RESEARCH PAPER

Evolution and ecology of lizard body sizes

Shai Meiri

NERC Centre for Population Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK

ABSTRACT

Aim Body size is instrumental in influencing animal physiology, morphology, ecology and evolution, as well as extinction risk. I examine several hypotheses regarding the influence of body size on lizard evolution and extinction risk, assessing whether body size influences, or is influenced by, species richness, herbivory, island dwelling and extinction risk.

Location World-wide.

Methods I used literature data and measurements of museum and live specimens to estimate lizard body size distributions.

Results I obtained body size data for 99% of the world's lizard species. The body size–frequency distribution is highly modal and right skewed and similar distributions characterize most lizard families and lizard assemblages across biogeographical realms. There is a strong negative correlation between mean body size within families and species richness. Herbivorous lizards are larger than omnivorous and carnivorous ones, and aquatic lizards are larger than non-aquatic species. Diurnal activity is associated with small body size. Insular lizards tend towards both extremes of the size spectrum. Extinction risk increases with body size of species for which risk has been assessed.

Main conclusions Small size seems to promote fast diversification of disparate body plans. The absence of mammalian predators allows insular lizards to attain larger body sizes by means of release from predation and allows them to evolve into the top predator niche. Island living also promotes a high frequency of herbivory, which is also associated with large size. Aquatic and nocturnal lizards probably evolve large size because of thermal constraints. The association between large size and high extinction risk, however, probably reflects a bias in the species in which risk has been studied.

Keywords

Body size, description dates, diversification rates, extinction risk, insularity, lizard diets, snout–vent length, size–frequency distributions, species richness.

*Correspondence: Shai Meiri, NERC Centre for Population Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK.
E-mail: s.meiri@imperial.ac.uk

INTRODUCTION

Body size is known to greatly influence many aspects of the morphology, physiology and ecology of organisms. Furthermore, size often is linked to the likelihood of speciation and extinction and to the rate of evolution, as well as to current levels of anthropogenically induced extinction risk (Stanley, 1973; Cardillo *et al.*, 2005; Olden *et al.*, 2007).

At large geographical and taxonomic scales, body size–frequency distributions are typically unimodal and right skewed on a logarithmic scale (Hutchinson & MacArthur, 1959; Gardezi & da Silva, 1999; Olden *et al.*, 2007. cf. Roy *et al.*, 2000; Boback & Guyer, 2003). Thus most species are smaller than the midpoint and mean of the size range. Most research on global-scale patterns of size distributions has focused on vertebrates and sampling is relatively complete for birds (65% of species; Maurer, 1998), mammals (73% of extant and historically extinct species; Smith *et al.*, 2003) and fishes (81%; Olden *et al.*, 2007). However, although lizards have featured prominently as model organisms in studies of the evolution of body size (e.g. Schoener, 1969; Case,

1978, Espinoza *et al*., 2004; Meiri, 2007) there have been no efforts to study patterns of size evolution for the whole group (but see Avery, 1996, and Greer, 2001 for skinks).

Here I examine the shape of the size–frequency distributions of lizards at the global and continental scales, both for the group as a whole and at the family level, where most of the variation of lizard body size lies (Dunham *et al*., 1988 and see below). I use these distributions to test the following hypotheses.

Body size and species richness

Because in many groups most species are small (Hutchinson & MacArthur, 1959; Stanley, 1973), and small animals have high rates of molecular evolution (Fontanillas *et al*., 2007), it is often thought that small size promotes high speciation rates (e.g. Maurer *et al*., 1992). However, Orme *et al*. (2002) have shown that richness is usually not associated with body size when clade ages and phylogenetic affinities are modelled. I therefore test for the association between body size, species richness and diversification rates.

Ecological correlates of body size

Small lizards can gain heat more quickly, but will also tend to lose heat quicker than larger ones. Therefore it is reasonable to expect body size to interact with factors related to thermal regimes such as daily activity patterns. Smaller size may facilitate faster heating and cooling rates in diurnal lizards (Huey & Slatkin, 1976), which are likely to be thermoregulators. Nocturnal lizards may be more likely to be thermoconformers (Huey & Slatkin, 1976), and thus less affected by body-size related cooling and heating rates. Thus I predict that diurnal species will be smaller to facilitate faster heating. Likewise aquatic species may be more likely to be affected by fast cooling. I therefore hypothesize they will tend to be large, to reduce the rates of heat loss. Fossorial habits are thought to be associated with large size (Dunham *et al*., 1988), perhaps because fossorial lizards often have reduced legs, and serpentiform movement is easier at large sizes (Avery, 1996; Greer, 2001). I therefore examine whether the use of space influences lizard size.

Some authors report that viviparous lizards are larger than oviparous ones (e.g. Shine, 1985; Dunham *et al*., 1988). Greer (2001) hypothesized that viviparity is difficult to fit into the short life cycle of very small species, and that over the long development times needed by large species embryos may be safer within the mother's body than inside a nest. However, his finding that small size may be constrained by minimum egg size can suggest that oviparous species are constrained to larger sizes (see also Kratochvil & Frynta, 2006).

While most lizards are carnivorous, Cooper & Vitt (2002) estimated that some 12% of lizard species include a significant amount of plant material (> 10%) in their diets. Plant consumption in lizards has frequently been associated with large body size (Sokol, 1967; Van Damme, 1999), and it is often assumed that large size is required for lizards to efficiently process plant material, or that herbivory allows lizards to grow large, or both (Pough, 1973; Cooper & Vitt, 2002; Herrel *et al*., 2004). This view

has been challenged by Espinoza *et al*. (2004), studying the evolution of herbivory in small-sized lizards of the genus *Liolaemus*. I therefore test whether there are associations between lizard size and activity times, use of space, mode of reproduction and dietary preferences.

Body size and insularity

Island living is thought to enable lizards to evolve large sizes in the absence of mammalian predators (Szarski, 1962; Pregill, 1986; Greer, 2001). However, cases of insular dwarfism are also well known (Hedges & Thomas, 2001). I test whether insular lizards tend to occupy more extreme sizes than mainland lizards (as was found intraspecifically; Meiri, 2007), or whether insular lizards tend to be show less extreme sizes than mainland ones, as predicted by theories of optimal body size (Marquet & Taper, 1998; Lomolino *et al*., 2005, cf. Meiri *et al*., 2005). These theories invoke the island rule to suggest that small taxa evolve larger size and large ones evolve smaller sizes on islands, a process that will result in insular size distribution tending towards medium body sizes (Price & Phillimore, 2007). I further test whether extreme sizes are more likely to have evolved on islands lacking mammalian carnivores.

Body size and extinction risk

Large size has often been associated with anthropogenically induced extinction risk (Cardillo *et al*., 2005; Olden *et al*., 2007). Many lizard species that went extinct in recent times were among the largest in their clades (Case *et al*., 1998). I therefore test whether current levels of threat are associated with lizard body size. Because risk status is published for only a small number of lizard species, this analysis may be biased if small species are less likely to have been assessed or described (e.g. Reed & Boback, 2002). However, if there is no such bias, or if most newly described species result from well-known species being split, then no relationship between size, description date and threat will be found.

