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Research article

When Rensch meets Foster: insular gigantism may reduce sexual dimorphism in anurans

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According to the Island rule, insular populations exhibit gigantism in small species and dwarfism in large species. These contexts offer opportunities to test for complementary aspects pertaining to the evolution of body size, and particularly sexual dimorphism (SSD). 'Rensch's rule' states that SSD should vary with increasing body size, depending on the larger sex. As a consequence, it is expected that dwarfism or gigantism occurring in insular populations should influence the magnitude of SSD. Using anuran amphibians as a study system (because most anuran species express a female-biased SSD and a marked lability in size), we investigated our hypothesis both in a specific comparison of continental and insular populations of a widespread coastal amphibian, and using a large-scale analysis across anurans (10 species across 62 sites). Both datasets yielded similar results, with increasing body size in insular populations reducing the magnitude of SSD through an increase of male body size, as expected by Rensch's rule. Detailed data on insular populations considering both sexes are scarce, and future studies are required to complement the existing literature in order to test for the validity of our hypothesis at a wider scale and to infer the mechanistic causes of size variations, which remain unknown. In addition, further investigations are required to explore the consequences of insularity on the magnitude of SSD including various taxa (e.g. mammals, birds, lizards and snakes) in which the Island rule has found support, and considering taxa in which males are the larger sex.

Keywords: amphibians, body size, insularity, Island rule, Rensch's rule, sexual dimorphism

Introduction

Islands constitute particular, isolated ecosystems characterized by lower species richness and different interaction networks than continental ecosystems (Traveset et al. 2016). Populations isolated on islands may often function as a closed system with limited gene



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flows (Everson et al. 2020), especially in larger species. As a consequence, insular populations usually differ from their continental counterparts for several key traits such as genetic richness and structure (Nieberding et al. 2006, Aubret and Shine 2009, Jensen et al. 2013, Diniz-Filho et al. 2021), physiology (Müller et al. 2007, Salazar et al. 2019), ecology (Blondel 1985, Pafilis et al. 2009), reproductive traits (Adler and Levins 1994, Russell et al. 2011), morphological characteristics (Adler and Levins 1994, Diniz-Filho and Raia 2017, Diniz-Filho et al. 2019, Avramo et al. 2021, Borzée and Min 2021) and behaviour (Adler and Levins 1994, Brodin et al. 2013). These patterns can be expressed over relatively short time scales (Diniz-Filho et al. 2019), and these differences between insular and continental populations have been generalized as the 'Island syndrome' (Adler and Levins 1994).

Morphological variations between insular and continental populations have attracted considerable interest and, in vertebrates, have led to the formalization of the 'Island rule' (also known as 'Foster's rule', Van Valen 1973). According to this rule, insular populations exhibit gigantism in small species and dwarfism in large species, because of specific insular conditions and because body size tends to converge to an optimal size according to these environmental conditions (Lomolino 2005). Insular conditions include, but are not limited to, change in predation pressure (Palkovacs 2003), competition (Li et al. 2011, Rebouças et al. 2018) or resource availability (Lomolino 2005). Although these trends have been validated in several vertebrate taxa (i.e. mammals: Lomolino 1985, birds: Clegg and Owens 2002, lizards: Pafilis et al. 2009, Novosolov et al. 2013, Siliceo-Cantero et al. 2020, Avramo et al. 2021, snakes: Keogh et al. 2005, Aubret 2012, amphibians: Borzée and Min 2021) and even in plants (Biddick et al. 2019), the Island rule has found support in some, but not all clades (Meiri et al. 2008, Lokatis and Jeschke 2018). Nonetheless, a recent meta-analysis suggested that the Island rule may be common across vertebrates despite the influence of multiple factors on body size evolution (Benítez-López et al. 2021). Indeed, body size evolution on islands can also depend on a variety of parameters such as island area, distance to the continent, island topography and habitat structure (Traveset et al. 2016), predation pressure and resource availability (Palkovacs 2003).

Insular settings offer unique opportunities to test for complementary aspects pertaining to the evolution of body size (Filin and Ziv 2004, Anaya-Meraz and Escobedo-Galván 2020), because their isolation and particular environmental conditions promote rapid evolution (Millien 2006), allowing investigation of micro-evolutionary processes of body size evolution (Anderson and Handley 2002, Renaud and Auffray 2010, Aubret 2015). This seems particularly relevant for the 'Rensch's rule' (Rensch 1950). This rule states that sexual size dimorphism (SSD) increases with increasing body size when males are the larger sex, and decreases with increasing body size when females are the larger sex (Rensch 1950, Fairbairn 1997, Dale et al. 2007), presumably because sexual selection acting on male size drives the evolution of this pattern (Abouheif and Fairbairn 1997). As a consequence, it

is expected that dwarfism or gigantism occurring in insular populations should, in turn, influence the magnitude of SSD depending on the larger sex. That is, in species characterized by male-biased SSD, the magnitude of SSD should decrease when insular populations are characterized by dwarfism and increase when insular populations are characterized by gigantism. Conversely, the magnitude of SSD in species with female-biased SSD should increase in insular populations characterized by dwarfism, and decrease in insular populations characterized by gigantism. In turn, sexual dimorphism itself may also influence the outcome of the Island rule. To date, very few studies have formally tested for the validity of Rensch's rule within the context of body-size evolution in insular settings, and those that did find diverging patterns (Anaya-Meraz and Escobedo-Galván 2020, Avramo et al. 2021, Toyama and Boccia 2021).

Amphibians are particularly well suited to test for the effects of Rensch's rule in the context of body size evolution in insular settings for two main reasons. First, female-biased SSD is the common pattern across amphibians with only very few species characterized by male-biased SSD (Kupfer 2007, Kraus 2008, Pincheira-Donoso et al. 2020), thereby simplifying the test of Rensch's rule. Second, amphibians are characterized by a relatively high plasticity in size, either due to environmental factors or to biological interactions (Laurila et al. 2002, Buskirk 2009, Urban et al. 2014, Levis and Pfennig 2019). In addition, amphibians are relatively well represented in island fauna (Hopkins and Brodie 2015, da Fonte et al. 2019) and, due to their low dispersal abilities (Wells 2007), insular individuals are restricted to these environments. The Island rule shows weak support in these taxa (Benítez-López et al. 2021). Yet, contrasted results have been highlighted in specific systems (Rebouças et al. 2018, Borzée and Min 2021), and the relative paucity of studies carried out on amphibians may well explain the fact that no general pattern was found between insular and continental amphibians (Benítez-López et al. 2021), particularly when accounting for studies in which both sexes were investigated. The fact that insular amphibians may express both dwarfism and gigantism (Wu et al. 2006, Benítez-López et al. 2021) may allow testing for the variations in SSD across all ranges of variation in body size.

