

Article

The geographical diversification in varanid lizards: the role of mainland versus island in driving species evolution

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Abstract

Monitor lizards (Varanidae) inhabit both the mainland and islands of all geological types and have diversified into an exceptionally wide range of body sizes, thus providing an ideal model for examining the role of mainland versus island in driving species evolution. Here we use phylogenetic comparative methods to examine whether a link exists between body size-driven diversification and body size-frequency distributions in varanid lizards and to test the hypothesis that island lizards differ from mainland species in evolutionary processes, body size, and life-history traits (offspring number and size). We predict that: 1) since body size drives rapid diversification in groups, a link exists between body size-driven diversification and body size-frequency distributions; 2) because of various environments on island, island species will have higher speciation, extinction, and dispersal rates, compared with mainland species; 3) as a response to stronger intraspecific competition, island species will maximize individual ability associated with body size to outcompete closely-related species, and island species will produce smaller clutches of larger eggs to increase offspring quality. Our results confirm that the joint effect of differential macroevolutionary rates shapes the species richness pattern of varanid lizards. There is a link between body size-driven diversification and body size-frequency distributions, and the speciation rate is maximized at medium body sizes. Island species will have higher speciation, equal extinction, and higher dispersal rates compared with mainland species. Smaller clutch size and larger hatchling in the island than in mainland species indicate that offspring quality is more valuable than offspring quantity for island varanids.

Key words: body size, island, mainland, trait-driven diversification, Varanidae

Islands are the hotspots of biodiversity for their high levels of endemism, even if the number of species is lower than that on the mainland (Whittaker and Fernández-Palacios 2007). As a result of the strong oceanic influence, island climates are fairly anomalous

(Whittaker and Fernández-Palacios 2007). Island-specific environment, combined with other factors (i.e., geographical isolation and ecological release), may affect lineage diversification (Losos and Ricklefs 2009). Yet as natural laboratories, it remains unclear

whether island species have higher diversification rates. Compared with their fellow mainland organisms, island species face fewer competitors and predators (lower interspecific predation pressures) and few preys (stronger intraspecific competition; MacArthur et al. 1972; Novosolov et al. 2016), thus having a suite of traits variation (Adler and Levins 1994). These include morphology (e.g., a tendency toward medium body size; Clegg and Owens 2002; Lomolino et al. 2012; Sandvig et al. 2019), behavior (increased intraspecific aggression; Robinson-Wolrath and Owens 2003), and life-history strategy (a shift to K strategy; Slavenko et al. 2015; Schwarz and Meiri 2017). Besides those biotic factors, some abiotic factors, such as isolation and area, have an indirect effect on animal body sizes, by influencing the identities and numbers of species that occur on islands (Raia and Meiri 2006).

There are 2 opposing arguments on the morphological difference between island and mainland species. The “island rule” describes a trend toward gigantism of small species and dwarfism of large species on islands (van Valen 1973). This rule represents the combined influences of ecological release (lacking competitors and predators), immigrant selection (small species likely to be limited by dispersal distances), thermoregulation and endurance climatic and environmental stress, and resource limitation (Lomolino et al. 2012). But the pattern is not general, especially for reptiles: snakes support the rule at the intraspecific level, whereas turtles and lizards disagree (Boback and Guyer 2007; Meiri 2007; Itescu et al. 2018).

The other argument “island syndrome” suggests that island species have a tendency toward greater body size, as higher population densities lead to reduced reproductive output (Adler and Levins 1994). Natural selection can alter female strategies with a change of population density (Chitty 1960; Sinervo et al. 2000). At high density, females favor laying fewer but high-quality offspring. At low density, females tend to lay many but small offspring. Thus, for life-history, island animals will shift toward “ K strategy”, selecting for offspring quality, rather than offspring number (MacArthur and Wilson 1967; MacArthur et al. 1972; Adler and Levins 1994; Slavenko et al. 2015). In reptiles, trait shifts following the predictions of the “island syndrome” are common. Island lizards lay smaller clutches of larger hatchlings than the closely-related similar-size mainland species (Raia et al. 2010; Novosolov et al. 2013; Schwarz and Meiri 2017). Meanwhile, lizards with different kinds of reproduction (variable/invariant clutch sizes) respond differently to “island syndrome”: lizards with variable clutch size decrease clutch size and increase egg volume and hatchling size; the other lizards decrease clutch size and increase brood frequency, but not hatchling or egg size (Schwarz and Meiri 2017).