METHODS

Data

I used data obtained from published literature on the body size of lizards (Appendix S1 in Supplementary Material), and supplemented it by measurements of live lizards (mostly at the Meier Segal's Garden for Zoological Research, Tel-Aviv University), museum specimens and personal communication with museum curators. Taxonomy follows Uetz (2006).

Snakes and amphisbaenians probably evolved from lizards (e.g. Townsend *et al*., 2004; Kumazawa, 2007; but see Zhou *et al*., 2006, who found snakes and lizards are sister taxa). However, these taxa are highly derived (e.g. in respect to life history and skull kinetism; see Dunham *et al*., 1988, Zug *et al*., 2001, and Pough *et al*., 2003), and are both, on average, much larger than lizards (Avery, 1996). Using the Squamata as a whole, while making the group examined monophyletic, may therefore

obscure rather than clarify the forces affecting size evolution (see below). The omission of highly morphologically and ecologically derived taxa is commonplace in macroecology. For example, marine mammals and bats are often omitted from studies of mammals (e.g. Brown & Maurer, 1989), seabirds are routinely omitted from studies of birds (Orme *et al.*, 2006) and tetrapods are excluded from studies of fishes (Olden *et al.*, 2007). I therefore excluded amphisbaenians and snakes from the analyses.

I used maximum snout–vent length (SVL; in mm, log-transformed in all analyses) as a measure of size. Maximum SVL is a good measure of the size potential in a population, and is tightly correlated with mean adult SVL and SVL at sexual maturity (Greer, 2001). Although this index is sensitive to unequal sample sizes (Stamps & Andrews, 1992; Meiri, 2007) it is reasonable that such sampling effects are relatively minor when species across the lacertilian size range are compared. Furthermore, maximum SVL is by far the most common size index reported for lizards (author's unpublished work). Moreover, measurements of juveniles are often included when mean SVLs are reported, but this is not always stated explicitly. Mass data for adults are also hard to come by (I obtained mass data for only 615 species), and I therefore used maximum SVL throughout. I included estimates of maximum SVL for recently extinct species and populations (see Pregill, 1986), if these species were included in the taxonomy I use (Uetz, 2006).

Distribution data from Uetz (2006) and regional guides (Appendix S1) were used to assign each species to a continent and to determine whether it is endemic to islands. Data on the presence or absence of mammalian carnivores from islands were from Meiri *et al.* (2005), discarding historic introductions. Biological data were from the same sources used to derive body-size (Appendix S1).

I classified lizards as either diurnal or nocturnal, with crepuscular and cathemeral species regarded as nocturnal because they are active when basking is impossible. I used five categories of space use: fossorial, scansorial (arboreal and/or saxicolous), terrestrial, semi-aquatic and variable (species active in more than one of the above categories). Dietary categories followed Cooper & Vitt (2002): predators (< 10% plant material or species that, e.g., 'occasion-ally' take plants), omnivores (10–50% plant material, species described as 'omnivorous' etc.) and herbivores (> 50% plant materials). Species are classified as either oviparous or viviparous (including ovoviviparous). Species showing both modes (*n* = 14) were omitted.

Because quantitative data regarding lizard ecology are mostly lacking, and when they are reported sometimes show considerable intraspecific variation, the categorizations for all biological attributes are best viewed as qualitative.

Analyses

All analyses were conducted in R 2.7.0. (R Development Core Team, 2007). I described the shape and moments of central tendency of the lizard body size–frequency distribution and examined the variance attributed to different levels of the taxonomic hierarchy using the R package 'ape'.

I examined the relationship between SVL and species richness within both families and genera. To account for phylogenetic structure (Orme *et al.*, 2002) I repeated the analysis using the family-level phylogeny of Townsend *et al.* (2004). Because some recognized lizard families are polyphyletic in the Townsend *et al.* (2004) phylogeny I used subfamily data from Uetz (2006) in the phylogenetic comparative analysis. Phylogenetic data are insufficient to explore the relationship at lower taxonomic levels. For the family-level analyses I used a generalized least squares method to test, and account for, the strength of phylogenetic non-independence in the model using the scaling parameter λ (Freckleton *et al.*, 2002). I estimated and applied the maximum likelihood value of λ using R code written by R. P. Freckleton. I calculated the within-family diversification rate as log(species richness)/family age. In another analysis I used family species richness as the response.

I used mixed-effects models with species nested in genera and families to best control for evolutionary relationships because species-level phylogenies are mostly lacking. When studying ecological attributes I used only species for which I had data on all relevant traits.

Data on the extinction risk were from the IUCN Red Data Book (Cox *et al.*, 2006). Because data were scarce (only 358 species assessed) I repeated the analyses for two additional groups: Iguanidae, which is the family (except Helodermatidae, *n* = 2) with the highest proportion of lizards with an IUCN assessment (24 of 36 species, 67%), and Mediterranean endemics, for which risk data were recently published (Cox *et al.*, 2006). I analysed risk data by assigning codes to risk categories: least concern (and LR/lc), 1; near threatened (and LR/nt), 2; vulnerable, 3; endangered, 4; critically endangered, 5; and extinct, 6 (no lizards are listed as extinct in the wild). I also compared threatened lizards (categories 3–6 above) with non-threatened (categories 1–2), data-deficient (DD) and never-assessed species.

RESULTS

Body size–frequency distributions

Data on the maximum SVL of 4875 species of lizards (99% of the 4916 species recognized by Uetz [2006], 457 of 459 genera) are shown in Appendix S2. The largest specimen in a species is a male in 1249 species and female in 943 (including 32 partheno-genetic species). Otherwise the sex of the largest specimen is not reported. I was unable to obtain size data for 15 species, four of which I considered invalid (including members of the mono-typic genera *Oreodeira* and *Chabanaudia*). Twenty-six species, as far as I know, are only known from juveniles, and were not analysed (see Appendix S3 for exclusions). Mean lizard SVL is 91 mm (median 74 mm). The mean of the log-transformed values was 1.89 (77 mm). The smallest lizard was *Sphaerodactylus elasmorhynchus* (maximum SVL 17 mm) and the largest was *Varanus komodoensis* (1540 mm). The family (*n* = 26) was the level where most of the variation in lizard size resided: 47.4% of the variation in maximum log(SVL) lay at this level, compared with 34.8% at the genus level and 17.7% at the species level.
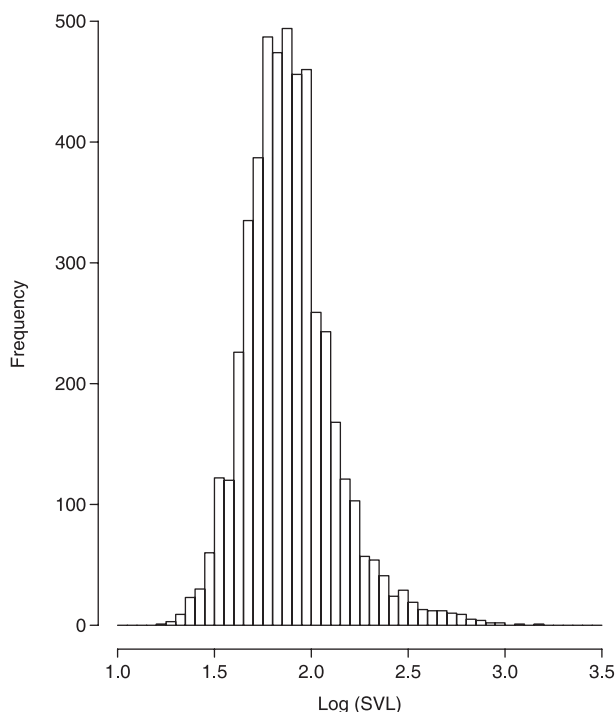
Figure 1 Body size–frequency distribution of all lizards ($n = 4875$ species). Size is the $\log_{10}$(snout–vent length) (SVL) in mm.

