on wild adult Lesser Antillean iguanas at seven sites across the French Lesser Antilles (Fig. 1, Table S1). In Martinique, individuals were sampled from populations on both the main island and Chancel island. On Saint-Barthélemy, only individuals from the main island were included. Iguanas from Basse-Terre, Désirade island, and the two islands of Petite-Terre made up the study populations for Guadeloupe.

Data collection

Data collection spanned from 2009 to 2021, involving a total of 6878 individuals (2734 males and 4144 females; Table S1). We used three databases compiled by different agencies. Data from Saint-Barthélemy were sourced from the ATE (*Agence Territoriale de l'Environnement*), while data from Martinique and Guadeloupe were provided by iguana conservation managers, specifically those from the DEAL (*Direction de l'Environnement, de l'Aménagement et du Logement*) and the ONF (*Office National des Forêts*). Data on iguanas from Chancel island, Petite-Terre, and Désirade island was obtained through CMRs (capture-mark-recapture) conducted in spring and summer as part of a national action plan. Data collection occurred over different years for each population, as detailed in Table S1. Individuals were identified individually with a PIT-tag, and only those captured once were included in the analyses. To determine the sex of iguanas, we used visual observation and identified the presence of large femoral pores in males, following the method described by Dellinger and von Hegel (1990). This non-invasive approach is preferred to hemipenial eversion and is practical for use in field conditions (Rivas et al., 1996). Individual iguanas were measured using the standard size index for iguanas and lizards, the snout-vent-length (SVL). Live body measurements were taken, with the iguanas positioned belly-down and measured using flexible fiberglass tape at 0.1 cm precision, as in a previous study (Warret Rodrigues et al., 2021). The survey methodology was standardized across all sites and maintained consistency from year to year to ensure reliable data collection. It should be noted that individuals resulting from the interbreeding of *Iguana delicatissima* and the invasive common iguana (*Iguana iguana*) were present on several of the islands. We distinguished between *Iguana delicatissima* and its hybrids based on their morphological differences. Specifically, hybrids exhibit distinctive characteristics such as a ringed tail and a large subtympanic scale, both of which are absent in *Iguana delicatissima* (Breuil, 2013).

Most studies on iguana morphology focus on body size and weight, often demonstrating strong correlations between these variables (Bakhuis, 1982; Werner, 1983; Wikelski & Trillmich, 1997). Previous research has not found significant