Monitor lizards of the family Varanidae (containing 80 species that all belong to 1 genus, *Varanus*; Uetz and Hošek 2019) provide an ideal model for examining the role of mainland versus island in driving species evolution. This group inhabits mainland east to Africa and south to Australia continent, and also inhabits islands of all geological types (oceanic, land-bridge, and continental fragment islands) in New Guinea, Philippines, Indonesia, and Solomon Islands (Pianka et al. 2004; Koch et al. 2013). Varanid lizards have diversified into an exceptionally wide range of body sizes the smallest short-tailed monitor *Varanus sparnus* (116 mm snout–vent length [SVL]; Doughty et al. 2014) to the largest Komodo dragon *V. komodoensis* (1,540 mm SVL; Ciofi et al. 2007).

Here we hypothesize that island lizards differ from mainland species in evolutionary processes, morphological trait (body size), and life-history traits (clutch size and hatchling mass) using

phylogenetic comparative methods. We predict that: 1) since body size drives rapid diversification in groups, a link exists between body size-driven diversification and body size-frequency distributions 2) because of various environments on island, island species will have higher speciation, extinction, and dispersal rates, compared with mainland species; and 3) as a response to stronger intraspecific competition, island species will maximize individual ability associated with body size to outcompete closely-related species, and island species will produce smaller clutches of larger eggs to increase offspring quality.

Materials and Methods

Data collection

We collected the following morphology and life-history data of monitor lizards from published literature: largest SVL of males (60 species) and females (50 species), largest clutch size (44 species), and largest hatchling mass (35 species; Supplementary Table S1). For geographic state speciation and extinction (GeoSSE) analysis, we classified species as island (21 species), mainland (14 species), or both (25 species; Figure 1A), using distribution data from Lin and Wiens (2017) and distribution map of IUCN (<https://www.iucnredlist.org/>). For Brownian motion (BM), Ornstein–Uhlenbeck (OU), ordinary least squares (OLS), and phylogenetic generalized least square (PGLS) analyses, we classified species as mainland species (>80% of their distribution area is on the mainland) and island species (<20% of their distribution area is on the mainland, that is, excluding *V. dumerilii* and *V. salvator*).

We obtained a time-calibrated phylogeny from Lin and Wiens (2017), including 60 varanid species (75% of the 80 currently described species; Uetz and Hošek 2019). For each consequent analysis, we prune the phylogeny according to extant trait data, using packages “ape” (Paradis et al. 2004) and “geiger” (Harmon et al. 2008).

Body size-driven diversification

To determine if body size influences rates of species diversification, we used the quantitative state speciation and extinction (QuaSSE) model implemented in package “diversitree” (FitzJohn 2010, 2012) to examine continuous speciation rate. We used the lowest delta Akaike information criterion (Δ AIC) score to choose the best-fit model among models (see Supplementary Table S2) with following changes in speciation rate: constant (no relationship), linear (increases or decreases linearly), sigmoidal (with a sigmoidal curve) and hump (i.e., maximum rate occurs in median body size value), and 3 drift models.

We tested whether the pattern of body size evolution in island lizards differed from mainland species by fitting 2 BM models and 3 OU models using package “OUwie” (Beaulieu et al. 2012). Three key parameters describing morphological evolution in these models: the rate of adaptation to the optimal state (α), evolutionary rate (σ^2), and optimum value (θ). Single-rate BM (BM1) is the simplest BM model, with a single σ^2 . Multi-rate BM (BMS) is a complex BM model, with different σ^2 between the island and mainland. OU1 is the simplest OU model with a single θ . The OUM model has different θ , but with a single σ^2 for island and mainland species. Finally, the OUMV model is an OU model with different σ^2 and θ for island and mainland species. We sampled potential histories for distribution in proportion to their posterior probability (Huelsenbeck et al.