In this study, we tested for both the Island rule and Rensch's rule in an island-continental system using pairs of continental and insular populations of a widespread coastal amphibian, the western spadefoot toad *Pelobates cultripes*. Specifically, we investigated differences in body size between continental and insular populations, and whether the magnitude of SSD was different between continental and insular populations according to variations in size observed on islands. According to Rensch's rule (Rensch 1950, Dale et al. 2007), we predicted that larger body size in insular populations should reduce the magnitude of SSD. Finally, we complemented our approach with a large-scale analysis of the effects of body size shift in insular populations of anurans on the magnitude of SSD in order to test whether Rensch's rule applies globally in insular amphibians.

Material and methods

Study species

The western spadefoot *Pelobates cultripes* is a nocturnal amphibian species, distributed in the Iberian Peninsula and on the southeastern and Atlantic coast of France (Lizana et al. 1994, Leclair et al. 2005, Thirion 2014). This medium-sized species (50–80 mm in adults) is characterized by a strong female-biased SSD (Salvador et al. 1986, Lizana et al. 1994, Priol 2015, Lorrain-Soligon et al. 2022). It lives in coastal environments, including islands (Stănescu et al. 2013, Thirion 2014), where it shelters in sandy soils (Speybroeck et al. 2018).

Study sites

Four sites were sampled on the western coast of France, in areas previously identified as being favorable to the presence of the species: the Réserve Naturelle Nationale de Moëze-Oléron (45°53'33.36"N, 01°04'59.16"W, hereafter MO), the Réserve Naturelle Nationale du marais d'Yves (46°02'40.735"N, 01°03'16.906"W, hereafter MY), Oléron Island (46°00'13.91"N, 01°23'15.72"W, hereafter OI) and Ré Island (46°14'47.4"N, 01°31'48.86"W, hereafter RI) (Fig. 1). Each site was sampled for two years, in 2019 and 2020 for MO, MY and RI, and in 2020 and 2021 for OI. Sampling was carried out in autumn when the western spadefoot toad resumes activity after aestivation (Priol 2015, Speybroeck et al. 2018). The two islands are comparable, both being 1.5 km from the continent, and are 13 km from each other. OI measures 17 680 ha and RI measures 9250 ha (Fig. 1).

Field procedures

All field surveys were carried out at night, between 21:00 and 4:00. Sampling was conducted on 3–6 different field trips separated by 1–2 weeks, by teams of 2–10 people. To avoid pseudoreplication in our analyses, individuals were identified with microchips (trovan ID-100VB/1.4), or via photo identification, and if individuals were captured multiple times, only data from the first capture event were included in our analyses. We only kept individuals captured within 500 m from the seashore as this was the greatest distance common to all our study sites, and because distance to the ocean can influence body size in this species (Lorrain-Soligon et al. 2022). We kept only adult individuals in our analyses, using the smallest size (45 mm) for which secondary sexual characters might be observed in males at all our study sites (Lorrain-Soligon et al. 2022). Individuals larger than 45 mm snout-to-vent length (SVL) were classified as adults, while smaller individuals were classified as juveniles (Leclair et al. 2005, Lorrain-Soligon et al. 2022). Individuals lacking male sexual characters were considered as females. This led to a total of 879 individuals (Supporting information).

All detected individuals were captured; their SVL was measured using a caliper (± 1 mm); they were weighed using a pesola spring scale (± 0.5 g); and shortly afterwards were released at the site of capture. Sex was assessed by the presence of secondary sexual characters (Speybroeck et al. 2018).

Literature review of size shift in insular amphibians

We used data gathered by Benítez-López et al. (2021) in their up-to-date meta-analysis from which we kept records concerning amphibians when data for both sexes were

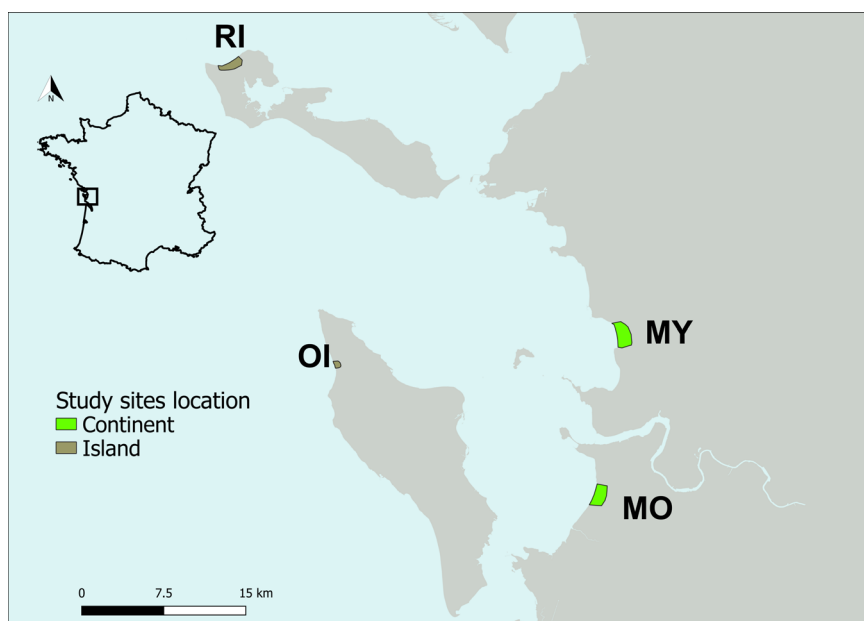


Figure 1. Map of the study area relative to western France illustrating the four study sites (Réserve Naturelle Nationale de Moëze-Oléron, MO; Réserve Naturelle Nationale du marais d'Yves, MY; Oléron Island, OI; and Ré Island, RI).

available (i.e. papers in which only one sex was monitored were excluded). This selection led to data being available on 10 species (across 62 sites). We used body size and not body mass in our analyses. We then used the information available on each island and on the continental sites to calculate the SSD, expressed as the size dimorphism index (SDI) of Lovich and Gibbons (1992). SDI was expressed as $[(\text{size of larger sex} / \text{size of smaller sex}) - 1]$, and defined as positive when females were the larger sex and negative when males were the larger sex. This index is commonly used in studies investigating Rensch's rule (Peñalver-Alcázar et al. 2019, Liang et al. 2022). To compute changes in size between continental and insular populations, for each species we pooled the information of each study concerning continental populations to obtain a single mean value for continent, but kept separate values for each insular site (Supporting information). We then computed the change in size (difference between the mean size of insular individuals and that of continental individuals, divided by the mean size of continental individuals), the change in female size and the change in male size. As data available for Caudates and Gymnophiones were very scarce, we focused our analyses on anurans. We also excluded studies in which phylogenetically close, albeit different, species were found on the continent and on nearby insular sites. See the Supporting information for details of the data retained for these analyses.