The body size–frequency distribution for the Sauria was highly modal, right skewed and leptokurtic (Fig. 1). Nine out of 16 families with at least 30 species (taxonomy follows Uetz, 2006) had a significantly right-skewed body size–frequency distribution (Fig. 2). Five families showed significant kurtosis: four had leptokurtic distributions, while the Phrynosomatidae distribution was platykurtic (Table 1).

Lizards inhabiting different realms come in different sizes, and there was a significant interaction between family and geography (two-way ANOVA, family d.f. = 25, $F = 116.47$, $P < 0.0001$; realm d.f. = 7, $F = 26.17$, $P < 0.0001$; interaction d.f. = 37, $F = 11.64$, $P < 0.0001$). Nearctic lizards were the largest ($n = 154$, mean $\log$(SVL) = 100 mm) while Malagasy and Neotropic ones were the smallest (73 mm). All realms (except Madagascar, $P = 0.068$) were characterized by significantly right-skewed body size–frequency distributions, and all distributions except for that of Madagascar were significantly leptokurtic (Table S1).

Body size and species richness

There was a strong negative correlation between log(species richness) within families (using numbers of all the species in each family, not only sampled ones) and SVL (mean SVL, $n = 26$, $r = -0.695$, $P < 0.0001$; median SVL $r = -0.691$, $P < 0.0001$). However, there was only a weak correlation between SVL and log(species richness) within genera (Fig. 3) [mean log(SVL) of sampled species versus log total number of species per genus, including missing species. $n = 457$, $r = -0.045$, $P = 0.036$, for

medians $r = -0.103$, $P = 0.028$]. Within families with at least 10 genera ($n = 9$), only skinks (Scincidae) showed a significant negative relationship between species richness within genera and average SVL of the genus. Gymnophthalmids had a significant positive relationship. The mean of the nine slopes was $-0.573 \pm 0.367_{SE}$.

The taxa used in the phylogenetic comparative analysis and data for node ages (stem age), richness, diversification rates and SVL are shown in Appendix S4. The maximum likelihood value of lambda ($\lambda < 0.001$) did not differ significantly from zero for either mean or median SVL (likelihood ratio statistic, 1 df, $\chi^2 < 0.001$, $P > 0.99$ for both). Setting λ to its maximum likelihood value resulted in significant negative relationships between diversification rate [log(species richness) divided by stem age] and SVL [$n = 31$ clades; median SVL, slope = -0.024, $r^2 = 0.21$, $P = 0.009$, Akaike information criterion (AIC$_c$) = -181.3; mean SVL, slope = -0.024, $r^2 = 0.17$, $P = 0.012$, AIC$_c$ = -180.9]. Setting λ to 1 (equivalent to an independent contrast analysis; Freckleton *et al.*, 2002) also resulted in negative relationships between size and diversification rates (median SVL, slope = -0.028, $r^2 = 0.15$, $P = 0.029$, AIC$_c$ = -163.9; mean SVL, slope = -0.028, $r^2 = 0.14$, $P = 0.035$, AIC$_c$ = -163.5).

The number of species in each clade was negatively correlated with log(SVL) setting λ to its maximum likelihood ($\lambda < 0.001$ for both median and mean SVL; median SVL, slope = -2.32, $r^2 = 0.54$, $P < 0.0001$, AIC$_c$ = 56.8; mean SVL, slope = -2.38, $r^2 = 0.53$, $P < 0.0001$, AIC$_c$ = 57.3). Setting $\lambda = 1$ still resulted in a strong negative relationship between richness and body size (median SVL, slope = -2.12, $r^2 = 0.35$, $P = 0.0004$, AIC$_c$ = 70.6; mean SVL, slope = -2.17, $r^2 = 0.34$, $P = 0.0006$, AIC$_c$ = 71.1). Taxon age was not a significant predictor of richness in these models.

There was no relationship between species richness within a family and the average number of species in genera ($r = 0.12$, $P = 0.55$), and no relationship between the mean number of species per genus within families and mean SVL within families ($r = -0.02$, $P = 0.91$). Thus small body within lizard families was associated with high genera richness (both variables log-transformed, $n = 26$, slope = -0.118, $R^2 = 0.45$, $P = 0.0002$).

Ecology

Using mixed-effectss models with ecological variables nested within families and genera, I first examined univariate models, where maximum sample sizes could be attained. Viviparous lizards were no larger than oviparous ones ($t = 0.97$, d.f. = 2163, $P = 0.33$). Nocturnal lizards were larger than diurnal ones ($t = 2.54$, d.f. = 1844, $P = 0.011$). Space use was significantly related to body size, with planned comparisons showing that semi-aquatic lizards are larger than lizards in the other categories ($t = 5.90$, d.f. = 2786, $P < 0.0001$). Fossorial species were no different in size from species in the rest of the categories ($t = 0.79$, $P = 0.43$), species in the 'variable' space use category were larger than scansorial and terrestrial ones ($t = 2.41$, $P = 0.016$), and scansorial species were larger than terrestrial ones ($t = 2.40$, $P = 0.016$). Diet significantly affected size, with planned comparisons showing that species incorporating plants in their

Table 1 Body size of lizard families; moments of central tendency.