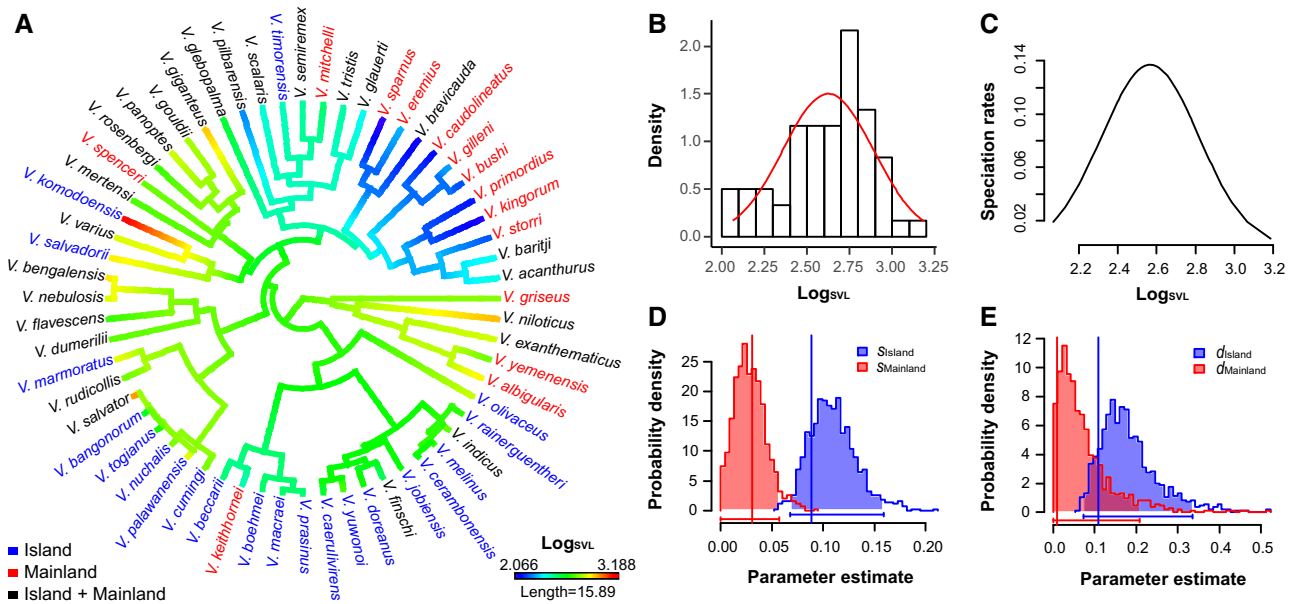


Figure 1. Phylogeny (A) is shown with colors indicating quantitative values for body size (SVL), colored fonts indicate regions [Lin and Wiens (2017) with some modifications]. Histogram of body size-frequency distributions (B), and the preferred models (C) of body size-driven diversification. Rates of speciation (D) and dispersal (E) for island and mainland varanids. Probability density plots are based on 1,000 MCMC samples of the best-fit model under GeoSSE.

2003) by creating 1,000 stochastic character maps with the *make-simmap* function in package “phytools” (Revell 2012).

Comparing diversification and dispersal between regions

We tested the differences in evolutionary processes (speciation, extinction, and dispersal rates) between island and mainland species using the GeoSSE model (Goldberg et al. 2011), implemented in package “diversitree” (FitzJohn 2012). The GeoSSE model is an extension of the binary state speciation and extinction model (Maddison et al. 2007), including 3 speciation parameters, 2 extinction parameters, and dispersal parameters. The speciation parameters s_{Island} and s_{Mainland} represent a species occurring on island or mainland; and s_{Btw} represents a species occurring on both islands and the mainland. The extinction parameters included in the model are x_{Island} and x_{Mainland} . Two dispersal parameters included the model are d_{Island} and d_{Mainland} , respectively, representing range expansion of island and mainland lineages. We tested a set of 13 distinct models (see Supplementary Table S3), all these 7 parameters can be allowed to vary freely or equally between island and mainland. We tested a model in which all parameters were free to vary, setting 1 or more parameters to be equal between 2 regions for a series of constrained submodels on this basis. We used the lowest ΔAIC score to choose the best-fit model. To account for model uncertainty, we sampled the posterior probability distribution of those parameters using Markov Chain Monte Carlo (MCMC), with a broad exponential prior (mean of 0.5), run for 1,000 generations.