Statistical analysis

Size change and SSD in *Pelobates cultripes*

We computed a scaled mass index (SMI) according to Peig and Green (2009), which is widely used as a body condition index in amphibians, making comparisons more reliable (MacCracken and Stebbings 2012, Brodeur et al. 2020). This index computes the mass of all individuals as if they were of the same size (average length of all individuals; Peig and Green 2009). B_{SMA} was calculated on log transformed data using the online software RMA (Bohonak and Van der Linde 2004).

Variations in SVL and SMI between sites were compared with two linear mixed-effects models (LMMs), with either SVL or SMI as a dependent variable, site as a covariate and year as a random effect, and with post hoc comparisons using the multcomp R package (www.r-project.org). To test for sex-specific variations in SVL and SMI, we performed LMMs with site and sex as covariates, and year as a random effect.

Size change and SSD in insular anurans

We tested for the hypothesis that changes in size will influence the magnitude of SSD using the subset (above) of the data gathered by Benítez-López et al. (2021). As phylogenetic control has been shown to be more robust for analyses using multiple species (Meiri et al. 2008, Benítez-López et al. 2021; here 10 species distributed around the globe), we used PGLMM (phylogenetic generalized linear mixed model, *pglmm()* function using the Gaussian distribution package *phyr*; Li et al. 2020). We constructed a phylogenetic tree using the amphibians

phylogeny from Jetz and Pyron (2018), including node age calibration (data available at: <https://datadryad.org/stash/dataset/doi:10.5061/dryad.cc3n6j5>). Their reference taxonomy contains 7238 species, extracted from AmphibiaWeb (<http://amphibiaweb.org>). We only retained the 10 species presented in our analysis (i.e. *Blommersia galani*, *Blommersia dejongi*, *Boophis tephraeomystax*, *Fejervarya limnocharis*, *Fejervarya kawamurai*, *Adenomera marmorata*, *Bufo bufo*, *Bufo viridis*, *Oophaga pumilio*, *Discoglossus pictus*) using the *drop.tip()* function from the ape library (Paradis and Schliep 2019). We then computed PGLMMs with SSD (SDI) as a dependent variable, and changes in size between continental and insular populations as an explanatory variable (either mean size, female size or male size, expressed as a percentage). To take into account the difference in phylogeny between species, and their difference in repartition (differentially distributed around the globe), we used species (with the associated phylogenetical Brownian matrix) and location (geographical area) as random effects. Model diagnostics were computed using the package DHARMA (Hartig 2022). See the Supporting information for the output of the three models.

All data analyses were performed using R ver. 3.6.3 (www.r-project.org).

Results

Size change and SSD in *Pelobates cultripes*

Morphology varied significantly across sites (Table 1). Both females and males were significantly larger in OI than females and males in any other site (Table 1). This led, overall, to larger individuals in OI compared to other sites (Fig. 2a, Table 1). Individuals in OI did not display SSD, while females were larger than males on continental sites and in RI (Fig. 2b, Table 1).

On one island (RI), individuals had a better body condition (SMI) than on the three other sites either for females (Table 2), males (Table 2), or both sexes (Fig. 2c, Table 2). No difference in SMI between sexes was observed at any site (Fig. 2d, Table 2).

Size change and SSD across insular anurans

In the 10 species investigated, the magnitude of SSD decreased with increasing body size in insular populations as compared to continental populations (coefficient = -0.001 , $SE < 0.001$, $z\text{-score} = -2.198$, $p\text{-value} = 0.027$; Fig. 3a). A similar effect was found when focusing our analyses on body size change in males (coefficient = -0.002 , $SE = 0.001$, $z\text{-score} = -2.626$, $p\text{-value} = 0.008$; Fig. 3b), but not in females (coefficient = -0.001 , $SE = 0.001$, $z\text{-score} = -1.103$, $p\text{-value} = 0.258$; Fig. 3c).

Discussion

In this study, we tested whether Rensch's rule can apply to the change in body size observed in insular contexts and

Table 1. Differences in snout-to-vent length (SVL) between sites for all adults and separately for males and females, and difference in SVL within sites between males and females.

Comparison		Estimate	SE	t	p
All adults	MY–MO	2.345	0.797	2.944	0.016
	OI–MO	13.057	1.111	11.756	< 0.001
	RI–MO	2.204	0.687	3.206	0.007
	OI–MY	10.711	1.139	9.402	< 0.001
	RI–MY	−0.142	0.733	−0.194	0.997
Females	RI–OI	−10.852	1.066	−10.186	< 0.001
	MY–MO	4.046	1.033	3.916	< 0.001
	OI–MO	12.429	1.497	8.305	< 0.001
	RI–MO	2.138	0.848	2.521	0.054
	OI–MY	8.383	1.544	5.431	< 0.001
Males	RI–MY	−1.908	0.929	−2.054	0.161
	RI–OI	−10.291	1.426	−7.214	< 0.001
	MY–MO	0.249	1.071	0.232	0.996
	OI–MO	14.421	1.42	10.158	< 0.001
	RI–MO	0.964	1.026	0.939	0.78
Differences between males and females	OI–MY	14.173	1.44	9.843	< 0.001
	RI–MY	0.715	1.054	0.678	0.904
	RI–OI	−13.457	1.407	−9.563	< 0.001
	MO	−3.335	1.056	−3.159	0.031
	MY	−7.132	1.147	−6.216	< 0.001
	OI	−1.343	1.867	−0.719	0.996
	RI	−4.51	0.941	−4.793	< 0.001

formalized as the Island rule. Using specific comparisons of continental and insular populations of the widespread coastal amphibian *P. cultripes*, we found that gigantism, expressed in one of our insular site, also affected the magnitude of SSD, with males from this population reaching a similar body size to that of females. Complementarily, using a large-scale analysis across anuran amphibians, we found that increased body size in insular populations reduced the magnitude of SSD through an increase in male body size, similar to our results focused on *P. cultripes*.

