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ORIGINAL ARTICLE

The relationship between limb reduction, body elongation and geographical range in lizards (*Lerista*, Scincidae)

Michael S. Y. Lee[1,2]*, Adam Skinner[1,2] and Agustín Camacho[3]

[1]*School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA 5005, Australia,* [2]*Earth Sciences Section, South Australian Museum, Adelaide, SA 5000, Australia,* [3]*Instituto de Biociências, University of São Paulo, São Paulo-SP, CEP: 05508-090, Brazil*

*Correspondence: Michael S.Y. Lee, Earth Sciences Section, South Australian Museum, North Terrace, Adelaide, SA 5000, Australia.
E-mail: mike.lee@samuseum.sa.gov.au

ABSTRACT

Aim The relationship between changes in body form (limb reduction and body elongation) and geographical range size was investigated across 68 species of *Lerista*, a species-rich clade of Australian scincid lizards that exhibits extensive interspecific variability in both body form and range size.

Location *Lerista* occurs across the entire Australian mainland, with diversity concentrated in arid and semi-arid regions.

Methods Geographical range size was estimated directly from *c.* 14,000 museum specimens using bioclimatic modelling in MaxEnt. Body form was quantified using principal components analysis of morphometric variables. Comparative analyses testing for a correlation between these two variables used a full Bayesian approach that accounts for uncertainties in trait optimization as well as in tree topology and branch lengths.

Results A serpentine body form (elongated with reduced limbs) was significantly associated with smaller geographical range size, in both phylogenetically corrected and uncorrected analyses – but only if species from single localities (whose ranges could not be modelled using the above methods) were excluded.

Main conclusions These results suggest a general predictive relationship between body form and geographical range size in lizards: elongate, limb-reduced lizards tend to exhibit more restricted geographical ranges that may reflect reduced dispersal ability and may also predispose them to greater vulnerability of extinction.

Keywords

Australia, Bayesian inference, bioclimatic modelling, geographical range size, *Lerista*, limb reduction, lizards, reptiles, Scincidae, squamates.

INTRODUCTION

Geographical range size varies widely among species and clades, but the evolutionary and ecological mechanisms underlying this variation remain contentious. One important facet of current debate concerns whether geographical range size is phylogenetically conserved ('heritable') over broad evolutionary time-scales. Do closely related species tend to share similar range sizes (e.g. Hunt *et al.*, 2005; Mouillot & Gaston, 2007; Borregaard *et al.*, 2012), and if range size is phylogenetically conserved, what mechanisms are responsible for such phylogenetic conservatism? Similarities in geographical range size among closely related species might be attributable to shared (inherited) biological attributes, such as dispersal ability or niche breadth (e.g. Böhning-Gaese *et al.*, 2006). Alternatively, they could result from extrinsic factors – for instance, species from different clades could occupy different landmasses, and so could be affected by different (e.g. narrow or wide) geographical barriers (e.g. Machac *et al.*, 2011). For certain broad comparisons, the observed patterns and their causes appear intuitive; for instance, on a global scale, geographical range size is typically much larger in birds than in freshwater fishes, in pelagic organisms than in spring-dwellers, and in species with planktonic rather than directly developing larvae, almost certainly reflecting differences in organismal or habitat attributes affecting dispersal ability (e.g. Brown *et al.*, 1996; Gaston, 2003). A more

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intriguing question is whether consistent phylogenetic patterns in geographical distribution persist when comparisons are made across closely related taxa. Such taxa are less likely to exhibit major biological and/or geographical differences that readily explain differing geographical range sizes. Analyses of relatively recent clades are therefore needed to assess the extent to which geographical distribution varies systematically at lower phylogenetic scales, and to elucidate more subtle evolutionary and ecological mechanisms that influence the evolution of range size. While these factors are potentially clade-specific, examination of multiple clades which each exhibit similar variation might reveal general correlations.