Comparing traits evolution between regions

To test if reproductive traits differed between island and mainland species, we used both OLS and PGLS regressions, with clutch size and hatchling mass as the response variables, and female body size and region (island versus mainland) as the explanatory variables. The ecological settings of large islands resemble the mainland, because of numerous predators and competitors (Badano et al. 2005).

Hence we also run similar analyses for species inhabiting small islands (excluding islands $>50,000\text{ km}^2$; Novosolov and Meiri 2013) and the mainland. We performed all analyses using packages “caper” (Orme et al. 2018) and “rms” (Harrell 2015).

Results

Body size-driven diversification in varanids

Body size-frequency distributions have a hump-shaped pattern (Figure 1B). QuaSSE analysis indicates that the hump model ($w=0.40$) is preferred among the 7 models (constant, linear, sigmoidal, hump, and 3 drift models) of body size-driven diversification (Figure 1C, Supplementary Table S2). The hump-shaped trait-driven speciation model indicates that speciation rates are highest ($\lambda_{\text{max}}=0.137$) close to medium values (\log_{SVL} around 2.568), and lowest ($\lambda_{\text{min}}=0.007$) at extreme value, consistent with body size-frequency distributions (Figure 1B).

The mean body size of island species is 2.70 (log-transformation, Standard deviation [SD]=0.17), and that of mainland species is 2.56 (SD=0.30). The best-supported and simplest model (BM1 model, $w=0.40$) among the 5 models (BM1, BMS, OU1, OUM, and OUMV) indicates that neither the evolutionary rates nor the optimum values in body size differ between mainland and island varanids (Table 1).

Comparing diversification and dispersal between regions

GeoSSE analysis indicates that the best-supported model is the model setting equal extinction rate for islands and the mainland ($x_{\text{Island}}=x_{\text{Mainland}}$; Supplementary Table S3). In this model, the speciation rate is higher for island species (s_{Island} , range from 0.06 to 0.21 lineages Myr^{-1}) than for mainland species (s_{Mainland} , range from 4.54×10^{-5} to 0.09 lineages Myr^{-1}), and the speciation rate is low for species occurring on both islands and mainland (s_{Btw} ; Figure 1D, Supplementary Table S3). Dispersal from island to

Table 1. Model fit and estimated parameters of supported BM and OU models

Model	ΔAIC	w	σ^2		θ	
			Island	Mainland	Island	Mainland
BM	BM1	0	0.40	2.50×10^{-3}		2.743
	BMS	0.85	0.26	3.43×10^{-3}	1.90×10^{-3}	2.655 2.745
OU	OU1	2.00	0.15		2.52×10^{-3}	2.742
	OUM	3.12	0.08		2.47×10^{-3}	2.617 2.760
	OUMV	2.85	0.10	3.43×10^{-3}	1.90×10^{-3}	2.655 2.745

The parameters are: σ^2 , the rate of stochastic trait evolution; θ , the evolutionary trait optimum. BM and OU models are: BM1, the simplest BM model with a single σ^2 for the whole clade; BMS, a complex BM model, with different σ^2 for mainland and island species; OU1, the simplest OU model, with a single θ ; OUM, a complex OU model with a single σ^2 but different θ ; OUMV, a complex OU model with different σ^2 and θ . Parameter estimates are reported as mean across 1,000 stochastic maps generated using SIMMAP.

mainland (d_{Island}) is almost 10 times more frequent than dispersal from mainland to island (d_{Mainland} ; Figure 1E, Supplementary Table S3).