Our species-specific investigations, focused on continental and insular populations of *P. cultripes*, led to contrasting results about the Island rule. One insular population (OI) was characterized by gigantism in both male and female individuals. Another insular population (RI), however, did not display any size modification as compared to continental populations. Nonetheless, these contrasted responses of two insular populations of the same species accord relatively well with other studies which have repeatedly found that the validity of the Island rule can depend on environmental factors affecting body size evolution, either in amphibians (Rebouças et al. 2018), or more broadly in other taxa (Lomolino 1985, Palkovacs 2003, Meiri et al. 2008). These differential responses to insular settings have been related to factors such as the degree of isolation (distance to the continent, Lomolino 2005, Traveset et al. 2016, Benítez-López et al. 2021) and the degree of seasonality (unpredictable versus predictable environments, Benítez-López et al. 2021), two parameters that are unlikely to apply in our context where the two islands are situated very close to each other and at similar distances from the continent. Additional factors are known to influence the validity of the Island

rule (Lomolino 1985, Palkovacs 2003, Meiri et al. 2008, Rebouças et al. 2018), supporting the hypothesis that size modification on islands can be population- and/or species-specific (Benítez-López et al. 2021). For instance, individuals that have colonized OI could have, by chance, already been larger, leading to a genetic drift (founder effect, Barton and Charlesworth 1984; as highlighted in Rebouças et al. 2020). In addition, ecological island-specific factors such as reduced predation pressure, competition and/or resources availability, could influence body size. These factors can influence the validity of the Island rule and, when valid, the direction (dwarfism versus gigantism) of body size changes (Lomolino 1985, Meiri et al. 2008, Rebouças et al. 2018). Unfortunately, we did not investigate such sources of variation, and the various factors that potentially influence body size on islands need to be monitored. These hypotheses remain to be tested in order to identify which factors, or combination thereof, induced gigantism in one insular setting but not in the other.

If gigantism was found only in one island (OI), variations of body condition were also contrasted between study sites. On one of our insular sites (RI), individuals were characterized by a better body condition (higher SMI). Although this pattern is linked to body condition and not body size, it can nonetheless be related to similar mechanisms that underlie the Island rule. Indeed, as island communities are generally less diverse (Lomolino 2005), this can lead to reduced competition (Li et al. 2011, Rebouças et al. 2018) and reduced predation (Palkovacs 2003). As a consequence, insular individuals may have access to larger amounts of and/or more diverse resources (Palkovacs 2003), leading to higher energy gain. In addition, larger individuals may also increase their

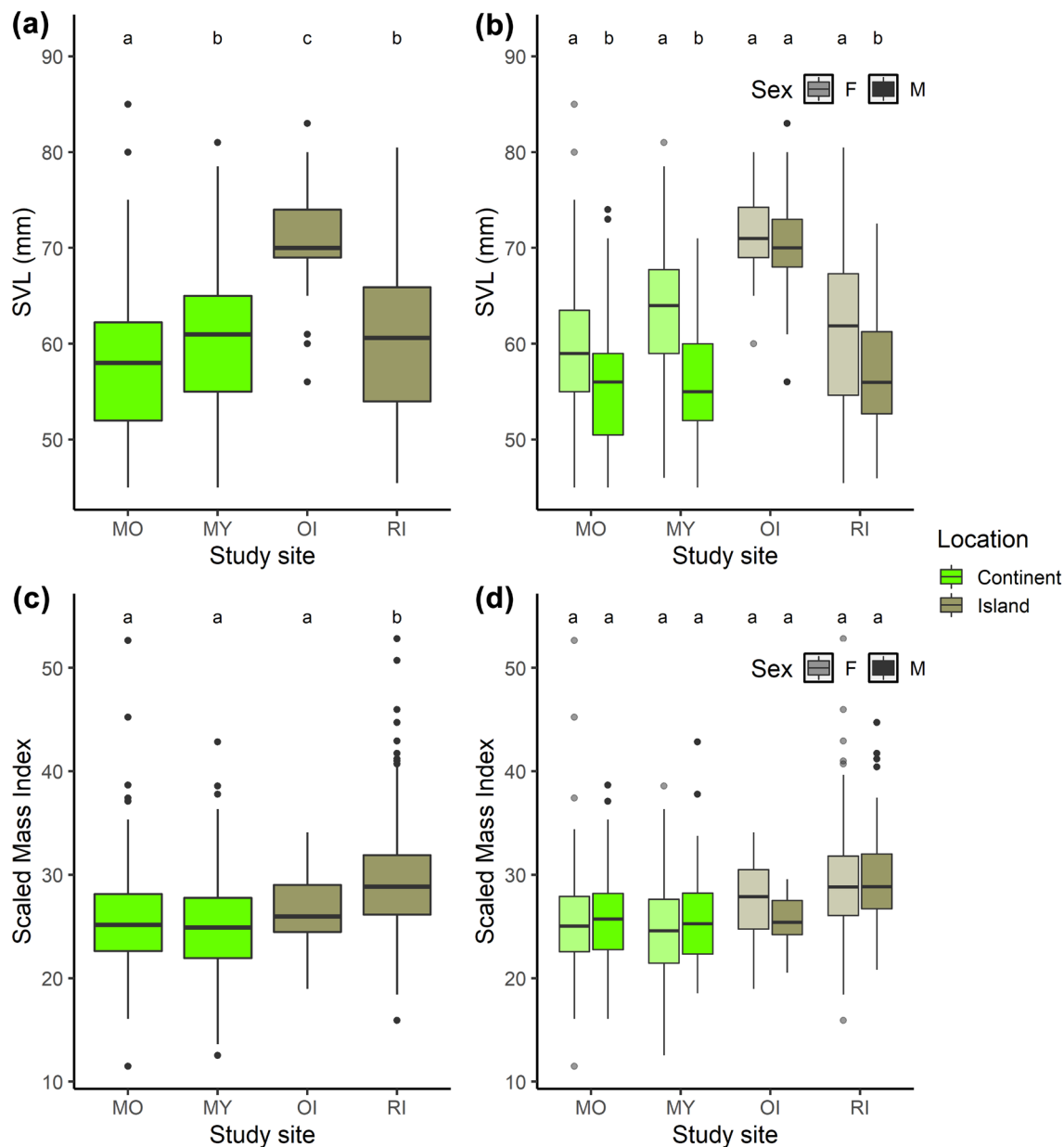


Figure 2. Differences in snout-to-vent length (SVL) between sites for all adults (a) and between males and females within sites (b). Differences in scaled mass index (SMI) between sites for all adults (c), and between males and females within sites (d), in Réserve Naturelle Nationale de Moëze-Oléron, MO; Réserve Naturelle Nationale du marais d'Yves, MY; Oléron Island, OI; and Ré Island, RI. Different letters represent a significant difference at $\alpha = 0.05$.

niche breadth, as they can feed on both larger and smaller prey items (Lomolino 1985). Competition and resources availability may also interact, because niche breadth increases with resource breadth, and decreases with the number of congeneric competitors (Costa-Pereira et al. 2019). In our settings, the two insular populations showed either an increase in body size, or an increase in body condition, both of which can be related to the factors described above. Nonetheless, as highlighted above, we have not monitored potentially underlying factors (e.g. predation pressure, competition or resources availability) at our study sites. As a consequence,

this hypothesis remains to be tested. Nevertheless, we suggest that body condition, in addition to body size, should be considered when investigating the variations between continental and insular populations.