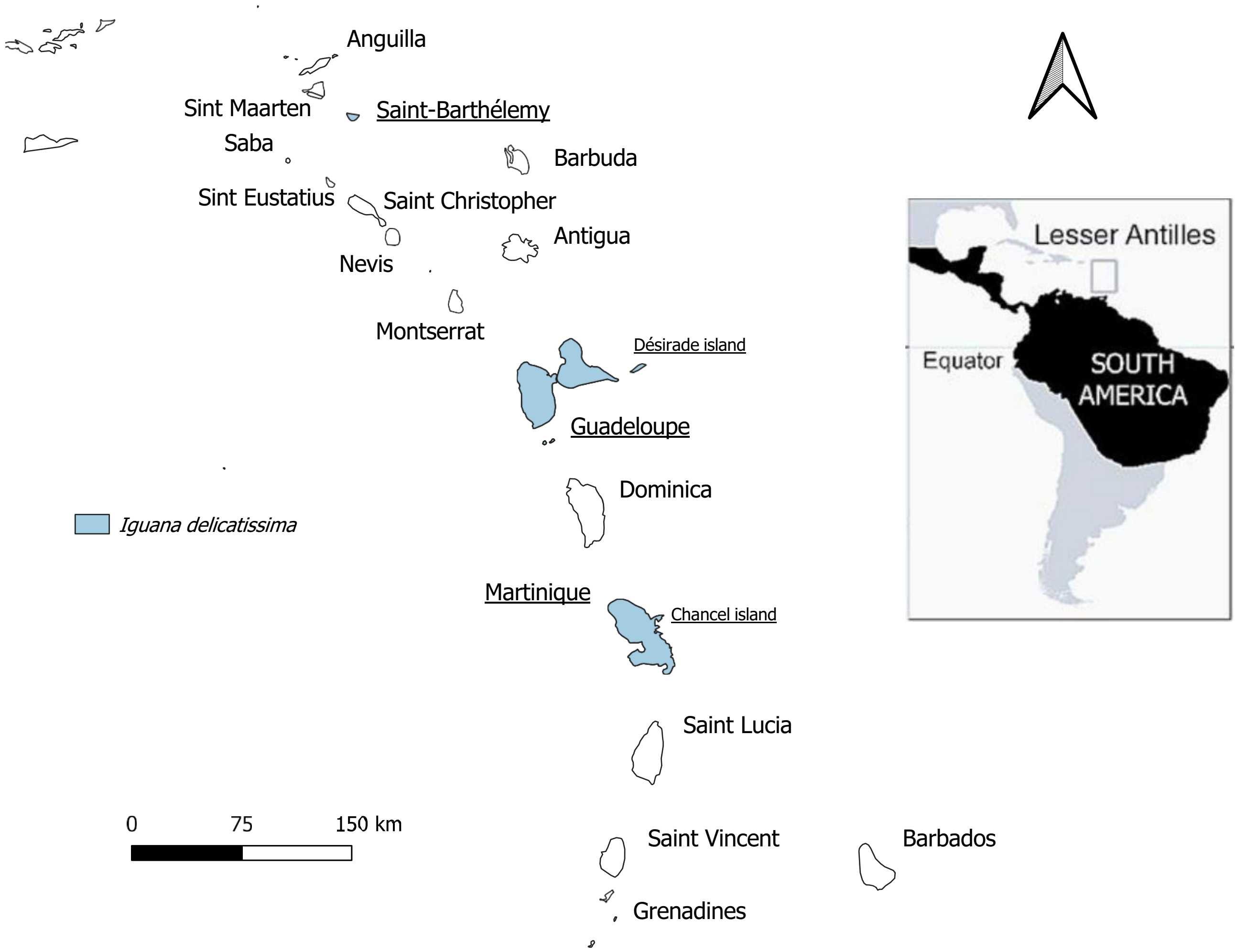

Figure 1 Localization of French island's living population of Lesser Antillean iguanas (in blue). Underlined islands represent the studied sites.

differences in the slopes of log mass against log SVL between male and female iguanas (Bakhuis, 1982; Wikelski & Trillmich, 1997). Our own data from *Iguana delicatissima* also revealed a strong correlation between body weight and size (Figs S1 and S2). Female body weight can vary considerably during the breeding season, with egg masses sometimes reaching up to 61% of the female's body weight (Stamps et al., 1998). Given the difficulty in determining the reproductive status of most females in our dataset, we opted to focus solely on SVL measures for this study and excluded weight as a variable. We considered iguanas to be adult when they reached an SVL of 24 cm, which corresponds to sexual maturity; this was the length at which the smallest female in our dataset was detected as gravid.

We obtained annual rainfall and ambient temperature data from local automatic weather stations operated by *Météo France*, located closest to the iguana capture sites. Monthly data were averaged over the years to derive representative values. For geographical measures of an island, we considered the surface area of the island and its closest distance to the mainland, as suggested by ecological studies (Itescu et al., 2018; Lomolino, 2005; Meiri et al., 2005). The distance from each island to the nearest mainland (South America) serves as an index of the islands' spatial isolation (Itescu et al., 2018). We used *Qgis* software (version 3.22.9) to calculate distances and areas. Based on the non-uniform distribution of island areas in our sample, we classified them into three size categories: small (<2 km^2), medium (between 20 and 30 km^2) and large (more than 1000 km^2) (Table 1). We were not able to investigate the influence of the shortest distance to the largest neighboring island, as recommended in some studies (Itescu et al., 2018, 2020), because the specific layout of the islands in our study region did not allow for all the necessary combinations of the islands' geographical characteristics to occur, as required for statistical analysis.

Statistical analysis

We performed a generalized linear mixed model (GLMM) using the *R* software (version 4.2.2, R Core Team, 2022) and

Table 1 Localization and characteristics of islands

Location	Latitude (N)	Longitude (O)	Distance to nearest mainland (km) (category[a])	Area (km^2) (category[b])	Ambient temperature (°C)	Rainfall (mm/year)
Basse-Terre	16°20′37″	61°45′47″	575 (2)	1628 (3)	27.2 ± 0.22	160.3 ± 14.2
Chancel	14°41′38″	60°53′20″	448 (1)	0.7 (1)	27.9 ± 0.18	90.3 ± 16.8
Désirade	16°18′45″	61°3′46″	617 (2)	21.1 (2)	27.6 ± 0.15	91.5 ± 21.9
Martinique	14°50′59″	61°12′13″	416 (1)	1128 (3)	27.3	141
Petite-Terre-de-Haut	16°10′38″	61°6′32″	603.8 (2)	0.3 (1)	27.6 ± 0.23	79.6 ± 16
Petite-Terre-de-Bas	16°10′16″	61°7′11″	603.4 (2)	1.17 (1)	27.6 ± 0.23	81.1 ± 15
Saint-Barthélemy	17°54′6″	62°50′7″	797.2 (3)	21 (2)	27.4 ± 0.29	83.4 ± 27.4

[a]1, short distance; 2, intermediate distance; 3, long distance.
[b]1, small area; 2, medium area; 3, large area.

the *glmer* function of the *lme4* package (Bates et al., 2015). The dependent variable was iguana size (SVL). Predictor variables included individual sex, annual rainfall (mm), annual ambient temperature (°C), total island area (km^2), and the shortest distance (km) to the mainland. Given that magnitude matters for the latter two variables, they were treated as ordinal variables, with each divided into three categories (Table 1). Location (island) and year of study were included as random factors in the model. We performed the GLMM analysis with a gamma distribution and a log link function, as it is suitable for modeling continuous, positive data with a constant coefficient of variation (Thiele & Markussen, 2012). We checked the absence of collinearity among the predictor variables, ensuring that the variance inflation factor was below 3 for all variables using the *check_collinearity* function of the *performance* package (Lüdecke et al., 2021). We assessed the quality of the model fit using four key diagnostic plots (Fig. S3). The quantile-quantile (QQ) plot showed that the residuals followed a normal distribution, supporting the assumption of normality in the model. Analysis of the residual plot showed no apparent bias in the residuals, indicating that the model assumptions of homoscedasticity and linearity were likely to be met. The leverage plot was used to identify any data points with a potentially large influence on the model. No observations were found to have unusually high leverage. Cook's distance plot, which measures the influence of individual observations on the regression results, showed no data points with a disproportionate influence on the model fit. Additionally, we performed post-hoc pairwise tests to compare categories, using the *emmeans* function of the *emmeans package* (Lenth et al., 2022), with a Tukey adjustment for multiple comparisons.

