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RESEARCH ARTICLE

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Predictors of geographic range size in Australian skinks

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Abstract

Aim: Geographic range size varies greatly across species. Climate, along with aspects of a species' biology, may influence its spatial extent. We investigate intrinsic and extrinsic predictors of range size in Australian skinks. We predicted that larger body size, longer limbs, and larger clutch sizes would be associated with larger ranges, and that ranges would be larger in colder, more arid, and more seasonal climates.

Location: Mainland Australia.

Taxon: Skinks (Scincidae).

Methods: We test for climatic and geographic correlates of range size of Australian skink species (417 of 462 described species), as well as investigate the effects of body size and clutch size (259 species). We compare detailed morphological measurements of 1,324 specimens across nine pairs of widespread and narrow-ranged congeneric species to investigate the roles of intrinsic (body size, clutch size, morphology) and extrinsic (mean temperature and precipitation) factors in determining range size.

Results: In the broader analysis, large range sizes were associated with the presence of fully developed limbs, low precipitation seasonality, high temperatures, and high precipitation. Ranges of species traversing the Great Dividing Range are larger by an order of magnitude than those east of the range, with western ranges being intermediate. Affinity to specific biomes explained less variation than climatic variables. For the nine species pairs, wide-ranging species share similar morphologies and clutch sizes with overlapping narrow-ranging congeners, but generally inhabit more arid regions.

Main conclusions: We found several extrinsic, but few intrinsic, factors were correlated with range size. The narrow mesic belts in Australia compared with the extensive expanse of arid and semi-arid regions may explain why desert species have larger ranges. This interpretation agrees with the notion that the size of the domain, here a climatic domain rather than a physical one, may exert strong influence on species' range sizes.

KEYWORDS

Australia, extrinsic trait, geographic distribution, intraspecific variation, intrinsic trait, narrow-ranged, Scincidae, skink, widespread

Shai Meiri and David G. Chapple contributed equally to the paper.

1 | INTRODUCTION

No species can live everywhere on Earth: multiple factors invariably limit where a species can occur. Understanding the factors that determine, and constrain, the geographic range of a species is a central focus in ecology and biogeography alike (Sexton et al., 2009). But there is extreme variation in geographic range extent among species. Why are some species widespread, whilst others are narrow ranged? (Gaston, 1996). The boundaries of a species' range often align with a discontinuation of preferred habitat or a significant barrier to dispersal (e.g., mountain range, river); however, in some cases, boundaries occur at a seemingly arbitrary point along a continuous gradient of environmental conditions (Kirkpatrick & Barton, 1997).

A number of factors have the potential to influence the size of a species' geographic range. Extrinsic factors, such as climate, soils, competition, predation, disease, as well as type and abundance of a resource, all have the capacity to influence species range margins (Bonino et al., 2015; Sexton et al., 2009). Ectotherms are especially sensitive to changes in climate, as their basic physiological processes, such as growth, reproduction, and locomotion, are all strongly affected by environmental temperature (Deutsch et al., 2008; Sexton et al., 2009). In addition to these extrinsic influences on range size, intrinsic characteristics of a species can limit its geographic range. Phylogenetic history may also be important, as closely related species (with similar ecology, life history, and morphology) often have more similar-sized ranges compared to distantly related species (Brown, 1995; Brown et al., 1996; Jablonski, 1987; Lee et al., 2013; but see Raia et al., 2011; Webb & Gaston, 2003). Thus, both extrinsic and intrinsic factors may act to determine the extent of a species' geographic range.