Can the Island rule affect the magnitude of SSD as stated by Rensch's rule? We found substantial support for this hypothesis from both our case study and our larger-scale analysis based on published data. Amphibians generally express a female-biased SSD (Wells 2007, Kraus 2008), a pattern that is also found in our study species (Salvador et al. 1986, Lizana et al. 1994, Lorrain-Soligon et al. 2022).

Table 2. Differences in body condition (scaled mass index, SMI) between sites for all adults and separately for males and females, and difference in body condition within sites between males and females.

Comparison		Estimate	SE	t	p
All adults	MY–MO	−0.517	0.506	−1.021	0.731
	OI–MO	0.828	0.725	1.142	0.657
	RI–MO	4.132	0.522	7.924	< 0.001
	OI–MY	1.345	0.743	1.809	0.262
	RI–MY	4.649	0.539	8.624	< 0.001
Females	RI–OI	3.304	0.776	4.257	< 0.001
	MY–MO	−0.886	0.675	−1.312	0.547
	OI–MO	1.923	1.001	1.921	0.212
	RI–MO	4.211	0.676	6.232	< 0.001
	OI–MY	2.809	1.032	2.723	0.031
Males	RI–MY	5.097	0.702	7.259	< 0.001
	RI–OI	2.288	1.045	2.189	0.122
	MY–MO	0.021	0.746	0.028	0.999
	OI–MO	−0.248	0.989	−0.251	0.994
	RI–MO	3.863	0.715	5.404	< 0.001
Differences between males and females	OI–MY	−0.269	1.003	−0.268	0.993
	RI–MY	3.843	0.734	5.234	< 0.001
	RI–OI	4.112	0.980	4.195	< 0.001
	MO	0.162	0.704	0.230	1
Differences between males and females	MY	1.056	0.762	1.387	0.855
	OI	−2.252	1.240	−1.816	0.592
	RI	0.296	0.625	0.474	0.999

However, in our insular site in which *P. cultripes* displayed gigantism (OI), the SSD was no longer significant. More generally, for anuran species found both on continental and insular sites (using 10 species), with data extracted from Benítez-López et al. (2021), we found that the magnitude of SSD in insular populations decreased when body size increased. This result dovetails remarkably well with Rensch's rule, which states that SSD should decrease with increasing

body size when females are the larger sex (Rensch 1950, Fairbairn 1997, Dale et al. 2007). Importantly, we found additional convergent results for both sets of analyses. In *P. cultripes*, although both sexes were larger in OI, the body size of males increased proportionally more than that of females, so that males and females had similar body size. Although this increased male size might be the consequence of directional selection (e.g. higher competition between males, as

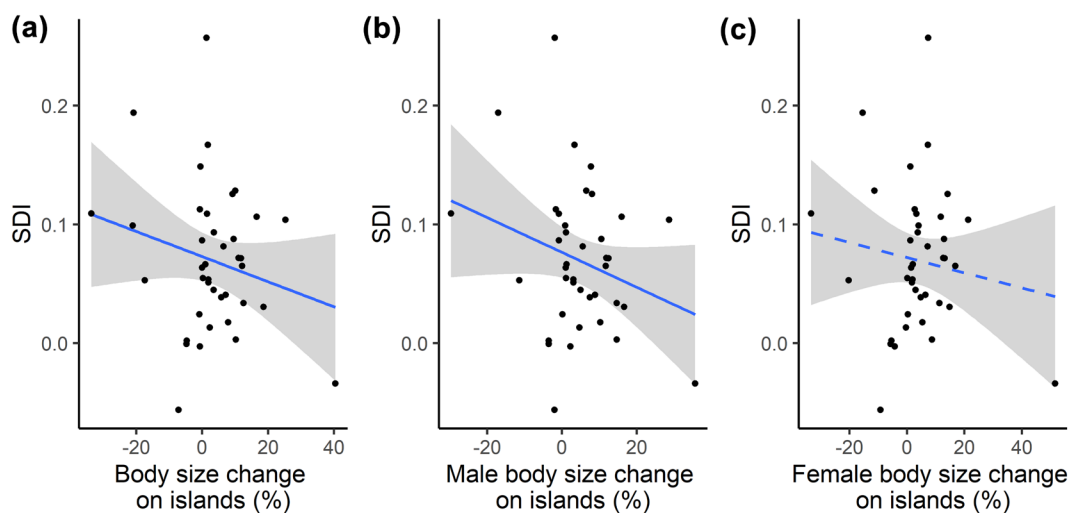


Figure 3. Sexual size dimorphism (SSD) as estimated by the size dimorphism index (SDI) in relation to change in anuran body size (a) for combined males and females; (b) only males; and (c) and only females on islands, according to the review of Benítez-López et al. (2021; Supporting information). SDI was expressed as $[(\text{size of larger sex}/\text{size of smaller sex}) - 1]$, and defined as positive when females were the larger sex and negative when males were the larger sex (Lovich and Gibbons 1992). The change in size was expressed as the difference between the mean size of insular individuals (either for combined males and females, only for males, or only for females) and that of continental individuals, divided by the mean size of continental individuals. Points represent observed values, solid lines represent significant relationships and dashed lines represent non-significant relationships (details in text and the Supporting information).

highlighted in [Reboucas et al. 2020](#)), this led to a reduction in the SSD. More broadly, across anurans, we highlighted that decreased SSD with increasing body size was strongly linked to body size changes in male individuals, but not in females. Again, these complementary results dovetail remarkably well with the mechanistic basis of Rensch's rule, as sexual selection acting on male size has been suggested to drive the evolution of this pattern ([Abouheif and Fairbairn 1997](#)). Complementary, it has been suggested that female body size may be less impacted than that of males in insular settings ([Lu et al. 2014](#), [Avramo et al. 2021](#)). Despite these similar patterns found from both our case study and our larger-scale analysis based on published data, we emphasize that these results need to be taken with caution, as literature on the modification of anuran body size on islands is very scarce, particularly when considering both sexes. Indeed, our large-scale analysis based on published data only considered 12 studies, involving 10 species which represent ~0.16% of the current anuran diversity (about 6400 species, [Jetz and Pyron 2018](#)). Overall, available data lack the variations in environmental conditions needed to robustly assess the universal validity of Rensch's rule in insular settings ([Benítez-López et al. 2021](#)). We suggest that future studies investigating variations in size should consider both sexes in order to complement the existing literature and further test for the validity of our hypothesis. We also emphasize that further investigations should also take into account location (as size can vary with locality; [Bergmann 1848](#)), although this pattern has not been found to apply in amphibians ([Adams and Church 2008](#)); and different thermal conditions between localities (as in the study of [Benítez-López et al. 2021](#)). However, the small number of available data did not allow us to take into account these additional sources of variations, and future studies investigating the same hypotheses on a higher number of taxa should address these issues. The consequences of insularity on the magnitude of SSD need also to be investigated on the various taxa (e.g. mammals, birds, lizards and snakes) in which the Island rule has found support ([Benítez-López et al. 2021](#)).