The scincid lizard clade *Lerista* possesses numerous features that make it ideal for investigating the fine-scale heritability of geographical range size and its causes. First, all species are endemic to Australia, eliminating the broadest-scale (continental) influences on geographical range size (e.g. Machac *et al.*, 2011). Second, it is a highly diverse clade containing species that display an extensive array of geographical distributions (e.g. Greer, 1989) – the *c.* 91 described species have known ranges that vary from single localities (e.g. *L. robusta*) to half a continent (e.g. *L. bipes*). Third, the alpha taxonomy of the group (Cogger *et al.*, 1983) is being actively investigated, improving the reliability of the museum records from which geographical distributions are constructed (e.g. Amey *et al.*, 2005; Smith & Adams, 2007). Fourth, a recent, detailed evolutionary tree for the group (Skinner *et al.*, 2008) provides a phylogenetic framework for evolutionary inferences. Fifth, *Lerista* has been sampled reasonably well throughout Australia, while there exists a detailed environmental database, including climate and soil data, for the whole continent. Thus, it is possible to generate reliable distribution maps, refined by the use of environmental modelling. Sixth, all species are broadly similar in both general anatomy and body size (to the extent that they are placed in the same genus), but vary substantially in gross body shape, permitting explicit investigation of the potential effects of body elongation and limb reduction on geographical range size evolution. Finally, although differences in body form are associated with different foraging modes (highly elongated species are predominantly fossorial, whereas shorter-bodied species are surface-active), surveys of stomach contents indicate that the examined species have essentially the same generalist diet (Pianka, 1986; Pough *et al.*, 1997). Any relationship between body form and range size is therefore unlikely to be confounded by specialization on habitat-restricted prey. Indeed, preliminary observations suggest that highly limb-reduced species of *Lerista* tend to have smaller ranges.

We assess here whether body form (i.e. the degree of body elongation and limb reduction) is correlated with geographical range size in *Lerista*, employing Bayesian methods that explicitly account for uncertainties in both phylogeny and character optimization.

MATERIALS AND METHODS

Analysis of body form

We measured four morphometric variables for 68 species of *Lerista* (see Skinner & Lee, 2009): snout–vent length, forelimb and hindlimb lengths (measured from the axilla and groin, respectively, to the tip of the longest digit), and head width (at the widest point of the head). Tail length was not used due to missing data caused by tail loss, and '*L. muelleri*' was excluded, because this taxon has recently been recognized as a species complex (Smith & Adams, 2007). The first three variables were size-corrected by dividing by head width, because although snout–vent length is the most commonly used body size proxy in squamate reptiles, it is poorly correlated with body mass (size) if there is great variation in body shape (Pincheira-Donoso *et al.*, 2011). The size-corrected data were subjected to principal components analysis, employing the correlation matrix, using R Commander (Fox, 2005).

Range size

Geographical range sizes for the 68 species of *Lerista* included in the analyses were estimated using collection locality data for specimens held in Australian state and territory museums. We modelled ranges using MaxEnt in R 2.14.1 (R Development Core Team, 2011), following recommendations in the vignette of the R package dismo (Hijmans *et al.*, 2012), and calculated areas using a custom R script. MaxEnt has proved itself a reliable algorithm when modelling with different sample sizes (Pearson *et al.*, 2007). Environmental modelling of species distributions was performed using a raster database including both climatic and soil layers. The database contained all of the climatic variables, plus elevation, available from the WorldClim database (http://www.worldclim.org/), and all of the soil-derived attribute layers available from the Harmonized World Soil Database (http://www.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/). The resolution of these databases is measured by the dimensions of the sides of the square cells that compose the raster layers. For this work, we used the highest resolution available for soil layers (5 arc-minutes). Distributions were modelled using the package dismo in R (Hijmans *et al.*, 2012), following guidelines in the vignette. We used the area under the receiver operating characteristic curve (AUC) to assess the accuracy of model predictions in discriminating between places where the species is present and places where it is absent. Values over 0.5 indicate that the discriminations are better than random (Hanley & McNeil, 1982).

Generating reliable distribution sizes from museum records presents the following problems: (1) errors may be present in the locality or taxonomic data; (2) low sampling effort may underestimate the distribution size of species; (3) wide-ranging species may have been present in only a small portion of the modelled distribution generated by their records; (4) endemic species of very restricted areas (e.g. single localities) will be difficult to model using estimation algorithms. Thus, we chose a conservative strategy to model distribution sizes that attempted to address these issues.

Our steps were as follows:

1. Specimens and localities were personally revised by A.S. and obvious errors corrected (e.g. zero-value coordinates, implausible outliers, records at sea or 'mirrored' in the Northern Hemisphere).

2. We generated a distribution map of the each species based on sampling records. In this way, we could check if species with smaller ranges tended to be confined to regions with low sampling effort (e.g. remote arid areas), which would be consistent with sampling artefacts. This was not the case – most species with limited ranges tended to be found in coastal regions which are generally better sampled than inland regions (see Wilson & Swan, 2010).