Family	Number of species	Sampled species	Mean log(SVL)	SE	Median log(SVL)	g_1	$P(g_1)$	g_2	$P(g_2)$	CV
All lizards	4916	4876	1.89	0.003	1.87	0.88	< 0.0001	2.08	< 0.0001	12.14
Agamidae	394	386	2.00	0.01	1.97	0.36	0.00	−0.06	0.80	9.81
Anguidae	114	113	2.11	0.02	2.06	0.63	0.01	0.01	0.97	8.97
Anniellidae	2	2	2.20	0.05	2.20	NA	NA	NA	NA	3.21
Chamaeleonidae	162	161	1.93	0.02	1.90	0.11	0.56	−0.33	0.40	12.31
Cordylidae	55	55	1.97	0.02	1.95	0.85	0.01	0.40	0.55	6.16
Corytophanidae	9	9	2.24	0.05	2.28	NA	NA	NA	NA	6.80
Crotaphytidae	10	10	2.09	0.02	2.10	−0.32	0.69	−1.07	0.51	2.31
Dibamidae	21	21	2.12	0.03	2.11	0.07	0.89	−1.42	0.20	5.64
Gekkonidae	1115	1107	1.76	0.01	1.76	0.22	0.00	−0.02	0.89	11.23
Gerrhosauridae	33	33	2.05	0.03	1.99	0.37	0.40	−1.05	0.23	9.33
Gymnophthalmidae	206	206	1.77	0.01	1.77	−0.14	0.41	−0.32	0.34	7.59
Helodermatidae	2	2	2.62	0.06	2.62	NA	NA	NA	NA	2.97
Hoplocercidae	11	11	2.11	0.02	2.13	−0.14	0.86	−1.47	0.35	2.78
Iguanidae	36	36	2.51	0.03	2.52	−0.08	0.84	−1.26	0.13	8.06
Lacertidae	285	284	1.86	0.01	1.83	2.05	< 0.0001	7.95	< 0.0001	7.96
Lanthanotidae	1	1	2.60	NA	2.60	NA	NA	NA	NA	NA
Opluridae	7	7	2.09	0.04	2.07	NA	NA	NA	NA	4.69
Phrynosomatidae	128	128	1.91	0.01	1.91	0.22	0.32	−0.91	0.037	6.59
Polychrotidae	394	389	1.83	0.01	1.80	0.69	< 0.0001	−0.13	0.61	9.20
Pygopodidae	37	37	2.11	0.02	2.08	0.82	0.049	0.41	0.62	7.11
Scincidae	1345	1331	1.87	0.01	1.85	0.70	< 0.0001	0.88	< 0.0001	10.63
Teiidae	122	121	2.05	0.02	2.03	1.20	< 0.0001	1.60	0.0005	10.59
Tropiduridae	333	333	1.92	0.01	1.92	0.15	0.27	0.62	0.02	5.81
Varanidae	63	62	2.58	0.03	2.60	−0.07	0.82	−0.64	0.31	10.04
Xantusiidae	24	24	1.88	0.03	1.89	−0.17	0.74	−1.14	0.27	8.68
Xenosauridae	7	7	2.14	0.08	2.06	NA	NA	NA	NA	9.53

SVL, snout–vent length; SE, standard error; g_1, skewness; g_2, kurtosis, CV, coefficient of variation. *P* values for these statistics are deviations from normality, and were calculated using their standard errors by way of *t*-tests.

diet were significantly larger than strict predators ($t = 8.53$, d.f. = 1543, $P < 0.0001$). Herbivores were marginally but non-significantly larger than omnivores ($t = 1.75$, $P = 0.080$).

Data for all ecological variables were only available for 1128 species. Using mixed-effects models with ecological variables nested within families and genera, viviparous lizards were larger than oviparous ones but the difference was marginally non-significant ($t = 1.91$, d.f. = 818, $P = 0.057$). Nocturnal lizards were larger than diurnal ones ($t = 2.67$, $P = 0.008$), carnivorous lizards were smaller than omnivores and herbivores ($t = 7.87$, $P < 0.0001$) and omnivores were smaller than herbivores ($t = 3.49$, $P = 0.0005$). Semi-aquatic lizards were larger than other species ($t = 4.99$, $P < 0.0001$), and there were no significant differences between sizes within the other categories of space use (*t*-values between 0.06 and 0.84, $0.39 < P < 0.96$).

Using lizard species for which I had detailed dietary data, there was a positive correlation between the percentage of plants in the diet and SVL (ANCOVA with family as a factor, slope for the percentage of plants = 0.37, $n = 84$, $t = 5.42$, $P < 0.0001$, partial R^2 for the percentage of plants = 0.205, partial R^2 for family = 0.176). Within the genus *Liolaemus*, in which Espinoza *et al.*

(2004) found no association between body size and herbivory, omnivorous and herbivorous species were larger than strict predators (79 mm vs. 73 mm) but this result was marginally non-significant ($t_{63,40} = 1.78$, $P = 0.079$).