Australian skinks (Scincidae) represent an ideal study system to investigate the intrinsic and extrinsic correlates of range size for several key reasons:

1. There is an exceptionally high diversity of Australian skinks, with 490+ described species (Chapple et al., 2019; Tingley et al., 2019; Uetz et al., 2020).
2. There is high species diversity within genera, allowing comparisons to be made between widespread and narrow-ranged congeneric species (i.e., capacity to effectively control for phylogenetic history; Tingley et al., 2019; Uetz et al., 2020; Wilson & Swan, 2017)
3. Australia is a continental landmass, spanning from 10.687° S at Cape York Peninsula in Queensland to 39.136° S at South Point in Victoria. As such, there are many widespread and narrow-ranged skink species in Australia, which occur in a variety of ecological situations and experience differing climatic conditions (Powney et al., 2010; Wilson & Swan, 2017).
4. Ecological and life-history trait data (Meiri, 2018; Meiri et al., 2020), and distributional information (Roll et al., 2017), are available for the vast majority of species.
5. A large number of museum specimens are available for most Australian skink species (http://www.ozcam.org.au/), allowing intraspecific variation in phenotypic traits (e.g., body size, clutch size) to be quantified.

Here we investigate whether widespread and narrow-ranged Australian skink species differ in their extrinsic (temperature, precipitation, seasonality, productivity) and intrinsic traits (morphology, life history). We adopt two separate approaches: the first uses published distributional and trait data (Meiri, 2018; Roll et al., 2017; Supporting Information Table S1) for nearly all (*c.* 95%) mainland-Australia skinks, while the second incorporates additional morphological and trait data measured from museum specimens for nine congeneric species pairs (Supporting Information Table S2). We predicted that widespread species:

1. Occur in colder and more seasonal regions (Rapoport's rule: Böhm et al., 2017; Janzen, 1967; Rapoport, 1982; Stevens, 1989). In seasonal regions animals are exposed to a wide variety of climatic conditions, which could lead to adaptation to multiple climatic regions (Janzen, 1967).
2. Occur in drier, less productive regions, which presumably force individuals to forage over wider areas, promoting dispersal. Furthermore, in Australia, desert areas are both large and continuous, whereas more mesic, productive areas are small and often isolated from each other (e.g., by the Great Dividing Range, or the SW corner versus mesic regions with similar temperatures in SE Australia). Thus, we expect larger ranges in the arid, less productive deserts (Powney et al., 2010).
3. Occupy widespread biomes. Rather than varying smoothly with climate, range size might differ across natural breaks in climatic hyperspace that can be ascribed to different biomes. Furthermore, if most species are endemic to a single biome, the extent of this biome in Australia could limit the range size of species inhabiting it. Thus, species occurring in small biomes (e.g., mountains or tropical forests; Supporting Information Figure S1) will have smaller ranges than species inhabiting biomes that cover larger parts of Australia (e.g., deserts, tropical and subtropical savannas; Supporting Information Figure S1).
4. Are larger-bodied (e.g., Angielczyk et al., 2015; Gaston & Blackburn, 1996; Reed, 2003) and longer limbed, traits that facilitate dispersal (Bowman et al., 2002; Whitmee & Orme, 2013 – who also found home range size and geographic range size were positively associated).
5. Have larger clutch sizes, which select for higher dispersal of the young, while smaller clutches and litters are associated with philopatry (e.g., in the Egerniinae; Chapple, 2003).

2 | MATERIALS AND METHODS

2.1 | Species-rich analysis based on literature data

The distributional ranges of all mainland Australian skinks (excluding all species endemic to Tasmania or smaller islands) were obtained from an updated version of Roll et al. (2017) and Gumbs et al. (2020) (version known internally as GARD 1.7). For each species we obtained values for mean annual precipitation and temperature, and seasonality in these variables from Karger et al. (2017; 'CHELSA'), and net primary productivity (NPP) data from Imhoff et al. (2004), as mean values across the range of each species. We assigned to each species the biome where the largest part of its range occurred (according to Olson et al., 2001; Supporting Information Figure S1) to test whether the vegetation structure/climatic association manifest in this categorization is more important than the climatic values per se in influencing range size.