3. To avoid over-extrapolation of species ranges, for species with five or more locality records, we calculated the projected area of the initial distribution rectangle, using the highest and lowest longitudinal and latitudinal record of each species. The projected area (in raster cells) was then cropped using the range models generated in MaxEnt (see previous paragraph), using the package raster (Hijmans & van Etten, 2012). In this way, we used the distribution models to remove areas with unsuitable habitat from within the latitudinal and longitudinal extent of each species distribution. MaxEnt has been demonstrated to perform well with samples as small as five records (Pearson *et al.*, 2007).

4. For species with records from 2–4 localities, we calculated the projected area (in raster cells) of the initial distribution rectangle (without cropping from MaxEnt).

5. Finally, for species known from a single locality, which are insufficient to generate distribution rectangles, we simply used the area of the raster cell. The R scripts for generating MaxEnt models and calculating the distribution range sizes are available on request to A.C.

Phylogenetic analysis

Nucleotide sequence data for one nuclear locus (ATP synthase subunit β intron) and three mitochondrial loci (12S rRNA, 16S rRNA, ND4 and adjacent regions) are available for the above 68 species. We used the alignment, partitioning scheme and substitution models employed in Skinner *et al.* (2008). The trait correlation analyses described below only require relative (not absolute) branch lengths, but rather than use an arbitrary root age, we used the same calibration as Skinner *et al.* (2008), so the trees could also be interpreted as chronograms. The data were analysed using Bayesian Markov chain Monte Carlo (MCMC) phylogenetic methods in MrBayes 3.2 (Ronquist *et al.*, 2012). Stepping-stone estimates of marginal likelihoods strongly (10.9 log *L* units) favoured the relaxed clock with independent gamma rates over a strict clock, so the former was employed. Four separate runs of 30 million generations were performed, each employing four chains, with sampling every 2000 generations; the first 10 million generations were discarded as burn-in, leaving 10,000 trees (per run) for analysis, from which a majority-rule consensus tree was obtained. Full details (alignment, partitions, nucleotide models, chain length and number, heating, burn-in and clock parameters) are in the MrBayes file (Appendix S2).

Correlation between geographical range size and body form

Phylogenetically uncorrected and corrected analyses were employed to evaluate the relationship between geographical range size and body form. In the phylogenetically uncorrected analyses (which effectively assume a star phylogeny), species were (naïvely) treated as independent data points. Because inferred geographical distribution is likely to have much higher error (extrapolated using complex models, often from sparse sampling) than measures of limb reduction, least-squares (LS) regressions were used. LS regression results are also directly comparable to the phylogenetically corrected analyses.

The phylogenetically corrected analyses directly employed the pool of sampled trees: using any single (e.g. consensus) tree was inappropriate due to uncertainty over many (especially basal) nodes in the *Lerista* phylogeny (Fig. 1; see also Skinner *et al.*, 2008). Analyses were performed using the Continuous module in BayesTraits (Pagel, 1997, 1999; Pagel & Meade, 2007), which implements the generalized least-squares model, analytically equivalent to independent contrasts (Garland *et al.*, 2005). Eight (2^3) different analyses were performed: (1) with single-locality species either excluded or included; (2) with the lambda parameter, which models the variance attributable to phylogenetic conservatism or 'heritability', either freely estimated or fixed to zero; and (3) with the covariance parameter, which describes the variance attributable to the correlation between geographical range size and body form, either freely estimated or fixed to zero. Analyses were run for 11 million generations, with a sampling frequency of 10,000 generations and a burn-in of 1 million generations. To assess convergence, each analysis was replicated four times. Bayes factors were used for inferring whether the lambda or covariance parameters improved model fit; we used Kass & Raftery's (1995) criterion of twice the marginal $\log_n$-likelihood differences (herein abbreviated BF_{KR}). Marginal $\log_n$-likelihoods were estimated using the Bayes Factor function in Tracer 1.5 (Rambaut & Drummond, 2009). Regression equations were calculated from the BayesTraits parameter output (using the formula in Pagel, 1999, p. 10) for the analyses employing the best-fitting models.

RESULTS

Analysis of body form

The first principal component (PC1) explained 77% of the variation and was an index of limb reduction, with high and similar loadings for (size-corrected) snout–vent length (+0.62), forelimb length (−0.58) and hindlimb length (−0.53). The full morphometric data and PC1 loadings for each species are presented in Appendix S1.