Results

Males were significantly larger than females across all populations studied (males: mean ± SD = 30.03 ± 3.11; females: m ± SD = 29.04 ± 2.63) (Table 2). We found no statistically significant effect of rainfall on SVL (Table 2, Fig. S4). Although there was a tendency for SVL to increase with rising ambient temperature, this relationship was not statistically significant (Table 2, Fig. S5).

Table 2 Results of the generalized linear mixed model (GLMM): factors affecting body length (SVL) of Lesser Antillean iguanas

	Estimate	SE	t	P
Intercept	3.433	0.046	75.3	<0.001
Sex male	0.037	0.002	17.9	<0.001
Rainfall	0.002	0.002	1.33	0.185
Ambient temperature	0.004	0.002	1.88	0.061
Medium island area	0.112	0.067	1.67	0.094
Large island area	0.165	0.038	4.38	<0.001
Intermediate distance to mainland	−0.169	0.042	−4.07	<0.001
Long distance to mainland	−0.076	0.085	−0.89	0.372

Island area had a significant effect on iguana size. Specifically, iguana SVL increased significantly with increasing island size (see Table 2). Post-hoc analyses revealed that iguanas on small islands were significantly smaller than those on larger islands (pairwise comparison with Tukey correction: estimate = −0.165, SE = 0.038, $P < 0.0001$; Fig. 2a). There were no significant differences in SVL between medium and small islands (pairwise comparison with Tukey correction: estimate = −0.112, SE = 0.067, $P = 0.216$), or between medium and large islands (estimate = −0.053, SE = 0.065, $P = 0.692$). The "shortest distance from the mainland" variable had a significant effect on SVL. SVL decreased significantly in iguanas from islands with a short or intermediate distance to the mainland (estimate = 0.1689, SE = 0.042, $P < 0.001$; Fig. 2b). There were no significant differences in SVL between islands with a long distance and those with an intermediate distance (estimate = −0.093, SE = 0.073, $P = 0.410$), or between islands with a long distance and those with a short distance (estimate = 0.076, SE = 0.085, $P = 0.650$).

Discussion

In line with our expectations, we found a significant influence of the geographical characteristics of the islands on the size of

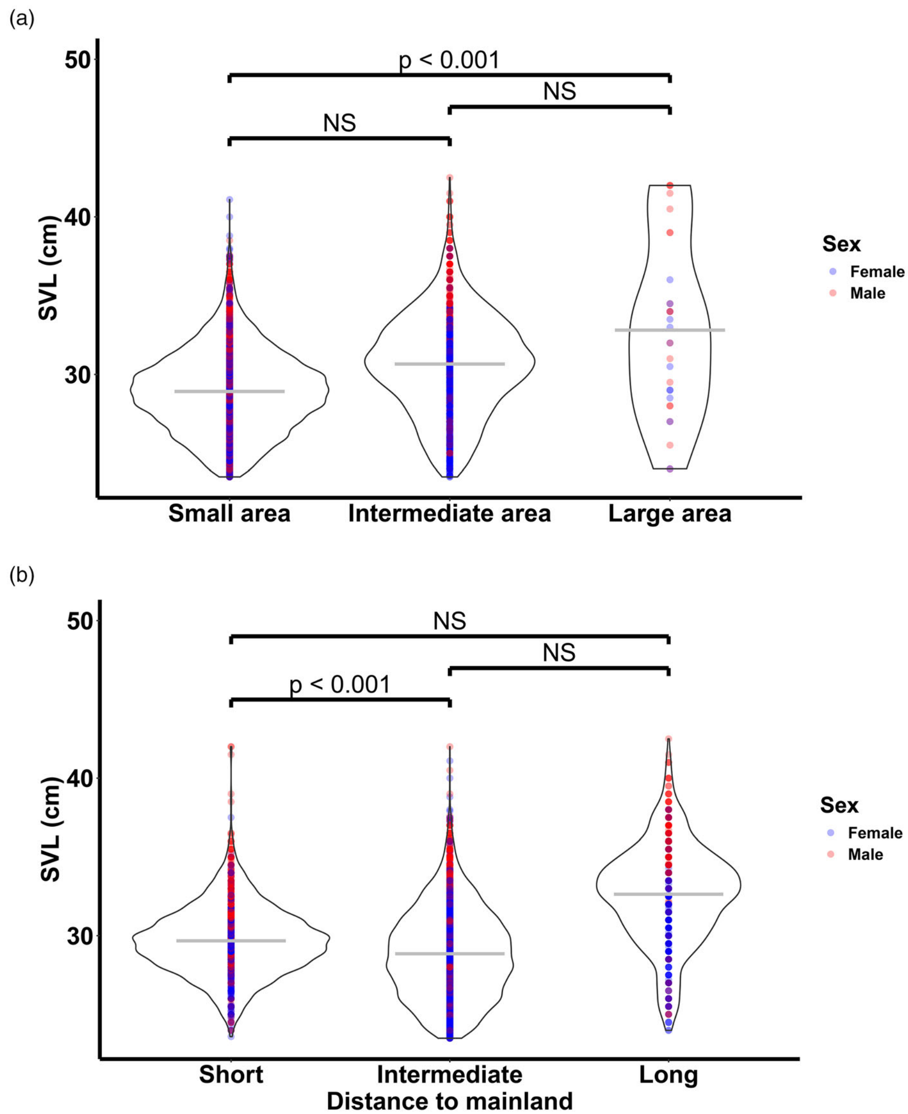

Figure 2 Violin plot showing SVL (cm) of Lesser Antillean iguana populations studied range as a function of (a) island area and (b) distance to mainland (the gray bar represents the average SVL for each island category). We provide the *P*-values from pairwise comparisons with Tukey correction (NS means non significant). Each coloured dot represents an individual.