Conclusion

Overall, we found that body size change linked to insularity can affect the magnitude of SSD in amphibians, thereby connecting the Island rule and Rensch's rule ([Anaya-Meraz and Escobedo-Galván 2020](#), [Avramo et al. 2021](#)). We emphasize that additional investigations are required to unequivocally confirm these patterns considering other taxa, to test the validity of Rensch's rule, and taking into account additional sources of body size variation. This hypothesis needs also to be tested for taxa in which males are the larger sex, in which case the magnitude of SSD is expected to increase with increasing body size. Such studies will be critical in order to understand the changes that can affect other isolated populations, not only on islands, but also those from anthropogenically fragmented ecosystems.

Significance statement

According to the Island rule, insular populations are characterized by gigantism in small species and dwarfism in large species. Independently, Rensch's rule states that SSD should increase with increasing body size when males are the larger sex, and decrease with increasing body size when females are the larger sex. Here, we connected these two global rules in biology. Using amphibians as a study system, we investigated this hypothesis both in a case study of continental and insular populations of a widespread coastal amphibian (the spadefoot toad) and using a large-scale analysis (published records) across anurans. We found substantial support for the association between the Island rule and Rensch's rule, with increased body size in insular populations reducing the magnitude of SSD through an increase in male body size, which needs to be further validated with additional data considering both sexes in amphibians.

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Author contributions

Léa Lorrain-Soligon: Conceptualization (lead), Data curation (lead), Formal analysis (lead), Investigation (lead), Methodology (lead), Resources (lead), Software (lead), Visualization (lead), Writing – original draft (lead), Writing – review and editing (lead). **Frédéric Robin:** Conceptualization-Supporting, Data curation-Supporting, Funding acquisition (equal), Investigation (equal), Project administration (equal), Validation-Supporting, Writing – review and editing-Supporting. **Marko Jankovic:** Conceptualization-Supporting, Data curation-Supporting, Investigation-Supporting, Validation-Supporting, Writing – review and editing-Supporting. **Vincent Lelong:** Conceptualization-Supporting, Data curation-Supporting, Investigation-Supporting, Validation-Supporting, Writing – review and editing-Supporting. **Simon Baudouin:** Conceptualization-Supporting, Data curation-Supporting, Investigation-Supporting, Validation-Supporting, Writing – review and editing-Supporting. **François Brischoux:** Conceptualization (equal), Funding acquisition (equal), Investigation (equal), Methodology (equal), Project administration (equal), Supervision (lead), Validation (equal), Visualization (equal), Writing – original draft (equal), Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k98sf7mb0> (Lorrain-Soligon et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Abouheif, E. and Fairbairn, D. J. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. – *Am. Nat.* 149: 540–562.
- Adams, D. C. and Church, J. O. 2008. Amphibians do not follow Bergmann's rule. – *Evolution* 62: 413–420.
- Adler, G. H. and Levins, R. 1994. The island syndrome in rodent populations. – *Q. Rev. Biol.* 69: 473–490.
- Anaya-Meraz, Z. A. and Escobedo-Galván, A. H. 2020. Insular effect on sexual size dimorphism in the clouded anole *Anolis nebulosus*: when Rensch meets Van Valen. – *Curr. Zool.* 66: 589–591.
- Anderson, R. P. and Handley Jr, C. O. 2002. Dwarfism in insular sloths: biogeography, selection, and evolutionary rate. – *Evolution* 56: 1045–1058.
- Aubret, F. 2012. Body-size evolution on islands: are adult size variations in tiger snakes a nonadaptive consequence of selection on birth size? – *Am. Nat.* 179: 756–767.
- Aubret, F. and Shine, R. 2009. Genetic assimilation and the post-colonization erosion of phenotypic plasticity in island tiger snakes. – *Curr. Biol.* 19: 1932–1936.
- Aubret, F. 2015. Island colonisation and the evolutionary rates of body size in insular neonate snakes. – *Heredity* 115: 349–356.
- Avramo, V., Senczuk, G., Corti, C., Böhme, W., Capula, M., Castiglia, R. and Colangelo, P. 2021. Evaluating the island effect on phenotypic evolution in the Italian wall lizard, *Podarcis siculus* (Reptilia: Lacertidae). – *Biol. J. Linn. Soc.* 132: 655–665.
- Barton, N. H. and Charlesworth, B. 1984. Genetic revolutions, founder effects, and speciation. – *Annu. Rev. Ecol. Syst.* 15: 133–164.
- Benítez-López, A., Santini, L., Gallego-Zamorano, J., Milá, B., Walkden, P., Huijbregts, M. A. and Tobias, J. A. 2021. The island rule explains consistent patterns of body size evolution in terrestrial vertebrates. – *Nat. Ecol. Evol.* 5: 768–786.
- Bergmann, C. 1848. *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*, Göttingen: Vandenhoeck und Ruprecht.
- Biddick, M., Hendriks, A. and Burns, K. C. 2019. Plants obey (and disobey) the island rule. – *Proc. Natl Acad. Sci. USA* 116: 17632–17634.
- Blondel, J. 1985. Breeding strategies of the blue tit and coal tit (*Parus*) in mainland and island Mediterranean habitats: a comparison. – *J. Anim. Ecol.* 54: 531–556.
- Bohonak, A. J. and Van der Linde, K. 2004. RMA: software for reduced major axis regression, JAVA version (v. 1. 21). – <http://www.kimvdlinde.com/professional/rma.html>, <http://www.biosdsu.edu/pub/andy/rma.html> (in press).
- Borzée, A. and Min, M.-S. 2021. Disentangling the impacts of speciation, sympatry and the island effect on the morphology of seven *Hynobius* sp. salamanders. – *Animals* 11: 187.
- Brodeur, J. C., Damonte, M. J., Candiotti, J. V., Poliserpi, M. B., D'Andrea, M. F. and Bahl, M. F. 2020. Frog body condition: basic assumptions, comparison of methods and characterization of natural variability with field data from *Leptodactylus latrans*. – *Ecol. Indic.* 112: 106098.
- Brodin, T., Lind, M. I., Wiberg, M. K. and Johansson, F. 2013. Personality trait differences between mainland and island populations in the common frog (*Rana temporaria*). – *Behav. Ecol. Sociobiol.* 67: 135–143.
- Buskirk, J. V. 2009. Natural variation in morphology of larval amphibians: phenotypic plasticity in nature? – *Ecol. Monogr.* 79: 681–705.
- Clegg, S. M. and Owens, P. F. 2002. The 'island rule' in birds: medium body size and its ecological explanation. – *Proc. R. Soc. B* 269: 1359–1365.
- Costa-Pereira, R., Araújo, M. S., Souza, F. L. and Ingram, T. 2019. Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions. – *Proc. R. Soc. B* 286: 20190369.
- da Fonte, L. F. M., Mayer, M. and Lötters, S. 2019. Long-distance dispersal in amphibians. – *Front. Biogeogr.* 11: e44577.
- Dale, J., Dunn, P. O., Figuerola, J., Lislevand, T., Székely, T. and Whittingham, L. A. 2007. Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. – *Proc. R. Soc. B* 274: 2971–2979.
- Diniz-Filho, J. A. F. and Raia, P. 2017. Island Rule, quantitative genetics and brain–body size evolution in *Homo floresiensis*. – *Proc. R. Soc. B* 284: 20171065.
- Diniz-Filho, J. A. F., Jardim, L., Rangel, T. F., Holden, P. B., Edwards, N. R., Hortal, J., Santos, A. M. C. and Raia, P. 2019. Quantitative genetics of body size evolution on islands: an individual-based simulation approach. – *Biol. Lett.* 15: 20190481.
- Diniz-Filho, J. A. F., Santos, A. M., Barreto, E., Naves, F., Santos, W., Souza, K. S., Santos-Silva, R., Dobrovolski, R., Soares, T. N., Tidon, R., Spigoloni, Z. A., Rangel, T. F., Raia, P., Hortal, J. and Jardim, L. 2021. Quantitative genetics of extreme insular dwarfing: the case of red deer on Jersey. – *J. Biogeogr.* 48: 1720–1730.
- Everson, K. M., Gray, L. N., Jones, A. G., Lawrence, N. M., Foley, M. E., Sovacool, K. L., Kratovil, J. D., Hotaling, S., Hime, P. M., Storfer, A., Parra-Olea, G., Percino-Daniel, R., Aguilar-Miguel, X., O'Neill, E. M., Zambrano, L., Shaffer, H. B. and Weisrock, D. W. 2020. Geography is more important than life history in the recent diversification of the tiger salamander complex. – *bioRxiv* 118: e2014719118.
- Fairbairn, D. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. – *Annu. Rev. Ecol. Syst.* 28: 659–687.
- Filin, I. and Ziv, Y. 2004. New theory of insular evolution: unifying the loss of dispersability and body-mass change. – *Evol. Ecol. Res.* 6: 115–124.
- Hartig, F. 2022. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. – R package, ver. 0.4.6, <https://CRAN.R-project.org/package=DHARMA>.
- Hopkins, G. R. and Brodie, E. D. 2015. Occurrence of amphibians in saline habitats: a review and evolutionary perspective. – *Herpetol. Monogr.* 29: 1–27.
- Jensen, H., Moe, R., Hagen, I. J., Holand, A. M., Kekkonen, J., Tufto, J. and Sæther, B. E. 2013. Genetic variation and structure of house sparrow populations: is there an island effect? – *Mol. Ecol.* 22: 1792–1805.