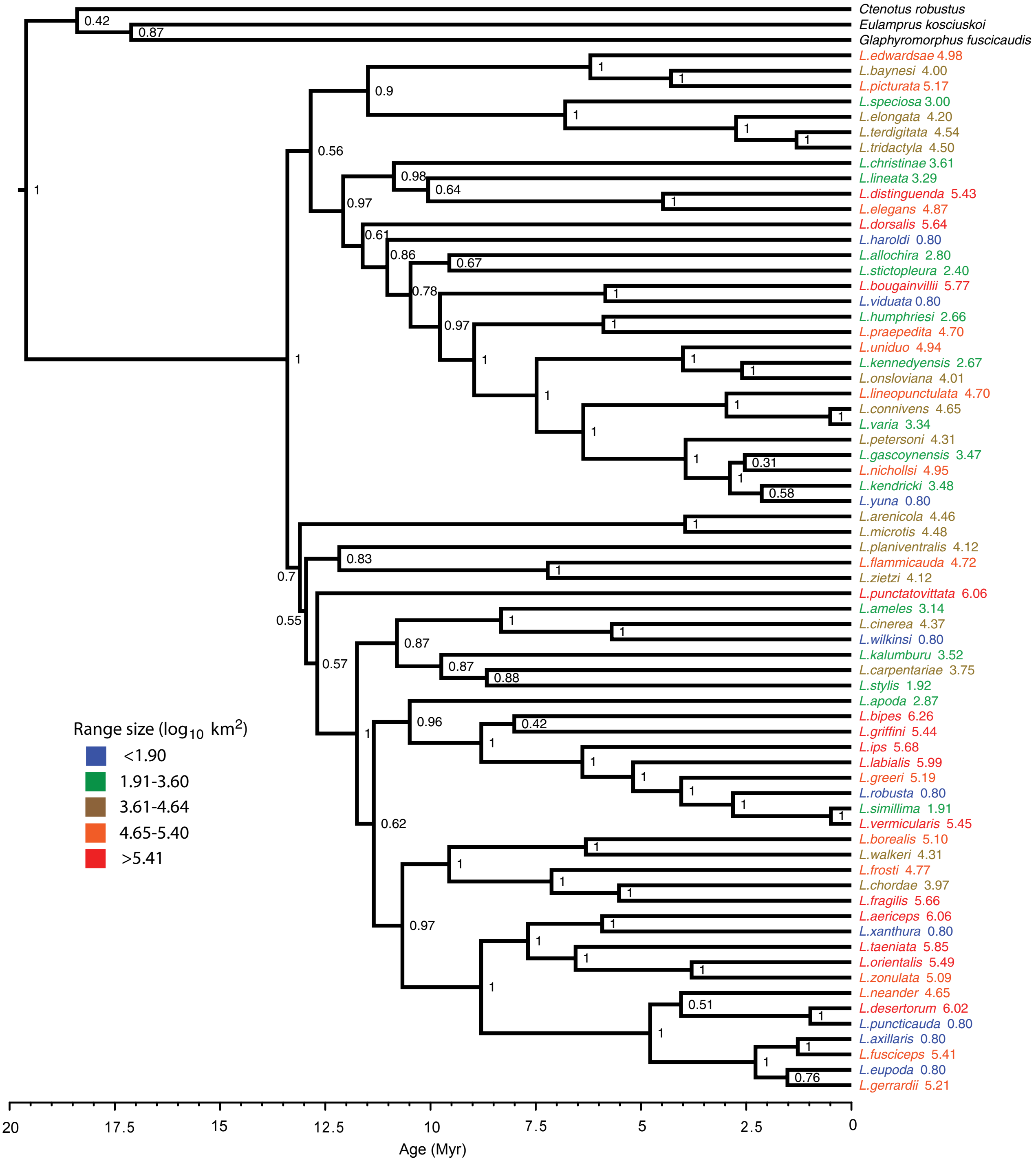

Figure 1 Phylogeny of 68 species of the Australian lizard genus *Lerista*. Majority-rule Bayesian consensus tree, with posterior probabilities at nodes; the time-scale is in million years (Myr). Geographical range size of each species ($\log_{10}$ km^2) is indicated; note substantial lability, but also some apparent degree of phylogenetic conservatism.

Range size

The *Lerista* species considered here are represented by more than 14,000 specimens with locality data in Australian museums, with the sample size for each species ranging from four (for *L. eupoda*) to 1290 (for *L. bipes*). This produced a total of 1663 locality records across all 68 species (median = 42, range = 1–168) for distribution modelling. All AUC values obtained were above 0.78, suggesting good general accuracy of the models generated. The resultant estimates of geographical range size are presented in Appendix S1. As these exhibited heteroscedasticity they were log-transformed (Fig. 1) before analyses.

Phylogenetic analysis

The majority-rule consensus tree from the Bayesian analysis (Fig. 1) is highly concordant with a previous analysis that used the same genes but with slightly more extensive taxon sampling (Skinner *et al.*, 2008). In both analyses, many of the basal clades of *Lerista* are poorly supported.