the Lesser Antillean iguanas. Our results showed a positive correlation between island area and body size. Similar correlations have been documented across various animal species (Benítez-López et al., 2021; Clegg & Owens, 2002; Lomolino, 2005; Stadler et al., 2023), including snakes (Hasegawa & Moriguchi, 1989: *Elaphe quadrivirgata* and *Elaphe climacophora*; Meik et al., 2010, 2012; *Crotalus mitchellii*) and marine iguanas (Wikelski, 2005: *Amblyrhynchus cristatus*). Several explanations have been proposed to explain this pattern of body size relative to island size. Larger islands often resemble continents in terms of their diversity and abundance of resources such as food, water, and habitat space (Whittaker & Fernández Palacios, 2007); this abundance can support larger individuals by providing ample nutrients that are necessary for growth (Whittaker & Fernández Palacios, 2007). Additionally, larger islands may offer more diverse microhabitats for effective thermoregulation and energy efficiency, thus allowing iguanas to move between cool and warm areas as needed (Kearney, 2002). Another hypothesis posits that larger islands support larger populations, leading to increased competition among individuals for resources (MacArthur et al., 1972); larger individuals may have a competitive advantage in securing and monopolizing resources, thereby facilitating their growth (Adler & Levins, 1994).

We observed that iguanas on islands closest to the mainland were larger than those on islands at intermediate distances. This result indicates that the individuals farthest from the mainland were subject to the island syndrome for a longer period of time than the larger individuals closer to the mainland. This suggests that the potential source of island colonization by a common ancestor of the *Iguana* genus was by the nearest land, that is, the region of Venezuela. This result aligns with the understanding that the greater contrast between island and mainland habitats imposes stronger selective pressures, leading to evolutionary changes in species (Adler & Levins, 1994; Boback, 2003; Kisel & Barraclough, 2010; Pergams & Ashley, 2004). It is important to note that we did not find a significant difference in iguana body size between the islands farthest from the mainland and the other islands. However, it is crucial to acknowledge that the category including the most distant islands was represented solely by Saint-Barthélemy, limiting the robustness of this particular result at this stage. Furthermore, the results concerning islands closest to the mainland are influenced by the predominance of data from the main island of Martinique. Further research across different environments, populations, and species is needed to validate the accuracy of our conclusions.

Body size in iguanas, as in other animals, has a strong genetic component (Wikelski, 2003). It is understandable that it may vary on an evolutionary timescale depending on the geographical location of islands. If an island is highly isolated, individuals are unlikely to interbreed. This results in reduced gene flow, which favors the maintenance of different body sizes within island populations (Itescu et al., 2020). In populations with a limited number of individuals, body size differences may be influenced by small gene pools within these isolated populations. This difference will be more pronounced if the iguana populations have experienced genetic drift like founding effects or bottlenecks in their history, as suggested by Lorvelec et al. (2004). Conversely, on the less isolated and larger islands, gene flow will be greater, implying greater genetic diversity, which may translate into greater morphological variability in iguanas.

Another factor influencing body size variation relative to distance from the mainland is human-mediated transportation over historical time. The larger Antillean islands can no longer be considered as spatially isolated entities, as individuals from other populations have been regularly introduced, both intentionally and unintentionally, during the past centuries (Breuil, 2013). This human-mediated gene flow may have altered the gene pools of insular populations, impacting the body size variation established over thousands of years. Over a time span of several centuries, it appears that selection pressure, potentially reinforced by pre-Columbian hunting, could also have influenced genetic diversity and, consequently, the morphological characteristics of populations. Prior to European colonization, *I. delicatissima* populations thrived and were remarkably large, even under the pressure of extensive hunting by pre-Columbian inhabitants (Bochaton et al., 2016). Paleontological data indicate that human activities, particularly European colonization of the Caribbean, likely led to significant changes in iguana body size (Bochaton et al., 2016). It has been documented that pre-Columbian populations of Lesser Antillean iguanas on Désirade and Petite-Terre islands had mean SVLs of 35.8 cm and 33 cm, respectively, with maximum lengths of 46 and 46.2 cm (Bochaton et al., 2016). In our database, the mean SVLs of Lesser Antillean iguanas on Désirade and Petite-Terre are 29.7 ± 7.3 cm and 28.4 ± 12.7 cm, respectively, with maximum SVLs of 37 cm and 41.1 cm. This indicates that current Lesser Antillean iguanas on Désirade island and Petite-Terre islands are approximately 20% smaller in size than those from the pre-Columbian period (Bochaton et al., 2016). When considered over the timescale of several centuries, it appears that selection pressure can exert a significant influence on genetic diversity, thereby influencing the morphological characteristics of populations.