The most striking major geographic discontinuity in Australia is the Great Dividing Range (GDR). This extensive (*c.* 3,500 km long) array of plateaus and mountain chains runs in the east of the continent roughly from Cape York in the north all the way to the Grampian mountains in southern Victoria in the south, and divides Australia into two very unequal parts. It serves as a major watershed and separates the general more mesic east from the more arid west. While the mountains are not particularly high, reptile beta diversity is greater along the Great Dividing Range than anywhere else in mainland Australia (Powney et al., 2010). Reptile ranges are generally much smaller to the east of the range than west of it, perhaps because the east simply has less space before the continent ends. To account for the effect of this major biogeographic filter, we designated species as either being from the east of the range (226 species), west of it (136 species), or traversing it (77 species traversing its centre, sometimes going over to the east, or west, or both). We then coded species according to this trichotomy for use in statistical models.

Mass estimates for each species are derived from maximum snout–vent length data, converted to masses using allometric equations that take leg development into account (Feldman et al., 2016). Mass and leg development (fully legged, limb-reduced, or limbless) data are from Meiri (2018). We obtained mean clutch or litter sizes for all species for which data were available from Meiri et al. (2020).

2.2 | Data-rich analysis incorporating museum specimen data

We identified nine pairs of species for which one was wide-ranging and the other narrow-ranged, and met four criteria: (a) they are congeneric and have similar degrees of limb development; (b) sufficient sample sizes (at least 20 adult specimens of the narrow-ranging species and 50 of the wide-ranging species) were available in natural history museums to enable statistical analyses to be conducted; (c) the wide-ranging species' range size is at least 10 times as large as that of the narrow-ranged species (this condition was met for eight pairs, for the ninth, the range of *Menetia maini* is 9.5 times as large as that of *Menetia alanae*; all other ratios are > 20; range 9.5–93849, median = 57); and (d) there was substantial overlap in the ranges of the species (at least 90% of the range of the narrow-ranging species is nested within that of the wide-ranged species) (Figure 1).

We measured 1,324 specimens (Supporting Information Table S6) belonging to these nine species pairs at the following Australian museums: Museums Victoria, Western Australian Museum, South Australian Museum, Museum and Art Gallery of the Northern Territory, Australian Museum, and the Queensland Museum. Maps of the distributions of these nine species pairs are shown in Figure 1.

Between 21 and 50 specimens of each narrow-ranged species were examined (depending on the number of specimens available in museum collections), and 50–168 specimens were examined for each widespread species (Supporting Information Table S2). Specimens whose bodies were preserved in a flat, straight posture with all limbs, toes, and original tails present were preferentially selected, to improved measurement accuracy. External morphological measurements were taken for each specimen as outlined in Supporting Information Table S3, using digital callipers (Mitutoyo 500–763–20 8"/200 mm Coolant Proof Digimatic Calipers with data output). As *Lerista bipes* contains no apparent groove or scale to indicate the location of the vestigial front limb, the snout–axilla length (SAL) and interlimb length (ILL) were unable to be measured. In order to estimate these values, measurements of 50 specimens of the similar-sized *Lerista onsloviana* (a congener lacking forelimbs, but with a consistent external marker of the location of the vestigial front limb, a groove where the front limb structure would be; Wilson & Swan, 2017) were used to estimate these values. The ILL and SAL of each specimen of *L. bipes* was calculated by determining the relationship between SVL and ILL and SAL in *L. onsloviana* specimens, and then using the SVL of *L. bipes* specimens to predict their ILL and SAL.

To examine clutch size and age, a small ventral incision along the left side of the specimen was made in order to determine the sex and sexual maturity of each individual. If an existing incision was already present, that was used instead. Male specimens were considered sexually mature if they had large testes and the ductus deferens appeared to be rough (rather than smooth, as found in juveniles). Maturity of females was determined based on the presence of a folded oviduct extending cranially from the ovary. In juvenile females this portion of the oviduct is smooth and not folded. For specimens that appeared to be gravid upon external examination, the incision was made down the midline to easily count the number of eggs. The reproductive condition (gravid or non-gravid) was recorded for each sexually mature female, along with the clutch or litter size. Only adult specimens were used to calculate trait means.