Correlation between geographical range size and body form

In the phylogenetically uncorrected analyses, when single-locality species were excluded, there was a significant negative relationship between geographical range size and body form ($P = 0.0322$; $r^2 = 0.078$, $F = 4.822$ with 57 d.f.), i.e. distributions were smaller for serpentine species (Fig. 2, thick dashed line). However, when single-locality species were included, this relationship was insignificant ($P = 0.289$, $r^2 = 0.017$, $F = 1.141$ with 66 d.f.; Fig. 2, thin dashed line). In the phylogenetically corrected analyses (Table 1), all eight analyses converged on essentially identical solutions for all four replicate runs, with effective sample sizes for all parameters > 35,000. Estimating lambda (i.e. allowing for phylogenetic conservatism) always greatly improved model fit (BF_{KR} 13.22–23.94: compare analyses 1 vs. 3, 2 vs. 4, 5 vs. 7, 6 vs. 8). Lambda was estimated for both variables simultaneously (see Pagel, 1999) and was always large (*c.* 0.7; theoretical range 0–1), with the lower limit of the 95% highest posterior density (HPD) never falling below 0.45. Thus, there is a significant tendency for closely related species to be more similar in geographical range size (Fig. 1) and body form (Figure 1 in Skinner *et al.*, 2008) despite high lability in both traits. The following discussion therefore focuses on those analyses in which lambda was estimated (analyses 3, 4, 7 and 8).

When species from single localities were excluded, there was positive evidence that higher PC1 scores (i.e. elongate, limb-reduced body forms) were correlated with smaller geographical distributions ($BF_{\mathrm{KR}} = 3.24$). The covariance, a measure of trait correlation, was estimated at −3.82, and neither the 95% HPD (−2.92, −4.77) nor even the entire sampled interval (−1.16, −7.82) approached zero. However, when single-locality species were included, the evidence for correlated evolution was marginal ($BF_{\mathrm{KR}} = 0.16$). The covariance between body form and geographical range size was much lower (−1.23), the 95% HPD approached zero (−0.19, −2.37), and the sampled interval included zero (+3.08, −5.04).

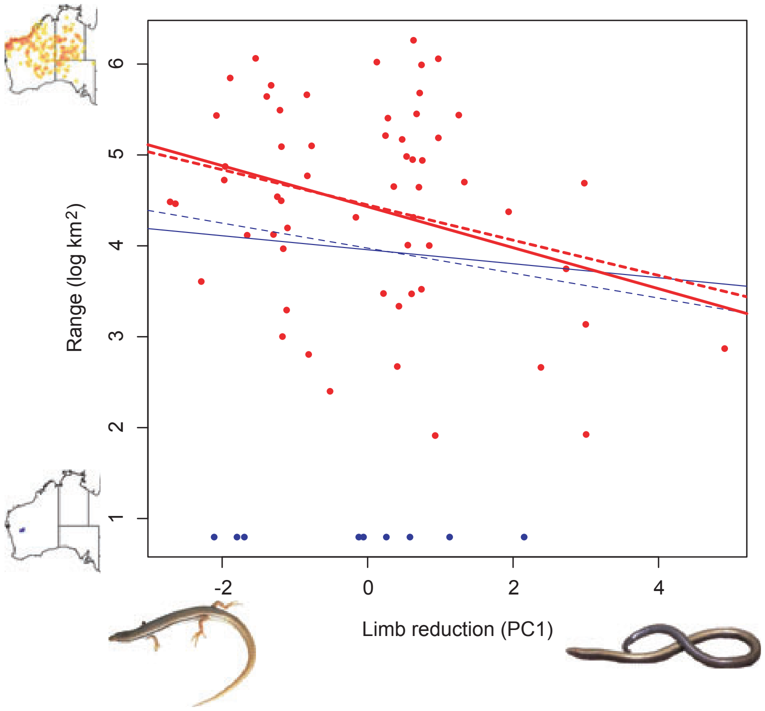

Figure 2 Relationship between modelled range size ($\log_{10}$ km^2) and limb reduction (indexed by the first principal component, PC1) in the Australian lizard genus *Lerista*; least-squares regressions with modelled range size as the dependent variable. Dots along the horizontal row at the bottom (blue) represent taxa known from single localities whose ranges could not be accurately modelled. Solid lines are phylogenetically corrected generalized least-squares regressions (integrated across Bayesian tree samples; Pagel & Meade, 2007); dashed lines are uncorrected least-squares regressions. Thick lines (red) are analyses excluding single-locality taxa ($n = 59$; both gradients significantly less than 0: Table 1, analyses 9 and 10); thin lines (blue) are for analyses including single-locality taxa ($n = 68$; both gradients indistinguishable from 0: Table 1, analyses 11 and 12). Regression coefficients are given in Table 1; *F*-values are given in the main text.