Body size and insularity

Island-endemic lizards and lizards inhabiting mainlands were similar in size [mean log(SVL) 75 mm vs. 78 mm, mixed-effects model, $t = 0.36$, d.f. = 4417, $P = 0.72$]. The size–frequency distributions of island endemic ($n = 1479$) and mainland lizards ($n = 3396$), however, were significantly different (Fig. 4; Kolmogorov–Smirnov $D = 0.088$, $P < 0.0001$). Dividing lizards into 10 size classes at 30-mm intervals (except the 10th class > 270 mm), the first and tenth classes contained many more island endemics (54 and 53 species, respectively versus 50 and 73 species of continental lizards in these classes) than expected by chance given continental lizards outnumber island endemics 2.29 to 1 (overall $\chi^2 = 73.1$, d.f. = 9, $P < 0.0001$). Thus island endemic lizards tended to have a less clumped size distribution than lizards inhabiting mainlands.
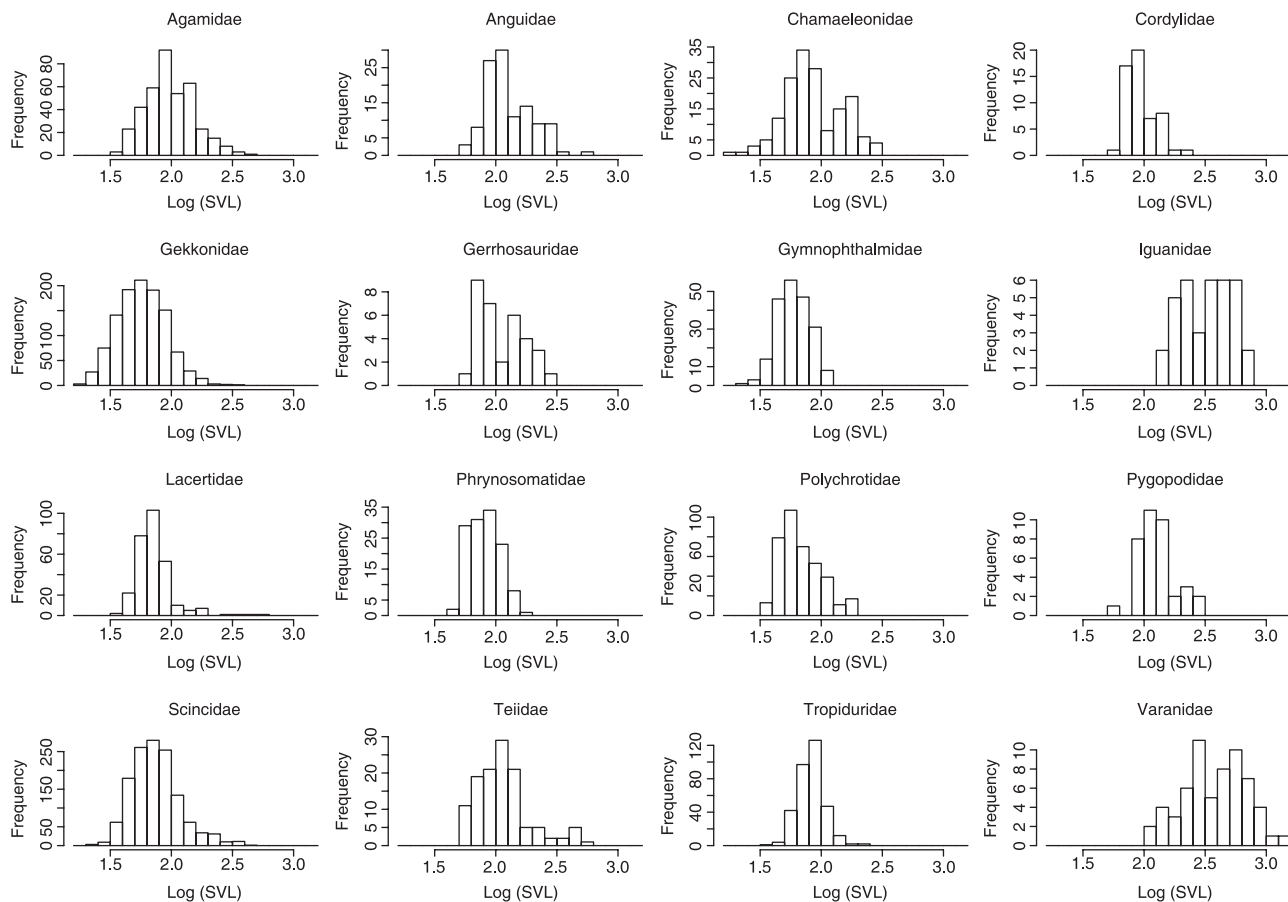
Figure 2 Body size–frequency distribution within lizard families with at least 30 species. Size is the $\log_{10}$(snout–vent length) (SVL) in mm.
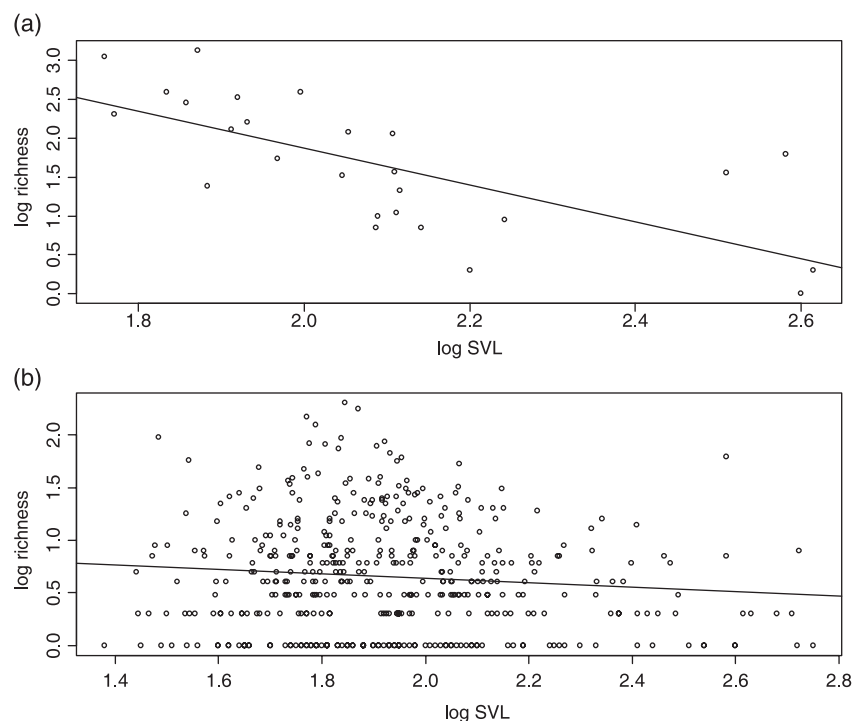

Figure 3 Relationship between body size and species richness. Species richness (log transformed) versus mean body size [log(snout vent length) (SVL), in mm] within (a) lizard families and (b) lizard genera.
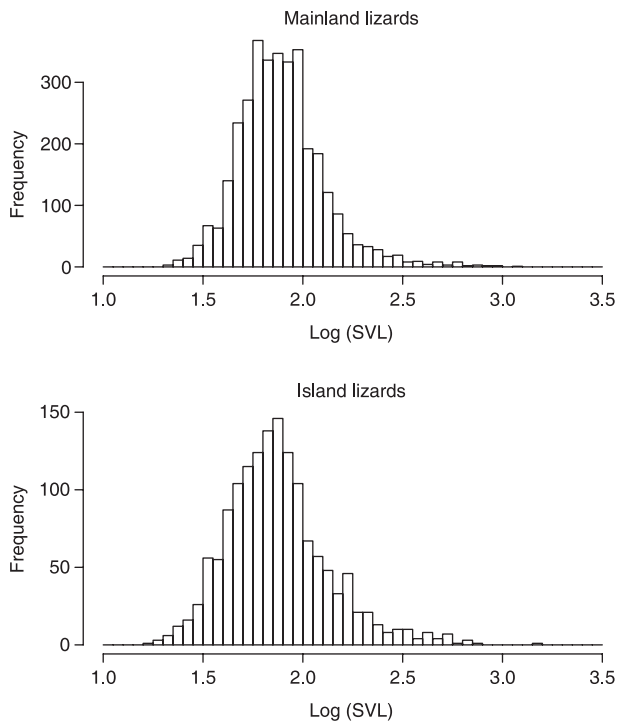
Mainland lizards

Island lizards

Figure 4 Body size–frequency distribution of lizards inhabiting continents (top) versus size–frequency distribution of island-endemic lizards (bottom). SVL is snout–vent length.

Lizards inhabiting carnivore-free islands ($n = 769$, mean log(SVL) 73 mm) were similar in size to island endemics from islands inhabited by mammalian carnivores ($n = 710$, 76 mm, mixed-effects model, $t = 1.30$, $P = 0.19$). Again, however, the size–frequency distributions of island endemics on islands with and without carnivores were significantly different ($D = 0.09$, $P = 0.003$, Fig. S1). The first and tenth classes contained fewer lizards from islands with mammalian carnivores (15 and 13, versus 39 and 40, respectively, on islands lacking carnivores) than expected by chance (overall $\chi^2 = 31.8$, $P = 0.0002$).

In none of the dietary categories were insular lizards different in size from mainland ones (mixed-effects models, predators, $t = 0.56$, d.f. = 1208, $P = 0.58$; herbivores, $t = 1.09$, d.f. = 67, $P = 0.28$; omnivores, $t = 0.47$, d.f. = 172, $P = 0.64$). However, the relative frequency of insular herbivores and omnivores (11% and 23% of the species, respectively) was much higher than that of continental herbivores and omnivores (4% and 11% of the species, respectively, $\chi^2 = 69.3$, d.f. = 2, $P < 0.0001$); thus carnivorous and omnivorous lizards were not larger on islands but they formed a much larger part of insular lizard faunas.