The locations and areas of islands are likely to have exerted long-lasting directional selective pressures on the iguana populations over extensive timescales. The most important finding of this study is that the geographical characteristics of islands had stronger effects on the body size of Lesser Antillean iguanas than ecological factors. Contrary to our expectations, and despite their influence on the production of ecological resources, we did not observe a significant effect of climatic variables on the body size of Lesser Antillean iguanas in recent years. On a shorter time scale of around 10 years, temperature, which plays a crucial role in thermoregulation and metabolic processes, had only a marginal effect. It is possible that it did not emerge as a major determinant of iguana size because of the limited variation in the temperature values measured during the study. There was also no evidence that annual rainfall, which affects ecological productivity and resource availability, had a significant influence on iguana body size. These findings might seem surprising when compared to broader ecological patterns where such variables often play a more prominent role (Sterner & Elser, 2002). For instance, it was described that marine iguanas (*Amblyrhynchus cristatus*) exhibit larger body sizes during periods of higher algae abundance in non-El Niño years, highlighting the direct link between climatic conditions, food availability, and iguana size (Wikelski, 2005).

A possible explanation for the limited effect of climatic variables on Lesser Antillean iguanas could be their ability to adapt their diet, consuming available plants also during dry periods. This ability to consume resources that limit iguanas body size during periods of drought (see Wikelski & Thom, 2000) is likely related to their demographic situation. Lesser Antillean iguanas' populations are classified as critically endangered, with a decline of more than 75% (van den Burg, Breuil, & Knapp, 2018), and appear to be well below the carrying capacity of their environment. This imbalance between abundant resources and low numbers of individuals would enable them to exploit a wide range of food without suffering from strong inter-individual competition. It is not expected that carrying capacity affects the body size of the iguanas in the short term, as the environment offers sufficient resources. It should be assessed taking into account several key factors that directly affect iguana survival. Measuring the population density per island would indicate the level of food competition within the population and whether or not resources are being overexploited. It would be necessary to determine the dietary preferences of iguanas, as well as the availability and quality of food resources, which are influenced by climatic conditions.

In addition, a study of interspecific competition with other herbivores present on the island would be useful to ascertain whether iguanas have to share or compete for resources with other species. Habitat characteristics need also to be considered, such as nesting sites and their numbers, hiding places for protection from predators, and sun-exposed sites. Extreme climatic events such as hurricanes and droughts can threaten the survival of populations on short time scales, so it would also be worthwhile to identify the habitat characteristics that iguanas need to withstand them. For instance, the iguana population on the Petite-Terre islands collapsed during the hurricanes of 1995 and the severe drought of 2001 (Breuil, 2002). Such events could have caused a bottleneck, leading to low genetic diversity and making the population more vulnerable.

Another ecological factor that can potentially influence the variation in body size over a period of several years is predation pressure. Predation is known to drive size increases in small species and decreases in large species, and size could be directly linked to predator– prey selection and prey anti-predator responses (Heaney, 1978). During hunting, the largest iguanas, containing more meat, should be the preferred prey, especially because these iguanas are more easily identified visually. Today, although it is now illegal, hunting was a significant problem on many islands, especially during periods when food reserves diminish, such as after hurricanes (van den Burg, Breuil, et al., 2018), leading to iguana population collapses (van den Burg, Madden, et al., 2018) and probably a drop in the number of large individuals. Predation by invasive species could be another major factor affecting iguana size because juvenile iguanas are regularly preyed upon by rats, cats, dogs, and mongooses (van den Burg, Breuil, et al., 2018; van den Burg, Madden, et al., 2018). The combination of predator richness, predation intensity, and interspecific competition related to island characteristics could also exert iguana size selection.

In addition to the need for ecological studies of Lesser Antillean iguanas, this study suggests several avenues for future research. It is necessary to confirm our present conclusions by studying the other endemic iguana species of the Lesser Antilles, as well as the invasive species. More generally, it would be beneficial to expand the study to include larger samples of populations and species in different geographical locations. This expansion should aim to test a wider range of factors, such as distance to the nearest major landmass, distance to the nearest species-rich landmass, and predation (see Itescu et al., 2020).

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Conflict of interest

The authors declare no competing interests.

Author contributions

F.D., study design, data processing; F.D., B.T., K.M., N.R.: statistics; F.D., B.T., writing; all authors contributed critically to the manuscript drafts and have approved the final version for submission.

Data availability statement

The data that support the findings of this study are available in Data S2.

References

Adler, G. H., & Levins, R. (1994). The Island syndrome in rodent populations. *Quarterly Review of Biology*, **69**, 473–490.

Adolph, S. C., & Porter, W. P. (1993). Temperature, activity, and lizard life histories. *American Naturalist*, **142**, 273–295.

Alroy, J. (1998). Cope's rule and the dynamics of body mass evolution in north American fossil mammals. *Science*, **280**, 731–734.

Anderson, R. P., & Handley, C. O. (2002). Dwarfism in insular sloths: Biogeography, selection, and evolutionary rate. *Evolution*, **56**, 1045–1058.

Angilletta, M. J. (2009). *Thermal adaptation: A theoretical and empirical synthesis*. Oxford University Press.

Angilletta, M. J., Niewiarowski, P. H., & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, **27**, 249–268.

Angilletta, M. J., Niewiarowski, P. H., Dunham, A. E., Leaché, A. D., & Porter, W. P. (2004). Bergmann's clines in ectotherms: Illustrating a life-history perspective with sceloporine lizards. *American Naturalist*, **164**, E168–E183.

Arnold, E. N. (1979). Indian Ocean giant tortoises: Their systematics and Island adaptations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **286**, 127–145.

Ashton, K. G., & Feldman, C. R. (2003). Bergmann's rule in nonavian reptiles: Turtles follow it, lizards and snakes reverse it. *Evolution*, **57**(5), 1151–1163. https://doi.org/10.1111/j.0014-3820.2003.tb00324.x

Ashton, K. G., Tracy, M. C., & Queiroz, A. D. (2000). Is Bergmann's rule valid for mammals? *American Naturalist*, **156**, 390–415.