2.3 | Data analyses

All statistical analyses were performed using the statistical program R version 3.6.0 (R Core Team, 2020). Log10 transformations were applied to NPP, precipitation, body mass, and clutch/litter size data, as well as to range size, to normalize residuals and reduce heteroscedasticity. A minimum adequate model was derived via backwards

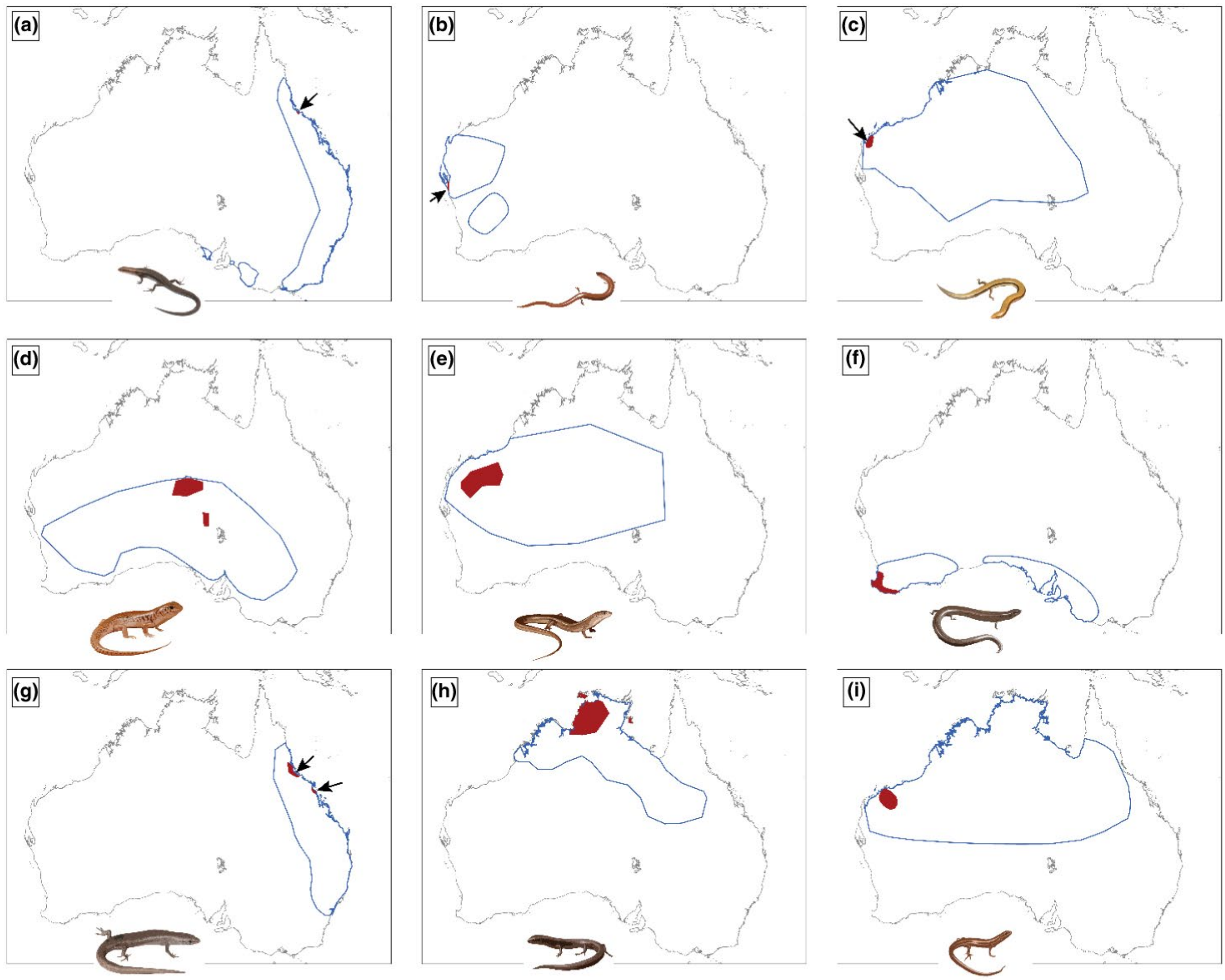

FIGURE 1 Maps of the distributions of wide-ranging (blue outline) and narrow-ranging (red fill, no outline) species pairs. Drawings are only of the wide-ranging species: (a) *Lampropholis delicata*; (b) *Lerista macropisthopus*; (c) *Lerista bipes*; (d) *Liopholis inornata*; (e) *Ctenotus helenae*; (f) *Hemiergis peronii*; (g) *Lygisaurus foliorum*; (h) *Menetia maini*; (i) *Notoscincus ornatus*. Narrow-ranging species (red ranges, no drawings): (a) *Lampropholis mirabilis*; (b) *Lerista kendricki*; (c) *Lerista onsloviana*; (d) *Liopholis slateri*; (e) *Ctenotus rutilans*; (f) *Hemiergis gracilipes*; (g) *Lygisaurus zuma*; (h) *Menetia alanae*; (i) *Notoscincus butleri*. All drawings are by Marco Camaiti

selection, starting with the least significant terms in the model. Statistical significance was set at $\alpha = .05$.

We tested for correlates of range size in all skink species using phylogenetic generalized least squares (PGLS) in the CAPER R package (Orme et al., 2014). For this analysis, we pruned the phylogenetic tree of Tonini et al. (2016) to include only the species used in the analysis of all Australian skinks. We ran the analyses with the scaling parameter λ set to its maximum likelihood value. We used range size (in km^2, log10 transformed) as the response variable and mean annual precipitation and temperature, precipitation and temperature seasonality, NPP, position relative to the Great Dividing Range (east, west or both), body mass, clutch/litter size, and leg development mode as the predictors. We used separate models with biome in lieu of mean annual precipitation, temperature, precipitation and temperature seasonality, and NPP, to test whether biomes or climate per se had greater influence on range size.