Extinction risk

Extinction risk increased with body size ($n = 358$, $R^2 = 0.08$, $P < 0.0001$), even when familiar and generic relationships were accounted for (mixed-effects model, $t = 2.07$, $P = 0.04$). Threatened lizards (128 mm, $n = 147$) were larger than non-threatened ones (93 mm, $n = 210$), DD species (83 mm, $n = 41$) and unassessed species [75 mm, $n = 4477$; $F_{3,4871} = 60.2$, $P < 0.0001$, Tukey honestly significant difference (HSD), $P < 0.001$ for all comparisons]. Non-threatened species were larger than unassessed ones (Tukey HSD, $P < 0.0001$), but data-deficient species were not different from either of these categories (Tukey HSD, DD versus non-threatened $P = 0.54$, DD versus non-assessed $P = 0.63$).

Within the Iguanidae there was no significant difference between threat categories ($F_{2,33} = 1.35$, $P = 0.27$). Neither was there a correlation between the degree of threat and SVL in Mediterranean lizards (DD species omitted, $n = 201$, $t = 0.53$, $r = 0.04$, $P = 0.60$).

Description dates were negatively correlated with SVL ($n = 4875$, $r = -0.29$, $P < 0.0001$). Nevertheless, when only lizards described since 1900 were considered, no significant effect of description year remained ($n = 2864$, $r = -0.01$, $P = 0.65$).

DISCUSSION

Lizards show a similar size distribution to that of many other taxa. Global, realm-specific and family-level distributions are mostly unimodal and right skewed. It is reasonable to assume that amniotes cannot grow significantly smaller than the smallest lizards (Pough, 1980; Greer, 2001; Kratochvil & Frynta, 2006) and thus that the decline in species numbers towards the smaller sizes may reflect a limitation on miniaturization (Stanley, 1973).

There are many more small lizard species than large ones (the mode is smaller than the mean and range midpoint in most families and realms), and families of small lizards contain more species than families of large lizards, even when phylogenetic effects are accounted for. High diversification rates are likewise associated with small body size. (cf. Orme et al., 2002). There is, however, little relationship between body size and richness of genera within families, as was previously found in agamids (Stuart-Fox & Owens, 2003). Thus genera richness, rather than high within-genera richness, leads to elevated species richness in small-bodied families. It may be that genera within families are ecologically distinct from one another whereas congeneric species share similar ecologies. If congenerics are also often allopatric, then perhaps the smaller size of lizards in species-rich families is a consequence of more niches being available to small-bodied genera. Alternatively, it may tell us more about taxonomic practice than about ecology and evolution. This supports Hutchinson & MacArthur's (1959) assertion that richness is related to the number of niche types, which peaks for small-bodied (but not the smallest) taxa.

The tendency of semi-aquatic lizards to be large may be explained by the relatively slow cooling rates of large species. Because heat loss is much more rapid in water, small species may not be able to maintain sufficient heat in aquatic habitats. Similarly, the smaller size of diurnal lizards may facilitate faster heating rates (Huey & Slatkin, 1976), whereas cooling is relatively less important for animals active during the hot hours of the day. Results of the dietary analysis support the hypothesis of a strong association between plant feeding and large body size in lizards (Sokol, 1967; Pough 1973; Cooper & Vitt, 2002). Phylogenetic

comparative analyses of some lizard groups also support such an association (e.g. Herrel *et al.*, 2004, but see Espinoza *et al.*, 2004). While the association of large size and herbivory seem well supported, it is not clear whether large size is an adaptation to herbivory, or whether large size evolved for other reasons, and enabled herbivory. Large lizards have more diverse prey size than smaller ones (Vezina, 1985; Vitt, 2000), and are more likely to include both invertebrates and vertebrates in their diet (S Meiri, unpublished). They are thus perhaps pre-adapted to dealing with more varied diets, including plant material.

Island lizards often evolve very small and very large sizes. This corroborates the conclusion of Arnold & Ovenden (2004) that large lizards often tend to evolve on predator-free islands. Lizards are likewise thought to grow large on islands where large prey or abundant food sources exist (Case & Schwaner, 1993; Raia & Meiri, 2006; Meiri 2007). The very large sizes attained by some insular lizards may result both as a direct response to release from predation (Case, 1982), and from lizards on mammalian-carnivore free islands being able to occupy the niche of the island top predator (e.g. *Phoboscincus bocourti*, *Varanus komodoensis*). Large lizards may also be better dispersers, which may help explain why, while islands have more large, herbivorous species than expected by chance, there are no differences between the sizes of insular and continental lizards within dietary categories. That islands also promote the diversification of very small lizards is more difficult to explain, as small size can be an anti-predatory adaptation in itself (Heaney, 1978). Extremely small size in island lizards may be an adaptation to a general shortage of insects (Janzen, 1973; Olesen & Valido, 2003). However, small insular lizards are often extremely abundant (Bennett & Gorman, 1979; Rodda *et al.*, 2001), so food shortage may not be a general characteristic of islands. Release from competition with homeo-therms is unlikely, as small lizards are much smaller than the smallest birds and mammals (Pough, 1980). It may be that small size often evolves on islands to facilitate feeding on very small arthropods (Janzen, 1973). Perhaps competition with amphibians and other arthropod predators is reduced on islands, but currently I have no data to support this hypothesis. Be that as it may, contrary to the expectation of theories of optimal body size (Marquet & Taper, 1998; Boback & Guyer, 2003, cf. Meiri *et al.*, 2005, 2006), islands seem to harbour an unusual number of both extremely small and very large lizards. I suspect that release from predation and the nature of the resource base on islands may drive the evolution of small size in predatory species, as well as that of very large size in both herbivores and vertebrate-eating species.

While most recently extinct lizards were large (mean size of extinct lizards is 190 mm, *n* = 17) the results of this study do not lend strong support to an association between large size and high extinction risk. Where relatively complete data exist, large size is not associated with risk. The relationship between risk and SVL is weak, and probably biased: risk in the vast majority of lizard species is not assessed and both non-assessed and DD species are small. Thus I suspect that there has been a greater tendency to assess the conservation status of large species.

The results of this study may be questioned if maximum SVL is a poor size index, or if a great many species still await description

and these are different in size from those I sampled. Maximum SVL disregards shape, which may strongly affect weight (Greer & Wadsworth, 2003). In 75 live lizards belonging to 21 species (in eight families, 24–530 mm SVL, 0.4–1760 g) I have measured, SVL explained 95% of the variation in body mass. However, the masses predicted for two specimens of the legless anguid *Pseudopus apodus* were 2.9 and 4.0 times their actual masses. Probably, however, across the six orders of magnitude of lizard body masses discrepancies between mass and SVL are relatively minor. Because maximum SVL is highly sensitive to sample size (Stamps & Andrews, 1992; Meiri, 2007), some species will appear to have shorter maximum SVL than the real value. However, there is no reason to assume it should bias the results in any particular direction, and the intraspecific variation is surely much smaller than the interspecific one. Similarly, museum specimens often shrink, but the degree of shrinkage is usually low (e.g. Lazell, 1972; Case, 1976; Reed, 2001) and probably does not bias my results.