Table 1 Model comparisons (analyses 1–8) and regressions using selected models (analyses 9–12; see also Fig. 2) of range size against limb size in Australian lizards of the genus *Lerista*. When single-locality species were excluded (1–4), leaving 59 species for analysis, there were significant improvements by including parameters accounting for phylogenetic conservatism (lambda) and correlation between the two variables (covariance). When single-locality species were included, and all 68 species were analysed (5–8), only the lambda parameter was supported. Similarly, in regression analyses, the gradient (relationship between range size and limb size) was significantly negative when single-locality species were excluded (9,10) but not when they were included (11,12).

Bayesian analysis: model comparisons	Lambda (95% HPD) [phylogenetic conservatism]	Covariance (95% HPD) [correlation between characters]	Log L (marginal)	BF_{KR} comparison ($2 \times \Delta\log L$)
1–4: Single-locality taxa excluded (n = 59)				
1. lambda 0, covariance 0	0; fixed	0; fixed	−200.04	−27.18
2. lambda 0, covariance estimated	0; fixed	−4.44 (−3.49, −5.36)	−197.66	−22.42
3. lambda estimated, covariance 0	0.75 (0.56, 0.92)	0; fixed	−188.07	−3.24
4. lambda estimated, covariance estimated	0.73 (0.54, 0.91)	−3.82 (−2.92, −4.77)	−186.45	0 (best)
5–8: Single-locality taxa included (n = 68)				
5. lambda 0, covariance 0	0; fixed	0; fixed	−255.56	−15.22
6. lambda 0, covariance estimated	0; fixed	−2.99 (−2.15, −3.90)	−254.56	−13.22
7. lambda estimated, covariance 0	0.70 (0.47, 0.90)	0; fixed	−248.03	−0.16
8. lambda estimated, covariance estimated	0.69 (0.45, 0.90)	−1.23 (−0.19, −2.37)	−247.95	0 (best)
Regression	**intercept**	**gradient**	**significance**	
9. **Single-locality taxa excluded (n = 59),** phylogenetically corrected	4.426	−0.225	$BF_{\mathrm{KR}} = 3.24$	
10. **Single-locality taxa excluded (n = 59),** uncorrected	4.466	−0.197	$P = 0.032$	
11. **Single-locality taxa included (n = 68),** phylogenetically corrected	3.975	−0.077	$BF_{\mathrm{KR}} = 0.16$	
12. **Single-locality taxa included (n = 68),** uncorrected	3.975	−0.137	$P = 0.289$	

HPD, highest posterior density; log L, log-likelihood; BF_{KR}, Kass & Raftery's (1995) criterion of twice the difference in marginal log-likelihoods.

The phylogenetically corrected regressions calculated from the BayesTraits parameter estimates (Fig. 2, solid lines) are very similar to the corresponding phylogenetically uncorrected regressions (Fig. 2, dashed lines).

DISCUSSION

We analysed geographical range size variability across closely related species using Bayesian approaches that integrate uncertainties both in model parameters and in phylogeny, and tested whether range size is consistently associated with body form. We found that elongate, limb-reduced species of *Lerista* have significantly smaller ranges, but only when single-locality species are excluded; when single-locality species are included, the relationship is much weaker and ceases to be statistically significant (Fig. 2). There might, however, be valid reasons justifying the exclusion of single-locality species. First, compared with species known from multiple localities, single-locality species are more likely to be rare and poorly sampled; if so, their known ranges might be particularly unrepresentative. Second, even if the known ranges of single-locality species are sampled as adequately as for other species, it was impossible to model the inferred ranges of these single-locality species using the same techniques used for other species, making the former data points methodologically inconsistent. Third, more detailed sampling and phylogeographical analyses could eliminate some single-point species, either by revealing they have wider ranges, or by demonstrating that they only represent local populations of species that are more widely distributed. For example, the single-locality species *L. puncticauda* is nested within the more widely occurring *L. desertorum* (A. Skinner, in prep.), raising questions about its taxonomic status. Additional research could of course confirm that single-locality taxa such as *L. puncticauda* should be recognized as species; however, even in these cases, taxa will have originated relatively recently (considering the absence of reciprocal monophyly), so that geographical range size is perhaps more likely to be determined by the mode of speciation than the ecological factors that control distributional limits for older taxa. An additional consideration is that elongated, limb-reduced taxa may be more likely to contain undiscovered species, and so have actual geographical ranges that are smaller than those estimated in our analyses. Among the 68 species of *Lerista* described in the past half-century (see Cogger *et al.*, 1983; Amey *et al.*, 2005; Smith & Adams, 2007), 40 (nearly 60%) have fewer than three digits for the forelimb or both limbs. Assuming this pattern of species discovery continues, and that species discovery primarily involves 'splitting' of existing taxa, estimates of geographical range size for limb-reduced species would be expected to further decline with improved taxonomic understanding, reinforcing the inferred relationship between body form and range size. If these arguments are accepted, there are reasons to prefer the results from analyses that exclude single-point ranges, which indicate that species displaying a serpentine body form have narrower distributions.