- Jetz, W. and Pyron, R. A. 2018. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. – *Nat. Ecol. Evol.* 2: 850–858.
- Keogh, J. S., Scott, I. A. and Hayes, C. 2005. Rapid and repeated origin of insular gigantism and dwarfism in Australian tiger snakes. – *Evolution* 59: 226–233.
- Kraus, F. 2008. Remarkable case of anuran sexual size dimorphism: *Platymantis rhipiphalcus* is a junior synonym of *Platymantis bouleengeri*. – *J. Herpetol.* 42: 637–644.
- Kupfer, A. 2007. Sexual size dimorphism in amphibians: an overview. – In: Fairbairn, D. J., Blanckenhorn, W. U. and Székely, T. (eds), *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*. Oxford Univ. Press, pp. 50–60.
- Laurila, A., Pakkasmaa, S., Crochet, P. A. and Merilä, J. 2002. Predator-induced plasticity in early life history and morphology in two anuran amphibians. – *Oecologia* 132: 524–530.
- Leclair, M. H., Leclair, R. and Gallant, J. 2005. Application of skeletochronology to a population of *Pelobates cultripes* (Anura: Pelobatidae) from Portugal. – *J. Herpet.* 39: 199–207.
- Levis, N. A. and Pfennig, D. W. 2019. Phenotypic plasticity, canalization, and the origins of novelty: evidence and mechanisms from amphibians. – *Semin. Cell Dev. Biol.* 88: 80–90.
- Li, D., Dinnage, R., Nell, L. A., Helmus, M. R. and Ives, A. R. 2020. phyr: an R package for phylogenetic species-distribution modelling in ecological communities. – *Methods Ecol. Evol.* 11: 1455–1463.
- Li, Y., Xu, F., Guo, Z., Liu, X., Jin, C., Wang, Y. and Wang, S. 2011. Reduced predator species richness drives the body gigantism of a frog species on the Zhoushan Archipelago in China. – *J. Anim. Ecol.* 80: 171–182.
- Liang, T., Meiri, S. and Shi, L. 2022. Sexual size dimorphism in lizards: Rensch's rule, reproductive mode, clutch size, and line fitting method effects. – *Integr. Zool.* 17: 787–803.
- Lizana, M., Márquez, R. and Martín-Sánchez, R. 1994. Reproductive biology of *Pelobates cultripes* in central Spain. – *J. Herpetol.* 28: 19–27.
- Lokatis, S. and Jeschke, J. M. 2018. The island rule: an assessment of biases and research trends. – *J. Biogeogr.* 45: 289–303.
- Lomolino, M. V. 1985. Body size of mammals on islands: the island rule reexamined. – *Am. Nat.* 125: 310–316.
- Lomolino, M. V. 2005. Body size evolution in insular vertebrates: generality of the island rule. – *J. Biogeogr.* 32: 1683–1699.
- Lorrain-Soligon, L., Robin, F., Lelong, V., Jankovic, M., Barbraud, C. and Brischoux, F. 2022. Distance to coastline modulates morphology and population structure in a coastal amphibian. – *Biol. J. Linn. Soc.* 135: 478–489.
- Lorrain-Soligon, L., Robin, F., Jankovic, M., Lelong, V., Baudouin, S., Brischoux, F. 2023. Data from: When Rensch meets Foster: insular gigantism may reduce sexual dimorphism in anurans. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.k98sf7mb0>.
- Lovich, J. E. and Gibbons, J. W. 1992. A review of techniques for quantifying sexual size dimorphism. – *Growth Dev. Aging* 56: 269–269.
- Lu, D., Zhou, C. Q., Zhao, L. J. and Liao, W. B. 2014. Pattern of sexual size dimorphism supports the inverse of Rensch's rule in two frog species. – *Anim. Biol.* 64: 87–95.
- MacCracken, J. G. and Stebbings, J. L. 2012. Test of a body condition index with amphibians. – *J. Herpetol.* 46: 346–350.
- Meiri, S., Cooper, N. and Purvis, A. 2008. The island rule: made to be broken? – *Proc. R. Soc. B* 275: 141–148.
- Millien, V. 2006. Morphological evolution is accelerated among island mammals. – *PLoS Biol.* 4: e321.
- Müller, C., Jenni-Eiermann, S., Blondel, J., Perret, P., Caro, S. P., Lambrechts, M. M. and Jenni, L. 2007. Circulating corticosterone levels in breeding blue tits *Parus caeruleus* differ between island and mainland populations and between habitats. – *Gen. Comp. Endocrinol.* 154: 128–136.
- Nieberding, C., Morand, S., Libois, R. and Michaux, J. R. 2006. Parasites and the island syndrome: the colonization of the western Mediterranean islands by *Heligmosomoides polygyrus* (Dujardin, 1845). – *J. Biogeogr.* 33: 1212–1222.
- Novosolov, M., Raia, P. and Meiri, S. 2013. The island syndrome in lizards. – *Global Ecol. Biogeogr.* 22: 184–191.
- Pafilis, P., Meiri, S., Foufopoulos, J. and Valakos, E. 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. – *Naturwissenschaften* 96: 1107–1113.
- Palkovacs, E. P. 2003. Explaining adaptive shifts in body size on islands: a life history approach. – *Oikos* 103: 37–44.
- Paradis, E. and Schliep, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. – *Bioinformatics* 35: 526–528.
- Peig, J. and Green, A. J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. – *Oikos* 118: 1883–1891.
- Peñalver-Alcázar, M., Galán, P. and Aragón, P. 2019. Assessing Rensch's rule in a newt: roles of primary productivity and conspecific density in interpopulation variation of sexual size dimorphism. – *J. Biogeogr.* 46: 2558–2569.
- Pincheira-Donoso, D., Harvey, L. P., Grattarola, F., Jara, M., Cotter, S. C., Tregenza, T. and Hodgson, D. J. 2020. The multiple origins of sexual size dimorphism in global amphibians. – *Global Ecol. Biogeogr.* 30: 443–458.
- Priol, P. 2015. Suivi d'une espèce rare en vue de sa conservation: dynamique spatiale et temporelle de populations de Pélobate cultripède (*Pelobates cultripes*) en Aquitaine. – École pratique des hautes études (EPHE).
- Rebouças, R., da Silva, H. R. and Solé, M. 2018. Frog size on continental islands of the coast of Rio de Janeiro and the generality of the Island Rule. – *PLoS One* 13: e0190153.
- Rebouças, R., Augusto-Alves, G. and Toledo, L. F. 2020. Evolution of treefrogs' calls in tropical islands might be under directional selection. – *J. Zool.* 312: 43–52.
- Renaud, S. and Auffray, J.-C. 2010. Adaptation and plasticity in insular evolution of the house mouse mandible. – *J. Zool. Syst. Evol. Res.* 48: 138–150.
- Rensch, B. 1950. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. – *Bonner Zoologische Beiträge* 1: 58–69.
- Russell, J. C., Ringler, D., Trombini, A. and Le Corre, M. 2011. The island syndrome and population dynamics of introduced rats. – *Oecologia* 167: 667–676.
- Salazar, J. C., del Rosario Castañeda, M., Londono, G. A., Bodensteiner, B. L. and Munoz, M. M. 2019. Physiological evolution during adaptive radiation: a test of the island effect in *Anolis* lizards. – *Evolution* 73: 1241–1252.
- Salvador, A., Alvarez, J. and Garcia, C. 1986. Reproductive biology of a northern population of the western spade foot *Pelobates cultripes* (Anura: Pelobatidae). – In: Rocek, Z. (ed), *Studies in herpetology*. Charles University, Prague, pp 403–408.
- Siliceo-Cantero, H. H., Benítez-Malvido, J. and Suazo-Ortuño, I. 2020. Insularity effects on the morphological space and sexual dimorphism of a tropical tree lizard in western Mexico. – *J. Zool.* 311: 277–285.