We tested for correlates of range size in the nine congeneric species pairs using phylogenetic mixed effects models in the mulTree package (Guillerme & Healy, 2014). We again used range size (in km^2, log10 transformed) as the response variable, with each morphological measurement and mean clutch size (log10 transformed) in turn treated as the predictor variable (i.e., one model for each trait). We added SVL as an additional predictor to all of these models (except for the model in which SVL was the sole predictor). We also fit separate models in which temperature, precipitation, and mean clutch size (not available for three species, as none of the museum specimens we examined were gravid) were included as predictors of range size. Random effects for 'species' and 'specimen' were also included, to account for the fact that multiple specimens of each species were measured. We used an inverse Wishart prior for the random effects (V = 1, nu = .02) and normal priors with a mean of 0 and a variance of 1,000 for the fixed effects. Models were run for 501,000 iterations, with the first 100,000 iterations discarded as 'burn- in', and every 10th sample retained. Convergence was evaluated via R-hat values.

3 | RESULTS

3.1 | Correlates of geographic range size

Geographic range sizes of Australian skink species are highly variable, from several species known only from their type locality (e.g., *Ctenotus aphrodite*, *Lerista quadrivincula*, *Cryptoblepharus wulbu*) to seven species with ranges that span more than half the continent (*Lerista timida*, *Ctenotus schomburgkii*, *Ctenotus inornatus*, *Ctenotus leonhardii*, *Ctenotus pantherinus*, *Eremiascincus richardsonii*, and *Menetia greyii*, the latter of which, with a range larger than 7 million km^2, spans 93% of mainland Australia). The distribution of range sizes is left-skewed (after logarithmic transformation), with a distinct mode around 300,000 km^2 (Figure 2).