Lizards are being described at an accelerating pace. Between 2000 and 2005, 285 new lizard species were described, and, if anything, the rate of description is increasing: Fitting year as an explanatory variable to the number of species described each year since the end of World War II (1946 to 2005) results in a strong positive correlation, explaining 67% (!) of the variation (slope 0.74 ± 0.07, Fig. S2). Therefore, while species sampling in this study is comprehensive relative to current listings, it is unlikely to remain so. Indeed 129 new reptile species have been described in 2007 alone, more than in any other year except 1854 (P. Uetz, pers. comm.). Again, however, I don't envisage that the discovery of new species will change the conclusions offered here. The SVL of 67 newly described (2005–08) species (Appendix S3) is not significantly different from that of previously described species (controlling for family, $F_{1,4915} = 0.41$, $P = 0.52$). Further-more, my impression is that new species are often being described based on very little differences from well-established ones, differences that may simply reflect minor geographical variation (Meiri & Mace, 2007). For example, many lacertid taxa that Boulenger (1920, 1921) considered as mere varieties (for example of *Lacerta muralis*, nowadays *Podarcis muralis*) are today recognized as specifically distinct (see also Harris, 2008). If this is the prevailing pattern, newly described species will be very similar in size to existing species, and newly described species, valid or not, will be a random sample of the body size distribution.

As lizards are paraphyletic in relation to snakes and amphis-baenians (Townsend *et al.*, 2004; Kumazawa, 2007; cf. Zhou *et al.*, 2006) it may be worth hypothesizing how the inclusion of these two taxa would have affected my results. Snakes and amphisbaenians (3055 and 164 species, respectively, Uetz, 2006) are larger than lizards. Amphisbaenians are, on average, three to four times as long (author's unpublished data) and snakes are even longer: Boback & Guyer's (2003) sample of 618 snake species has a uni-modal distribution, with a modal total length of 880–1080 mm. Therefore a frequency distribution for all squamates is likely to be highly bimodal. Snakes include by far the most speciose squamate family (Colubridae, 1832 species), as well as four other families

with more than 100 species (Uetz, 2006). It is therefore likely that the relationship between small size and high species richness would disappear if snakes were included. The high number of fossorial snake and amphisbaenians species, and the fact that these taxa contain almost exclusively predatory species (Pough *et al.*, 2003), probably means that when examined for all squamates, large size would be associated with burrowing habits, and with a carnivorous, rather than herbivorous diet. Taking phylogeny into account though, I predict that the results obtained here are likely to remain valid.

Using the most complete body size–frequency distribution of any large vertebrate group assembled so far, lizard body size distributions seem to resemble those of other taxa (Gardezi & da Silva, 1999; Olden *et al.*, 2007). Small-bodied families have more species, but this does not translate easily to elevated speciation rates at the lower end of the size spectrum. Neither does large body size seem to be tightly associated with extinction risk; rather it seems that large species are more likely to have been assessed. The association between lizard insularity and herbivory and large body size is corroborated, but the mechanisms responsible for these phenomena are still far from clear. Low predation pressures seem to play at least some role in the evolution of large body size. More puzzling is the fact that such a high proportion of the world's smallest lizards inhabit predator-free islands. Clearly much work is needed to address this and other questions regarding the evolution of lizard body size.

ACKNOWLEDGEMENTS

REFERENCES

Arnold, E.N. & Ovenden, D.W. (2004) *A field guide to the reptiles and amphibians of Britain and Europe*, 2nd edn. Collins, London.

Avery, R.A. (1996) Ecology of small reptile-grade sauropsids. *Symposia of the Zoological Society of London*, **69**, 225–237.

Bennett, A.F. & Gorman, G.C. (1979) Population density and energetics of lizards on a tropical island. *Oecologia*, **42**, 339–358.

Boback, S.M. & Guyer, C. (2003) Empirical evidence for an optimal body size in snakes. *Evolution*, **57**, 345–351.

Boulenger, G.A. (1920) *Monograph of the Lacertidae*, Vol. 1. London, Trustees of the British Museum (Natural History).

Boulenger, G.A. (1921) *Monograph of the Lacertidae*, Vol. 2. London, Trustees of the British Museum (Natural History).

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

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005) Multiple causes of high extinction risk in large mammal species. *Science*, **309**, 1239–1241.

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.

Case, T.J. (1982) Ecology and evolution of the insular giant chuckawallas, *Sauromalus hispidus* and *Sauromalus varius*. *Iguanas of the world: their behavior, ecology and conservation* (ed. by G.M. Burghardt and A.S. Rand), pp. 184–212. Noyes Publications, Park Ridge, NJ.

Case, T.J. & Schwaner, T.D. (1993) Island mainland body size differences in Australian varanid lizards. *Oecologia*, **94**, 102–109.

Case, T.J., Bolger, A.D. & Richman, A.D. (1998) Reptilian extinctions over the last ten thousand years. *Conservation biology for the coming decade*, 2nd edn (ed. by P.L. Fielder and P.M. Kareiva), pp. 157–186. Chapman and Hall, New York.

Cooper, W.E. & Vitt, L.J. (2002) Distribution, extent, and evolution of plant consumption by lizards. *Journal of Zoology*, **257**, 487–517.

Cox, N., Chanson, J. & Stuart, S. (compilers) (2006) *The status and distribution of reptiles and amphibians of the Mediterranean Basin*. IUCN, Gland, Switzerland and Cambridge, UK.

Dunham, A.E., Miles, D.B. & Reznick, D.N. (1988) Life history patterns in squamate reptiles. *Biology of the Reptilia. Vol. 16. Ecology B. Defense and life history* (ed. by C. Gans and R.B. Huey), pp. 441–522. Liss, New York.

Espinoza, R.E., Wiens, J.J. & Tracy, C.R. (2004) Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. *Proceedings of the National Academy of Sciences USA*, **101**, 16819–16824.

Fontanillas, E., Welch, J.J., Thomas, J.A. & Bromham, L. (2007) The influence of body size and net diversification rate on molecular evolution during the radiation of animal phyla. *BMC Evolutionary Biology*, **7**, 95, doi:10.1186/1471-2148-7-95.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**, 712–726.

Gardezi, T. & da Silva, J. (1999) Diversity in relation to body size in mammals: a comparative study. *The American Naturalist*, **153**, 110–123.

Greer, A.E. (2001) Distribution of maximum snout-vent length among species of scincid lizards. *Journal of Herpetology*, **35**, 383–395.

Greer, A.E. & Wadsworth, L. (2003) Body shape in skinks: the relationship between relative hind limb length and relative snout-vent length. *Journal of Herpetology*, **37**, 554–559.

Harris, D.J. (2008) Taxonomic inflation and red lists: how have Mediterranean reptile conservation issues been affected? *Proceedings of the Symposium on the Lacertids of the Mediterranean Basin*, **6**, 28.

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**, 29–44.

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

Herrel, A., Vanhooydonck, B., Joachim, R. & Irschick, D.J. (2004) Frugivory in polychrotid lizards: effects of body size. *Oecologia*, **140**, 160–168.

Huey, R.B. & Slatkin, M. (1976) Cost and benefits of lizard thermoregulation. *Quarterly Review of Biology*, **51**, 363–384.