- Speybroeck, J., Beukema, W. and Bok, B. 2018. Guide Delachaux des amphibiens & reptiles de France et d'Europe. – Delachaux et Nieslé.
- Stănescu, F., Iosif, R., Székely, D., Székely, P., Roşioru, D. and Cogălniceanu, D. 2013. Salinity tolerance in *Pelobates fuscus* (Laurenti, 1768) tadpoles (Amphibia: Pelobatidae). – *Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa"* 56: 103–108.
- Thirion, J.-M. 2014. Salinity of the reproduction habitats of the western spadefoot toad *Pelobates cultripes* (Cuvier, 1829), along the Atlantic coast of France. – *Herpetozoa* 27: 13–20.
- Toyama, K. S. and Boccia, C. K. 2021. Sexual size dimorphism and life history traits in an island-mainland system: an overview of the lizard genus *Microlophus*. – *Amphibia-Reptilia* 42: 511–517.
- Traveset, A., Tur, C., Trøjelsgaard, K., Heleno, R., Castro-Urgal, R. and Olesen, J. M. 2016. Global patterns of mainland and insular pollination networks. – *Global Ecol. Biogeogr.* 25: 880–890.
- Urban, M. C., Richardson, J. L. and Freidenfelds, N. A. 2014. Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. – *Evol. Appl.* 7: 88–103.
- Van Valen, L. M. 1973. A new evolutionary law. – *Evol. Theory* 1: 1–30.
- Wells, K. D. 2007. The ecology and behavior of amphibians. – Univ. of Chicago Press.
- Wu, Z., Li, Y. and Murray, B. R. 2006. Insular shifts in body size of rice frogs in the Zhoushan Archipelago, China. – *J. Anim. Ecol.* 75: 1071–1080.