The island syndrome in varanids

PGLS analysis shows a strong influence of female body size on reproductive traits (clutch size: $r^2 = 0.366$, $F_{3, 40} = 7.681$, $P < 0.001$; hatchling mass: $r^2 = 0.844$, $F_{3, 31} = 56.08$, $P < 0.001$), with no significant interaction between region and female body size. We adopted the results of the PGLS model, for the ΔAIC value in the PGLS model was lower than that in the OLS model (Table 2). The PGLS model indicates that: 1) clutch size is smaller on islands than on the mainland; and 2) there is no significant difference in hatchling mass between island and mainland varanids, but island varanids show a trend of increased hatchling mass (Table 2; Figure 2A,B). When excluding species inhabiting large islands ($>50,000 \text{ km}^2$), the PGLS model provides a better fit than the OLS model, which indicates that: 1) clutch size is smaller on islands than on the mainland; and 2) hatchling mass is larger on island than on the mainland (Supplementary Table S4, Figure 2C,D).

Discussion

Body size distributions and speciation

Body size plays a major role in geographic range size (Gaston and Blackburn 1996; Inostroza-Michael et al. 2018), and evolutionary history, including speciation, extinction, and dispersal rates (Cardillo et al. 2005; Fontanillas et al. 2007; Wollenberg et al. 2011). Body size among closely-related species may influence body size-frequency distributions through changing evolutionary history. In this study body size-frequency distributions have a hump-shaped pattern (Figure 1B), which was consistent with the speciation pattern (Figure 1C). Using the QuaSSE algorithm, a hump-shaped model for speciation was chosen, with the fastest rate slightly above the intermediate size. There are 3 scenarios about the evolutionary tendency in body sizes. First, Cope's rule claims that body size increases over evolutionary time because the largest body size has the greatest fitness (Cope 1887; Brown and Maurer 1989; Avaria-Llautureo et al. 2012). Previous studies on Oryzomyini rodents (Avaria-Llautureo et al. 2012), mammals in general (Raia et al. 2012) and 2 common groups of snakes in North America (Crotalinae and Thamnophiini; Burbrink and Myers 2014) supported Cope's rule. Second, miniaturization hypothesis: a

lineage unusually prefers the evolution of small adult size (Yeh 2002). Animals with small body sizes have smaller and more strongly fragmented ranges because of limited dispersal capabilities and low physiological tolerances, facilitating reproductive isolation, and speciation (Wollenberg et al. 2011). The studies on therocephalians and Lampropeltini snakes supported miniaturization hypothesis. Ancestral therocephalian was a large macro-predator, and later evolved toward small body size (Brocklehurst 2019). Diversification in Lampropeltini snakes decreased with increasing body size (Burbrink and Myers 2014). Third, the highest speciation rate is at the modal body size, such as primates (FitzJohn 2010) and Serpentes (Feldman et al. 2016). Our results support this last scenario. In a certain amount of time for speciation, high speciation rate lead to high species richness, which could be attributable to great reproductive potential (e.g., Brown et al. 1993; cf. Jones and Purvis 1997), ecological dominance in terms of population density (Damuth 1993), small geographic range sizes (and thus high spatial turnover, e.g., Brown and Nicoletto 1991; Agosta and Bernardo 2013), and great variety of ecological niches available to medium-sized species (e.g., Hutchinson and MacArthur 1959). Overall, there exists a link between trait-driven diversification and body size-frequency distributions, and the highest speciation rate is at the modal body size.

In a multivariate context, BM is the best model not just when evolution proceeds according to BM, but also when evolution is so complex that a single, simplistic model works best (Adams and Collyer 2018). BM1 model indicates that either the evolutionary rates or the optimum values in body size do not differ between mainland and island varanids (Table 1), which do not support the "island syndrome." The "island rule" cannot be agreed or opposed by our results, because we do not have enough island-mainland pairs of closely-related species to test.