Bakhuis, W. L. (1982). Size and sexual differentiation in the lizard *Iguana iguana* on a semi-arid Island. *Journal of Herpetology*, **16**, 322–325.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.

Benítez-López, A., Santini, L., Gallego-Zamorano, J., Milá, B., Walkden, P., Huijbregts, M. A. J., & Tobias, J. A. (2021). The Island rule explains consistent patterns of body size evolution in terrestrial vertebrates. *Nature Ecology & Evolution*, **5**, 768–786.

Bestion, E., Clobert, J., & Cote, J. (2015). Dispersal response to climate change: Scaling down to intraspecific variation. *Ecology Letters*, **18**, 1226–1233.

Black, I. R. G., Berman, J. M., Cadena, V. C., & Tattersall, G. J. (2019). Behavioral thermoregulation in lizards: Strategies for achieving preferred temperature. In V. Bels & A. Russell (Eds.), *Behavior of lizards* (pp. 13–46). CRC Press.

Blackburn, T. M., Gaston, K. J., & Loder, N. (1999). Geographic gradients in body size: A clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165–174.

Boback, S. M. (2003). Body size evolution in snakes: Evidence from Island populations. *Copeia*, **2003**, 81–94.

Boback, S. M., & Guyer, C. (2003). Empirical evidence for an optimal body size in snakes. *Evolution*, **57**, 345–451.

Bochaton, C., Bailon, S., Ineich, I., Breuil, M., Tresset, A., & Grouard, S. (2016). From a thriving past to an uncertain future: Zooarchaeological evidence of two millennia of human impact on a large emblematic lizard (*Iguana delicatissima*) on the Guadeloupe Islands (French West Indies). *Quaternary Science Reviews*, **150**, 172–183.

Bourn, D., & Coe, M. (1978). The size, structure and distribution of the giant tortoise population of Aldabra. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **282**, 139–175.

Breuil, M. (2001). Taxon reports: « *Iguana delicatissima* and *Iguana iguana* ». *Iguana Specialist Group Newsletter*, **4**, 9–11.

Breuil, M. (2002). *Histoire naturelle des amphibiens et reptiles terrestres de l'archipel guadeloupéen: Guadeloupe, Saint-Martin, Saint-Barthélemy*. Muséum National d'Histoire Naturelle.

Breuil, M. (2013). Caractérisation morphologique de l'iguane commun *Iguana iguana* (Linnaeus, 1758), de l'iguane des Petites Antilles *Iguana delicatissima* Laurenti, 1768 et de leurs hybrides. *Bulletin de la Société Herpétologique de France*, **147**, 309–346.

Brown, J. H., & Maurer, B. A. (1989). Macroecology: The division of food and space among species on continents. *Science*, **243**, 1145–1150.

Burness, G. P., Diamond, J., & Flannery, T. (2001). Dinosaurs, dragons, and dwarfs: The evolution of maximal body size. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 14518–14523.

Case, T. J. (1976). Body size differences between populations of the chuckwalla, *Sauromalus obesus*. *Ecology*, **57**, 313–323.

Case, T. J. (1978). A general explanation for insular body size trends in terrestrial vertebrates. *Ecology*, **59**, 1–18.

Clegg, S. M., & Owens, P. F. (2002). The 'Island rule' in birds: Medium body size and its ecological explanation. *Proceedings of the Royal Society of London B: Biological Sciences*, **269**, 1359–1365.

Cruz, F. B., Fitzgerald, L. A., Espinoza, R. E., & Schulte Ii, J. A. (2005). The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: Lessons from a clade of south American lizards. *Journal of Evolutionary Biology*, **18**, 1559–1574.

DaMatta, F. M., Grandis, A., Arenque, B. C., & Buckeridge, M. S. (2010). Impacts of climate changes on crop physiology and food quality. *Food Research International*, **43**, 1814–1823.

Dellinger, T., & von Hegel, G. (1990). Sex identification through cloacal probing in juvenile marine iguanas (*Amblyrhynchus cristatus*). *Journal of Herpetology*, **24**(4), 424–426. https://doi.org/10.2307/1565065

Dunham, A. E., Tinkle, D. W., & Gibbons, J. W. (1978). Body size in Island lizards: A cautionary tale. *Ecology*, **59**, 1230–1238.

Dzialowski, E. M., & O'Connor, M. P. (1999). Utility of blood flow to the appendages in physiological control of heat exchange in reptiles. *Journal of Thermal Biology*, **24**, 21–32.

Glaw, F., Köhler, J., Townsend, T. M., & Vences, M. (2012). Rivaling the world's smallest reptiles: Discovery of miniaturized and microendemic new species of leaf chameleons (*Brookesia*) from northern Madagascar. *PLoS One*, **7**, e31314.

Halliday, W. D., & Blouin-Demers, G. (2017). A test of the thermal coadaptation hypothesis with ultimate measures of fitness in flour beetles. *Journal of Thermal Biology*, **69**, 206–212.

Harvey, P. H., & Purvis, A. (1999). Understanding the ecological and evolutionary reasons for life history variation: Mammals as a case study. In J. McGlade (Ed.), *Advanced ecological theory: Principles and applications* (pp. 232–248). Blackwell Science.