Of the 438 skink species in mainland Australia for which we had data, 417 were represented in the phylogenetic tree of Tonini et al. (2016). Clutch sizes were only available for 259 of 417 species in the phylogeny, whereas all other traits were available for all species. Therefore, after the full model identified that clutch size was unrelated to range size (slope = −0.314 ± 0.354, p = .38) we removed this variable and reran the model for all 417 species. NPP (slope = 0.162 ± 0.274; p = .56 in the full model), temperature seasonality (slope = −0.0002 ± 0.0002; p = .26 in the full model), and mass (slope = 0.085 ± 0.079; p = .29 in the full model) were unrelated to range size. All other factors were significantly related to range size at α = .05. Range size increased with increasing temperatures and rainfall, and decreased with increasing precipitation seasonality, refuting the predictions of Rapoport's rule (Table 1). Range size was larger in fully-legged species (n = 313) than in limb-reduced (n = 91), but not limbless species (although n = 13) (Table 1). Ranges of species traversing the Great Dividing Range are larger by an order of magnitude than those east of the range, with western ranges being intermediate. Excluding this categorization and deriving a revised minimum adequate model results in positive effects of mass (0.175 ± 0.084; p = .039) and temperature seasonality (−0.0006 ± 0.0001; p ≤ .001), and effects of rainfall becoming non-significant (0.76 ± 0.54; p = .16). Interestingly, there was no phylogenetic signal in any model (λ = 0 regardless of whether models were simplified or not, and whether clutch size was used or not). A model with only the significant predictors explained 42.2% of the variation in range size. Variance inflation factors were ≤ 4.1.

When each species was assigned to the biome in which most of its range occurred, desert species had the widest ranges (Figure 3; Supporting Information Table S4), but a model with biome of origin as the sole predictor, and one with biome, body mass and leg development, explained substantially less variation in range size (11.7 and 18.7%) than the climatic/environmental model that only included significant predictors [Table 1; 32.7% of the variation in range size; Akaike's information criterion (AIC) values: 1,295.1, 1,282.3, and 1,199.9, respectively].

None of the 12 morphological traits differed between range-restricted species and their widespread overlapping congeners (Supporting Information Table S5). Clutch sizes were also similar between wide-ranging and small-ranging species (means: 2.52 eggs for small-ranged and 2.57 eggs for wide-ranging species). Narrow-ranging species experienced higher mean annual temperatures (by 1.09 ± 0.53 °C, although 95% credible intervals slightly overlapped 0) and more mesic conditions than wide-ranging congeners (by 42.5 ± 7.3%) (Supporting Information Table S5).

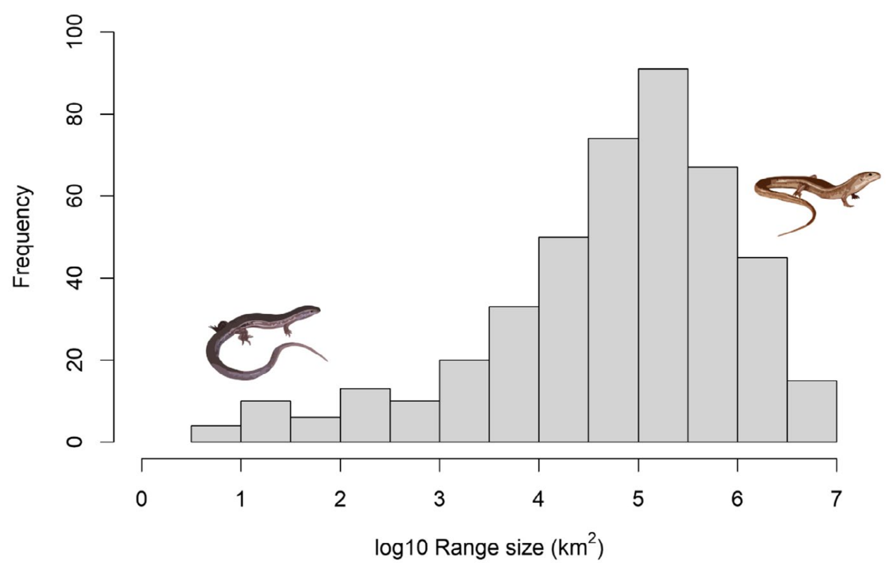

FIGURE 2 Distribution of geographic range sizes among all Australian skinks (log10 transformed). Skink images are placed approximately above their respective range sizes (*Ctenotus lancelini*, 1.08 = 12 km^2; *Ctenotus inornatus*, 6.65 = 4,467,000 km^2)