Island diversification and dispersal rates

Our GeoSSE analysis indicates that a model setting equal extinction rate for island and mainland species is preferred, whereas speciation and dispersal rates are higher for island species than mainland species (Supplementary Table S3). Higher extinction rates are found in insular and large-sized reptile species (Slavenko et al. 2016). Varanid lizards arose in Laurasia and subsequently spread to Africa and Australia, or arose in Gondwana and subsequently dispersed to other regions (Pianka et al. 2004). Molecular evidence indicates that varanid lizards disperse to Africa possibly via an Iranian route during 41 million years ago (Mya), and to Australia in the Late Eocene-Oligocene 32 Mya, consistent with an Asian origin (Vidal et al. 2012). Based on the phylogeny from Lin and Wiens (2017), the average node age is 4.211 (0.449–20.842) Mya for island species, and 8.153 (2.217–26.951) Mya for mainland species. The oldest varanid *V. griseus* (a node age of 26.951 Mya) is a mainland species, and the youngest *V. melinus* and *V. cerambonensis* (a node age of 0.449 Mya for both species) are island species (Lin and Wiens 2017). Given that varanids have originated on the mainland, mainland areas have more time to accumulate species.

The pattern of varanid species richness could be the result of the joint action of speciation time, speciation rate, and dispersal rate. As mentioned above, island species are younger than mainland species. Shorter time for island species to speciate and more frequently dispersal from island to mainland leads to lower species richness on island, whereas higher speciation rate for island species leads to higher species richness. These 3 factors result in roughly the same number of species between regions (39 on mainland and 46 on island, Figure 1A). Higher island dispersal may be related to considered

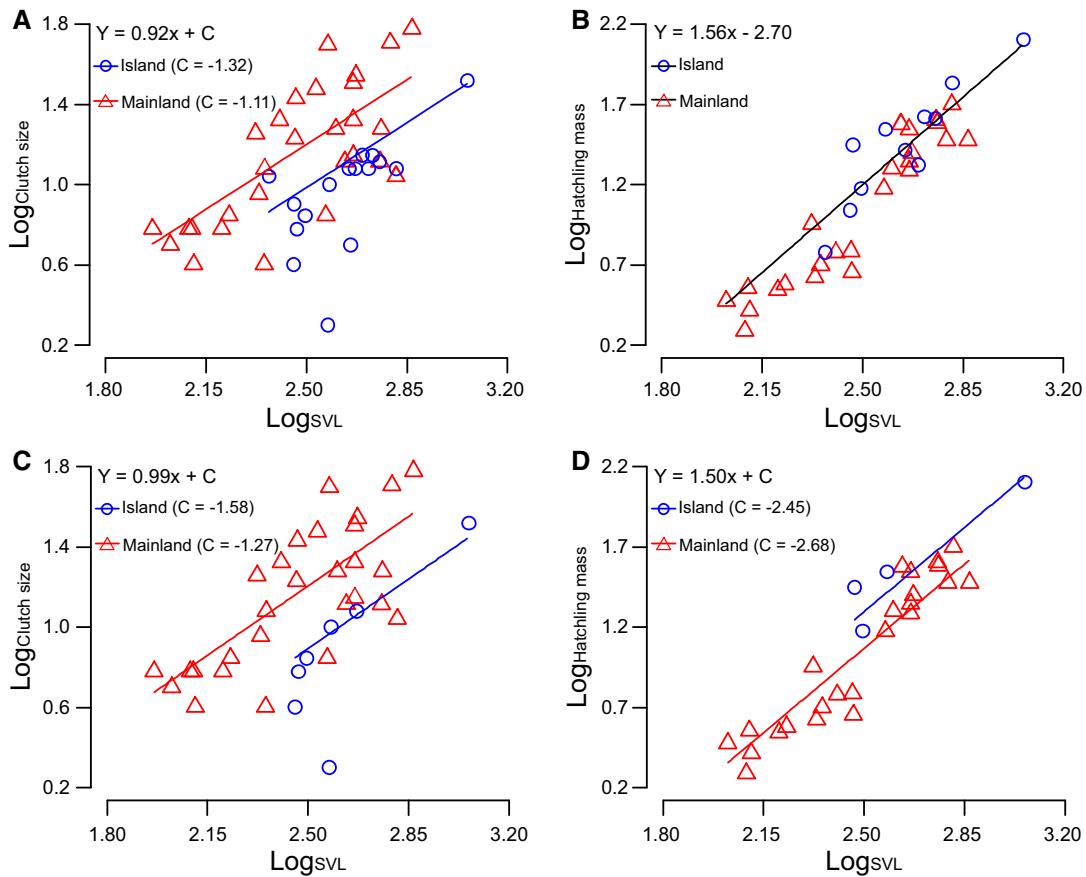


Figure 2. Relationship of clutch size and hatchling mass with female body size (SVL) on islands (blue circles) and the mainland (red triangles). Lines represent PGLS regressions, and 1 line was shown in Plot B because the difference between island and mainland species was not significant. (A, B) Results between all islands and mainland; (C, D) results between small islands (<50,000 km²) and mainland.