The analyses presented here are correlative, and do not directly evaluate the possible mechanisms responsible for a relationship between geographical range size and body form. Elongate, limb-reduced species of *Lerista* could be more affected by environmental patchiness if they are less likely to move long distances, more substrate-specific (e.g. sand-swimmers), or more cryptic in habit (e.g. see Greer, 1989). These traits could influence their dispersal ability and thus shape their geographical range sizes over evolutionary time-scales. Species with lower dispersal ability may be expected to display higher rates of local (population) extinction and lower rates of recolonization, restricting the number of potentially suitable sites occupied at any particular time, thus reducing geographical range. Moreover, dispersal limitation may facilitate the genetic differentiation of local populations, promoting speciation and the associated partitioning of ancestral distributions, again reducing geographical range. The potential for dispersal ability to affect geographical range size has been demonstrated for *Sylvia* warblers, where species lacking ecomorphological adaptations for long-range flight have smaller ranges (Böhning-Gaese *et al.*, 2006). Assessing whether the association between body form and geographical range in *Lerista* is mediated by dispersal limitation will depend on future ecological studies of a range of limb-reduced and surface-active species involving, for example, radio-tracking and behavioural tests of substrate preferences and performances. The relationship between limblessness and geographical range size also has conservation implications: for instance, the only two *Lerista* species on the International Union for Conservation of Nature's *Red List of Threatened Species* (http://www.iucnredlist.org/) are highly elongate, limb-reduced species with very restricted ranges, namely *L. allanae* and *L. vittata*.

Geographical range size is an important attribute of species, and the boundaries of species' ranges are likely to be influenced by a variety of factors, including physiological tolerances, competition, and past and present climatic and geographical barriers (e.g. Geber, 2011). However, with the notable exception of body size (e.g. Olifiers *et al.*, 2004), there have been few quantitative analyses of morphological attributes that could also play a significant role (Böhning-Gaese *et al.*, 2006). Given the large number of possible confounding factors, demonstrating a relationship between range size and morphology requires a large sample of species possessing morphological traits that display high homoplasy (leading to replicated changes), as well as great variation in geographical range size. *Lerista* fulfils all criteria, and our analysis suggests – with the above caveats – that body elongation and limb reduction are associated with more restricted distributions.

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REFERENCES

Amey, A.P., Kutt, A.S. & Hutchinson, M. (2005) A new species of *Lerista* (Scincidae) from central Queensland. *Memoirs of the Queensland Museum*, **50**, 125–131.

Böhning-Gaese, K., Caprano, T., van Ewijk, K. & Veith, M. (2006) Range size: disentangling current traits and phylogenetic and biogeographic factors. *The American Naturalist*, **167**, 555–567.

Borregaard, M.K., Gotelli, N.J. & Rahbek, C. (2012) Are range-size distributions consistent with species-level heritability? *Evolution*, **66**, 2216–2226.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.

Cogger, H.G., Cameron, E.E. & Cogger, H.M. (1983) *Zoological catalogue of Australia. Vol. 1: Amphibia and Reptilia*. Australian Government Publishing Service, Canberra.

Fox, J. (2005) The R Commander: a basic-statistics graphical user interface to R. *Journal of Statistical Software*, **14**, 1–42.

Garland, T. Jr, Bennett, A.F. & Rezende, E.L. (2005) Phylogenetic approaches in comparative physiology. *Journal of Experimental Biology*, **208**, 3015–3035.

Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.

Geber, M.A. (2011) Ecological and evolutionary limits to species geographic ranges. *The American Naturalist*, **178**, S1–S5.

Greer, A.E. (1989) *The biology and evolution of Australian lizards*. Surrey Beatty and Sons, Chipping Norton, NSW.

Hanley, J.A. & McNeil, B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, **143**, 29–36.