TABLE 1 Significant factors explaining range size across Australian mainland skinks ($n = 417$ species with phylogenetic data). t and p values for leg development specify differences from zero for species with fully developed limbs, and for differences from species with fully developed limbs for legless and leg reduced species (intercepts and standard errors are for each level, without reference to the others)

Variable	Estimate	*SE*	*t*	*p*
Intercept (both sides)	−0.790	1.352	−0.585	.559
GDR: east versus both sides	−1.270	0.145	−8.755	< .0001
GDR: east versus west	−0.508	0.131	−3.888	< .0001
GDR: both sides versus west	−0.761	0.13	−5.840	< .0001
Mean annual temperature	0.142	0.023	6.161	< .0001
Precipitation seasonality	−0.023	0.003	−6.946	< .0001
Precipitation (log10)	1.409	0.347	4.060	< .0001
Leg reduced versus fully legged	−0.672	0.118	−5.690	< .0001
Limbless versus fully legged	−0.266	0.269	−0.987	.324

Abbreviation: GDR, Great Dividing Range.

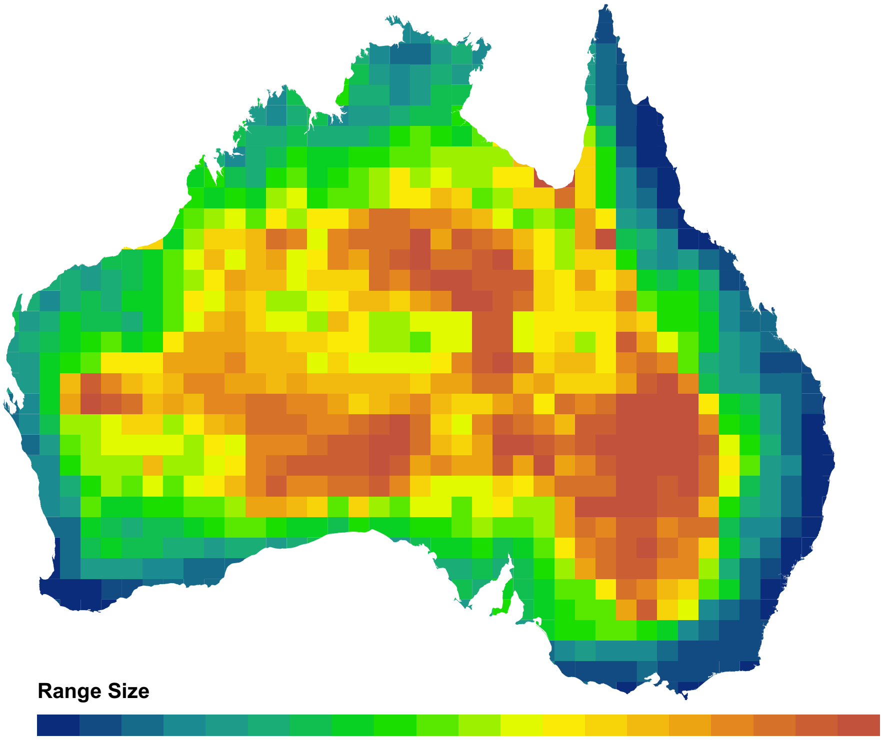

FIGURE 3 Range sizes of Australian mainland skinks. Values are averages of range sizes within 96.5 × 96.5 km grid cells (equal-area Behrmann projection). Each of the 20 colours represents a quantile: 5% of all cells with successively larger distributions from dark blue (smallest ranges: 584,000 km^2 minimum), via green and yellow (intermediate ranges) to dark brown (largest ranges; maximum: 3,223,000 km^2)

4 | DISCUSSION

Animals display significant variation in range size and Australian skinks are no exception. It is difficult to define the range size of species known only from their type series or type specimen (Meiri et al., 2018), as in 10 of the species we examined (e.g., *Lerista talpina*, *Lerista anyara*), but some species (such as *Saproscincus saltus* or the recently described *Egernia roomi*) are, in reality, found only at a single locality – such as a mountaintop or an isolated rock outcrop. Thus, range sizes of Australian skinks span about a million-fold range, with most species ranging over 30,000 to 3,000,000 km^2 (Figure 2). We aimed to uncover the causes of this substantial variation here and were only partially successful.