Hutchinson, G.E. & MacArthur, R.H. (1959) A theoretical ecological model of size distributions among species of animals. *The American Naturalist*, **93**, 117–125.

Janzen, D.H. (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, **54**, 687–701.

Kratochvil, L. & Frynta, D. (2006) Body-size effect on egg size in eublepharid geckos (Squamata: Eublepharidae), lizards with invariant clutch size: negative allometry for egg size in ectotherms is not universal. *Biology Journal of the Linnean Society*, **88**, 527–532.

Kumazawa, Y. (2007) Mitochondrial genomes from major lizard families suggest their phylogenetic relationships and ancient radiations. *Gene*, **388**, 19–26.

Lazell, J.D. (1972) The anoles (Sauria: Iguanidae) of the Lesser Antilles. *Bulletin of the Museum of Comparative Zoology*, **143**, 1–115.

Lomolino, M.V., Riddle, B.R. & Brown, J.H. (2005) *Biogeography*, 3rd edn. Sinauer, Sunderland, MA.

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

Maurer, B.A. (1998) The evolution of body size in birds. I. Evidence for non-random diversification. *Evolutionary Ecology*, **12**, 925–934.

Maurer, B.A., Brown, J.H. & Rusler, R.D. (1992) The micro and the macro in body size evolution. *Evolution*, **46**, 939–953.

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

Meiri, S. & Mace, G.M. (2007) New taxonomy and the origin of species. *PLoS Biology*, **5**, 1385–1386.

Meiri, S., Simberloff, D. & Dayan, T. (2005) Insular carnivore biogeography: island area and mammalian optimal body size. *The American Naturalist*, **165**, 505–514.

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

Olden, J.D., Hogan, Z.S. & Zanden, M.J.V. (2007) Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography*, **16**, 694–701.

Olesen, J.M. & Valido, A. (2003) Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology and Evolution*, **18**, 177–181.

Orme, C.D.L., Quicke, D.L.J., Cook, J.M. & Purvis, A. (2002) Body size does not predict species richness among the metazoan phyla. *Journal of Evolutionary Biology*, **15**, 235–247.

Orme, C.D.L., Davies, R.G., Olson, V.A., Thomas, G.H., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Owens, I.P.F., Blackburn, T.M. & Gaston, K.J. (2006) Global patterns of geographic range size in Birds. *PLoS Biology*, **4**, 1276–1283.

Pough, F.H. (1973) Lizard energetics and diet. *Ecology*, **54**, 837–844.

Pough, F.H. (1980) The advantages of ectothermy for tetrapods. *The American Naturalist*, **115**, 92–112.

Pough, F.H., Andrews R.M., Cadle, J.E., Crump, M.L., Savitzky, A.H. & Wells, K.D. (2003) *Herpetology*, 3rd edn. Prentice Hall, Upper Saddle River, NJ.

Pregill, G.K. (1986) Body size of insular lizards: a pattern of Holocene dwarfism. *Evolution*, **40**, 997–1008.

Price, T.D. & Phillimore, A.B. (2007) Reduced major axis regression and the island rule. *Journal of Biogeography*, **34**, 1998–1999.

R Development Core Team (2007) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Raia, P. & Meiri, S. (2006) The island rule in large mammals: palaeontology meets ecology. *Evolution*, **60**, 1731–1742.

Reed, R.N. (2001) Effects of museum preservation techniques on length and mass of snakes. *Amphibia-Reptilia*, **22**, 488–491.

Reed, R.N. & Boback, S.M. (2002) Does body size predict dates of species description among North American and Australian reptiles and amphibians? *Global Ecology and Biogeography*, **11**, 41–47.

Rodda, G.H., Perry, G., Rondeau, R.J. & Lazell, J. (2001) The densest terrestrial vertebrate. *Journal of Tropical Ecology*, **17**, 331–338.

Roy, K., Jablonski, D. & Martien, K.K. (2000) Invariant size-frequency distributions along a latitudinal gradient in marine bivalves. *Proceedings of the National Academy of Sciences USA*, **97**, 13150–13155.

Schoener, T.W. (1969) Size patterns in West Indian *Anolis* lizards: I. Size and species diversity. *Systematic Zoology*, **18**, 386–401.

Shine, R. (1985) The evolution of viviparity in reptiles: an ecological analysis. *Biology of the Reptilia*, Vol. 15 (ed. by C. Gans and F. Billett), pp. 605–694. John Wiley and Sons, New York.

Smith, F.A., Lyons, S.K., Morgan Ernest, S.K., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H. & Haskell, J.P. (2003) Body mass of late Quaternary mammals. *Ecology*, **84**, 3403.

Sokol, O.M. (1967) Herbivory in lizards. *Evolution*, **21**, 192–194.

Stamps, J.A. & Andrews, R.M. (1992) Estimating asymptotic size using the largest individuals per sample. *Oecologia*, **92**, 503–512.

Stanley, S.M. (1973) An explanation for Cope's rule. *Evolution*, **27**, 1–26.

Stuart-Fox, D.M. & Owens, I.P.F. (2003) Species-richness is agamid lizards: chance, body size, ecology or sexual selection? *Journal of Evolutionary Biology*, **16**, 659–669.

Szarski, H. (1962) Some remarks on herbivorous lizards. *Evolution*, **16**, 529.

Townsend, T.M., Larson, A., Louis, E. & Macey, J.R. (2004) Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology*, **53**, 735–757.

Uetz, P. (2006) *The reptile database,* CD-ROM edition, October 2006. Heidelberg, Germany.

Van Damme, R. (1999) Evolution of herbivory in lacertid lizards: effects of insularity and body size. *Journal of Herpetology*, **33**, 663–674.

Vezina, A.F. (1985) Empirical relationships between predator and prey size among terrestrial vertebrate predators. *Oecologia*, **67**, 555–565.

Vitt, L.J. (2000) Ecological consequences of body size in neonatal and small-bodied lizards in the neotropics. *Herpetological Monographs*, **14**, 388–400.

Zhou, K., Li, H., Han, D., Bauer, A.M. & Feng, J. (2006) The complete mitochondrial genome of *Gekko gecko* (Reptilia: Gekkonidae) and support for the monophyly of Sauria including Amphisbaenia. *Molecular Phylogenetics and Evolution*, **40**, 887–892.

Zug, G.R., Vitt, L.J. & Caldwell, J.P. (2001) *Herpetology*, 2nd edn. Academic Press, San Diego.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Literature sources for size and ecological data.

Appendix S2 Lizard body sizes.

Appendix S3 Lizard species not analysed and reasons for their exclusion.

Appendix S4 Taxa ages, species richness, diversification rates, SVL and phylogeny.

Table S1 Realm-specific moments of central tendency for size–frequency distributions.

Figure S1 Island endemic lizards and mammalian Carnivora.

Figure S2 Lizard description dates.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/ j.1466-8238.2008.0414.x
(This link will take you to the article abstract).

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

BIOSKETCH

Shai Meiri is interested in the evolution of body size and its implications, in biogeographical correlates of morphology and in the morphological signatures of speciation and community composition.

Editor: Tim Blackburn