Hijmans, R.J. & van Etten, J. (2012) *raster: geographic data analysis and modeling*. R package version 1.9-70. Available at: http://CRAN.R-project.org/package=raster.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2012) *dismo: species distribution modeling*. R package version 0.7-17. Available at: http://CRAN.R-project.org/package=dismo.

Hunt, G., Roy, K. & Jablonski, D. (2005) Species-level heritability reaffirmed: a comment on "On the heritability of geographic range sizes". *The American Naturalist*, **166**, 129–135.

Kass, R.E. & Raftery, A.E. (1995) Bayes factors. *Journal of the American Statistical Association*, **90**, 773–795.

Machac, A., Zrzavý, J. & Storch, D. (2011) Range size heritability in Carnivora is driven by geographic constraints. *The American Naturalist*, **177**, 767–779.

Mouillot, D. & Gaston, K.J. (2007) Geographic range size heritability: what do neutral models with different modes of speciation predict? *Global Ecology and Biogeography*, **16**, 367–380.

Olifiers, N., Vieira, M.V. & Grelle, C.E.V. (2004) Geographic range and body size in Neotropical marsupials. *Global Ecology and Biogeography*, **13**, 439–444.

Pagel, M. (1997) Inferring evolutionary processes from phylogenies. *Zoologica Scripta*, **26**, 331–348.

Pagel, M. (1999) *User's manual for Continuous*. Available at: http://www.evolution.reading.ac.uk/BayesTraits.html (last accessed 21 January 2013).

Pagel, M. & Meade, A. (2007) *BayesTraits 1.0. Software and documentation*. Available at: http://www.evolution.rdg.ac.uk/BayesTraits.html.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102–117.

Pianka, E.R. (1986) *Ecology and natural history of desert lizards*. Princeton University Press, Princeton, NJ.

Pincheira-Donoso, D., Fox, S.F., Scolaro, J.A., Ibargüengoytía, N., Acosta, J.C., Corbalán, V., Medina, M., Boretto, J., Villavicencio, H.J. & Hodgson, D.J. (2011) Body size dimensions in lizard ecological and evolutionary research: exploring the predictive power of mass estimation equations in two Liolaemidae radiations. *Herpetological Journal*, **21**, 35–42.

Pough, F.H., Preest, M.R. & Fusari, M.H. (1997) Prey-handling and the evolutionary ecology of sand-swimming lizards (*Lerista*: Scincidae). *Oecologia*, **112**, 351–361.

R Development Core Team (2011) *R: a language and environment for statistical computing*. Version 2.14.1. R Foundation for Statistical Computing. Vienna, Austria. Available at: http://www.r-project.org/.

Rambaut, A. & Drummond, A.J. (2009) *Tracer v1.5.0*. Available at: http://tree.bio.ed.ac.uk/software/tracer/.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, **61**, 539–542.

Skinner, A. & Lee, M.S.Y. (2009) Body-form evolution in the scincid lizard clade *Lerista* and the mode of macroevolutionary transitions. *Evolutionary Biology*, **36**, 292–300.

Skinner, A., Lee, M.S.Y. & Hutchinson, M.N. (2008) Rapid and repeated limb loss in a clade of scincid lizards. *BMC Evolutionary Biology*, **8**, 310.

Smith, L.A. & Adams, M. (2007) Revision of the *Lerista muelleri* species-group (Lacertilia: Scincidae) in Western Australia, with a redescription of *L. muelleri* (Fischer, 1881) and the description of nine new species. *Records of the Western Australian Museum*, **23**, 309–358.

Wilson, S. & Swan, G. (2010) *A complete guide to reptiles of Australia*, 3rd edn. New Holland Publishers, Sydney.

SUPPORTING INFORMATION

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

Appendix S1 Geographical range size and body form (PC1) data for 68 species of *Lerista*.

Appendix S2 MrBayes 3.2 file with molecular alignment and analytical settings.

BIOSKETCHES

Michael S. Y. Lee is a senior research scientist at the South Australian Museum and University of Adelaide. He investigates macroevolutionary questions at the interface of phylogenetics, molecular biology and palaeontology.

Adam Skinner is a research fellow at the University of Adelaide. He works on reptile evolution and systematics, and is currently focusing on the developmental genomics of limb reduction.

Agustín Camacho is a research fellow at the University of São Paulo. He works on the evolutionary ecology of Neotropical reptiles.

Author contributions: A.S. gathered the primary distribution data and morphometric measurements; A.C. performed the bioclimatic analyses; M.L. performed the phylogenetic, morphometric and correlation analyses; M.L. wrote the paper with input from A.S. and A.C.

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