Table 2. Results for OLS and PGLS regressions of clutch size ($\logCS \sim \logSVL + \text{region}$) and hatchling mass ($\logHM \sim \logSVL + \text{region}$) evaluating the effect of region on reproductive traits

Regression variables	Model	N	lnLik	ΔAIC	w	λ	Slope (\pm SE)	r^2	F	P-value
Clutch size versus body size	OLS	44	3.88	6.23	0.04	–	0.98 (0.15)	0.54	23.73	<0.001
	PGLS	44	5.99	0	0.96	0.67	0.92 (0.19)	0.37	11.8	<0.001
Hatchling mass versus body size	OLS	35	16.58	7.25	0.03	–	1.68 (0.11)	0.89	135.1	<0.001
	PGLS	35	19.21	0	0.97	0.61	1.56 (0.13)	0.84	86.83	<0.001

anomalous climate (strong oceanic influence) for similar latitude and limited carrying capacity (Whittaker and Fernández-Palacios 2007). In summary, our results confirm that joint effect of differential macro-evolutionary rates shapes species richness pattern of varanid lizards, with higher speciation rate for island species, equal extinction rate, and more frequent dispersal from islands to mainland.

Our finding of extremely high island to mainland colonization rate is surprising. Unfortunately, the fossil record of varanids is unavailable at this time. Groups with a more complete record may offer a more robust system to test for differences in island and mainland dispersal using fossil data.

The island effect in life-history evolution

Our PGLS model analysis indicates that clutch size is smaller on islands than on the mainland, and that there is no significant

difference in hatchling mass between island and mainland varanids, but island varanids show a trend of producing larger hatchlings (Figure 2). That trend for the hatchling size is significant when excluding species inhabiting large islands (>50,000 km²) from the island species (Figure 2). Smaller clutch size and larger hatchling in island than in mainland species indicate that island varanids prefer offspring quality over quantity. Laying fewer but larger offspring is considered to be a combined result of stronger intraspecific competition and lower interspecific competition (MacArthur and Wilson 1967; Adler and Levins 1994; Schwarz and Meiri 2017). Offspring size is a crucial life-history trait because of its direct consequences for both parental and offspring fitness (Sinervo et al. 1992; Sakai and Harada 2004; Ji et al. 2007). Natural selection can favor females producing fewer, high-quality offspring (K strategy) at high density (Sinervo et al. 2000). Larger islands (mainland-like; Whittaker and Fernández-Palacios 2007) contain more competitors

and predators, and more available niches, reducing the effects of insularity. Our result suggests that island area impacts the effect of “island syndrome,” particularly in a specific clade.

In summary, our results confirm the joint effect of differential macroevolutionary rates on the formation of species richness pattern in varanid lizards, a link between trait-driven diversification and body size-frequency distributions, and the highest speciation rate in species with medium body sizes. Speciation and dispersal rates are higher in island species, whereas extinction rate does not differ between island and mainland species. Island varanids produce fewer but larger offspring, suggesting that offspring quality is more valuable than offspring quantity for island species.

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Author Contributions

L.-H.L. and X.J. conceived the ideas. X.J. supervised the study. X.-M.Z., Y.D., Y.-F.Q., H.L., J.-F.G., C.-X.L., and L.-H.L. collected and analyzed the data. L.-H.L. and X.J. wrote the article. All authors reviewed and contributed to editing of the manuscript and approved of its final publication.

Supplementary Material

[Supplementary material](https://academic.oup.com/cz) can be found at <https://academic.oup.com/cz>.

Conflict of Interest

The authors declare no conflict of interest.

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