Hasegawa, M., & Moriguchi, H. (1989). Geographic variation in food habits, body size and life history traits of the snakes on the Izu Islands. In M. Matsui, T. Hikida, & R. C. Goris (Eds.), *Current herpetology in East Asia* (pp. 414–432). Herpetological Society of Japan.

Hatfield, J. L., & Prueger, J. H. (2015). Temperature extremes: Effect on plant growth and development. *Weather and Climate Extremes*, **10**, 4–10.

Heaney, L. R. (1978). Island area and body size of insular mammals: Evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution*, **32**(1), 29–44. https://doi.org/10.1111/j.1558-5646.1978.tb01096.x

Heaney, L. R. (2000). Dynamic disequilibrium: A long-term, large-scale perspective on the equilibrium model of Island biogeography. *Global Ecology and Biogeography*, **9**, 59–74.

Hedges, S. B. (2008). At the lower size limit in snakes: Two new species of threadsnakes (*Squamata*: *Leptotyphlopidae*: *Leptotyphlops*) from the Lesser Antilles. *Zootaxa*, **1841**, 1–30.

Hedges, S. B., & Thomas, R. S. (2001). At the lower size limit in amniote vertebrates: A new diminutive lizard from the West Indies. *Caribbean Journal of Science*, **37**, 168–173.

Itescu, Y., Foufopoulos, J., Pafilis, P., & Meiri, S. (2020). The diverse nature of Island isolation and its effect on land bridge insular faunas. *Global Ecology and Biogeography*, **29**, 262–280.

Itescu, Y., Karraker, N. E., Raia, P., Pritchard, P. C. H., & Meiri, S. (2014). Is the Island rule general? Turtles disagree. *Global Ecology and Biogeography*, **23**, 689–700.

Itescu, Y., Schwarz, R., Donihue, C. M., Slavenko, A., Roussos, S. A., Sagonas, K., Valakos, E. D., Foufopoulos, J., Pafilis, P., & Meiri, S. (2018). Inconsistent patterns of body size evolution in co-occurring Island reptiles. *Global Ecology and Biogeography*, **27**, 538–550.

Kearney, M. (2002). Hot rocks and much-too-hot rocks: Seasonal patterns of retreat-site selection by a nocturnal ectotherm. *Journal of Thermal Biology*, **27**, 205–218.

Kisel, Y., & Barraclough, T. G. (2010). Speciation has a spatial scale that depends on levels of gene flow. *American Naturalist*, **175**, 316–334.

Kohler, M., Moyasola, S., & Wrangham, R. (2008). Island rules cannot be broken. *Trends in Ecology & Evolution*, **23**, 6–7.

Kubisch, E., Piantoni, C., Williams, J., Scolaro, A., Navas, C. A., & Ibargüengoytía, N. R. (2012). Do higher temperatures increase growth in the nocturnal gecko Homonota darwini (Gekkota: Phyllodactylidae)? A skeletochronological assessment analyzed at temporal and geographic scales. *Journal of Herpetology*, **46**, 587–595.

Leisler, B., & Winkler, H. (2015). Evolution of Island warblers: Beyond bills and masses. *Journal of Avian Biology*, **46**, 236–244.

Lenth, R. V., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., & Singmann, H. (2022). *Emmeans: Estimated marginal means, aka least-squares means*. (Version 1.7.3) [Computer software]. https://CRAN.R-project.org/package=emmeans

Lomolino, M. V. (2005). Body size evolution in insular vertebrates: Generality of the Island rule. *Journal of Biogeography*, **32**, 1683–1699.

Lorvelec, O., Levesque, A., Barre, N., Feldmann, P., & Leblond, G. (2004). Évolution de la densité de population de l'iguane des Petites Antilles (*Iguana delicatissima*) dans la réserve naturelle des îles de la Petite Terre (Guadeloupe) entre 1995 et 2002. *Revue d'Écologie*, **59**, 331–344.

Lüdecke, D., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *The Journal of Open Source Software*, **6**, 3139.

MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in Island faunas. *Ecology*, **53**, 330–342.

Madsen, T., & Shine, R. (1993). Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution*, **47**, 321–325.

Marquet, P. A., & Taper, M. L. (1998). On size and area: Patterns of mammalian body size extremes across landmasses. *Evolutionary Ecology*, **12**, 127–139.

Martin, J. L., Knapp, C. R., Gerber, G. P., Thorpe, R. S., & Welch, M. E. (2015). Phylogeography of the endangered lesser Antillean iguana, *Iguana delicatissima*: A recent diaspora in an archipelago known for ancient herpetological endemism. *Journal of Heredity*, **106**, 315–321.

McShea, D. W. (2000). Trends, tools, and terminology. *Paleobiology*, **26**, 330–333.

Meik, J. M., Lawing, A. M., & Pires-daSilva, A. (2010). Body size evolution in insular speckled rattlesnakes (*Viperidae*: *Crotalus mitchellii*). *PLoS One*, **5**, e9524.

Meik, J. M., Schaack, S., Ingrasci, M. J., Lawing, A. M., Setser, K., Mociño-Deloya, E., & Flores-Villela, O. (2012). Notes on activity, body size variation, and diet in insular speckled rattlesnakes from the western sea of Cortés, Mexico. *Herpetological Review*, **43**, 556–560.

Meiri, S. (2007). Size evolution in Island lizards. *Global Ecology and Biogeography*, **16**, 702–708.

Meiri, S. (2008). Evolution and ecology of lizard body sizes. *Global Ecology and Biogeography*, **17**, 724–734.

Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, **30**, 331–351.

Meiri, S., Dayan, T., & Simberloff, D. (2004). Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society*, **81**, 579–588.

Meiri, S., Dayan, T., & Simberloff, D. (2005). Area, isolation and body size evolution in insular carnivores. *Ecology Letters*, **8**, 1211–1217.

Meiri, S., Dayan, T., & Simberloff, D. (2006). The generality of the Island rule reexamined. *Journal of Biogeography*, **33**, 1571–1577.

Melton, R. H. (1982). Body size and Island *Peromyscus*: A pattern and a hypothesis. *Evolutionary Theory*, **6**, 113–126.

Pergams, O. R., & Ashley, M. V. (2004). Microevolution in Island rodents. *Genetica*, **112–113**, 245–256.

Peters, R. H. (1983). *The ecological implications of body size*. Cambridge University Press.

Polis, G. A., Hurd, S. D., Jackson, C. T., & Pinero, F. S. (1997). El Nino effects on the dynamics and control of an Island ecosystem in the gulf of California. *Ecology*, **78**, 1884–1897.

Purwandana, D., Ariefiandy, A., Imansyah, M. J., Rudiharto, H., Seno, A., Ciofi, C., & Jessop, T. S. (2014). Demographic status of Komodo dragons populations in Komodo National Park. *Biological Conservation*, **171**, 29–35.

R Core Team. (2022). *R: A language and environment for statistical computing*. Version 4.2.2. R Foundation for Statistical Computing. https://www.R-project.org/

Rivas, J. A., Ávila, T. M., Rivas, J. A., & Avila, T. M. (1996). Sex identification in juvenile green iguanas (*Iguana iguana*) by cloacal analysis. *Copeia*, **1996**, 219–221.

Schmidt-Nielsen, K. (1984). *Scaling: Why is animals size so important?* Cambridge University Press.

Soule, M. (1966). Trends in the insular radiation of a lizard. *American Naturalist*, **100**, 47–64.

Stadler, S. R., Brock, K. M., Bednekoff, P. A., & Foufopoulos, J. (2023). More and bigger lizards reside on islands with more resources. *Journal of Zoology*, **319**, 163–174.

Stamps, J. A., Mangel, M., & Phillips, J. A. (1998). A new look at relationships between size at maturity and asymptotic size. *American Naturalist*, **152**, 470–479.

Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press.

Thiele, J., & Markussen, B. (2012). Potential of GLMM in modelling invasive spread. *CAB Reviews*, **7**, 1–10.

van den Burg, M., Breuil, M., & Knapp, C. (2018a). *Iguana delicatissima*. IUCN Red List of Threatened Species 2018, e.T10800A122936983.

van den Burg, M., Madden, P. H., van Wagensveld, T. P., & Buma, C. (2018b). Anthropogenic mortality in a population of the critically endangered lesser Antillean iguana (*Iguana delicatissima*). *IRCF Reptiles & Amphibians*, **25**, 120–124.

van Marken Lichtenbelt, W. D., Vogel, J. T., & Wesselingh, R. A. (1997). Energetic consequences of field body temperatures in the green iguana. *Ecology*, **78**, 297–307.

Warret Rodrigues, C., Angin, B., & Besnard, A. (2021). Favoring recruitment as a conservation strategy to improve the resilience of long-lived reptile populations: Insights from a population viability analysis. *Ecology and Evolution*, **11**, 13068–13080.

Watt, C., Mitchell, S., & Salewski, V. (2010). Bergmann's rule; a concept cluster? *Oikos*, **119**, 89–100.

Werner, D. I. (1983). Reproduction in the iguana *Conolophus subcristatus* on Fernandina Island, Galapagos: Clutch size and migration costs. *American Naturalist*, **121**, 757–775.

White, T. C. R. (2008). The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews*, **83**, 227–248.

Whittaker, R. J., & Fernández Palacios, J. M. (2007). *Island biogeography: Ecology, evolution, and conservation* (2nd ed.). Oxford University Press.

Wikelski, M. (2003). Body size, performance and fitness in Galapagos marine iguanas. *Integrative and Comparative Biology*, **43**, 376–386.

Wikelski, M. (2005). Evolution of body size in Galapagos marine iguanas. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **272**, 1985–1993.

Wikelski, M., & Thom, C. (2000). Marine iguanas shrink to survive El Niño. *Nature*, **403**, 37–38. https://doi.org/10.1038/47396

Wikelski, M., & Trillmich, F. (1997). Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: An Island comparison. *Evolution*, **51**, 922–936.

Supporting Information

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

Table S1 Year, number of individuals and their average size surveyed by island.

Figure S1 SVL (cm) as a function of log weight (g) for male (n = 2734) in all islands studied. The blue line corresponds to the correlation coefficient $r = 0.87$, $P < 0.001$.

Figure S2 Log SVL (cm) as a function of log weight (g) for female (n = 4144) in all islands studied. The blue line corresponds to the correlation coefficient $r = 0.81$, $P < 0.001$.

Figure S3 Assessment of the quality of the model fit evaluated using four key diagnostic plots (a) QQ-plot (b) Residual Graph (c) Leverage Graph (d) Cook's Distance Plot.

Figure S4 Influence of rainfall (mm) on the body size of iguanas (SVL) over all the years and islands monitored.

Figure S5 Influence of temperature (°C) on the body size of iguanas (SVL) over all the years and islands monitored.

Data S2.