Intriguingly, even closely related species often have very different range sizes. Indeed, we found no phylogenetic signal in range size, which is perhaps surprising given the high phylogenetic signal routinely found in most ecological and even biogeographic traits. Several groups of organisms, including lizards, do show such a phylogenetic signal in range size (e.g., Agosta et al., 2013; Whitmee & Orme, 2013). Interestingly, Lee et al. (2013) found a strong phylogenetic signal in the range size of Australian skinks of the genus *Lerista*. Studies of other taxa did not find such a signal (Webb & Gaston, 2003, in birds; Raia et al., 2011, and Whitmee & Orme, 2013, in mammals; Slove & Janz, 2011, in butterflies), and neither did we find it here. Indeed, our analyses of pairs of wide-ranging and narrow-ranging species hinge on the fact that even within the same genus ranges can vary several-fold. It may be that the PASTIS tree we used (Tonini et al., 2016), in which phylogenetic placement of species with no genetic data is inferred based on taxonomy, makes it inappropriate to estimate such phylogenetic signal. The fact remains, however, that several closely related species have very dissimilar range sizes (e.g., Figure 1).

Scale may be an important factor when assessing phylogenetic signal in range size. For example, Pigot et al. (2018) suggested that the intermediate level of phylogenetic signal in the range sizes of birds derived from the tendency of closely related species to be spatially clustered. Such clustering is very likely to manifest in global analyses where, for example, closely related species may share the same continent whereas others can be restricted to islands on an archipelago, enabling the first group, but not the second one, to have large range sizes. In Australia, physical barriers to dispersal (such as large rivers or high mountain chains) are few (with the Great Dividing Range perhaps coming closest, as revealed by our analysis). Abiotic and biotic filters related to climate and biomes may exert weak pressure on spatial clustering of closely related species. Furthermore, the exclusion of insular endemics from our analyses means all species in our dataset basically share the same domain. This, coupled with intrinsic traits having little influence, may explain the lack of phylogenetic signal in range size.

Our findings suggest that intrinsic factors, such as the size of different organs, were generally not associated with range size. The only exception was limb development mode, whereby, in the broader analysis, fully-legged species had larger ranges than limb-reduced and limbless species, potentially due to the effects of limb development on dispersal (interestingly, limb-reduced forms have smaller ranges than completely limbless species moving in serpentiform fashion). The final model for the broader analysis did not include an effect of body mass, although mass did have an effect in a univariate model. Brown and Maurer (1989) originally described the relationship between body size and range size as a triangle, in which small-bodied species are characterized by either small or large ranges and large-bodied species often have larger ranges. It has been thought that species with larger body sizes require larger ranges to persist due to their lower population densities (Brown & Maurer, 1989; Diniz-Filho et al., 2005). While even the largest Australian skinks are much smaller than the large bodied mammals previously analysed (Brown & Maurer, 1989), and being ectotherms need a fraction of the resources, the shape of the mass versus range size relationship of Australian skinks is very similar to that of mammals (Figure 4). No skink larger than 100 g in (maximum) mass has a small (< 10,000 km^2) range. We suspect that this relationship may be an artefact of the unimodal and skewed nature of both the body mass and range size distributions. Indeed, some of the largest described skinks have (or had) tiny distributions (e.g., the insular *Chioninia coctei* and *Phoboscincus bocourti*).

We did not find any relationship between clutch size and range size in either dataset. Seasonality and reproductive season length were recently found to affect clutch sizes in lizards globally (Meiri et al., 2020). Species inhabiting high latitudes are exposed to cooler, often more seasonal climates, with a smaller window for reproduction and growth. As such, lizards living in temperate (i.e., more seasonal) environments may accelerate growth (as some migrating birds do: Meiri & Yom-Tov, 2004), reproduce at smaller sizes, and as a result, have smaller clutch sizes. It is unlikely, however, that this is a

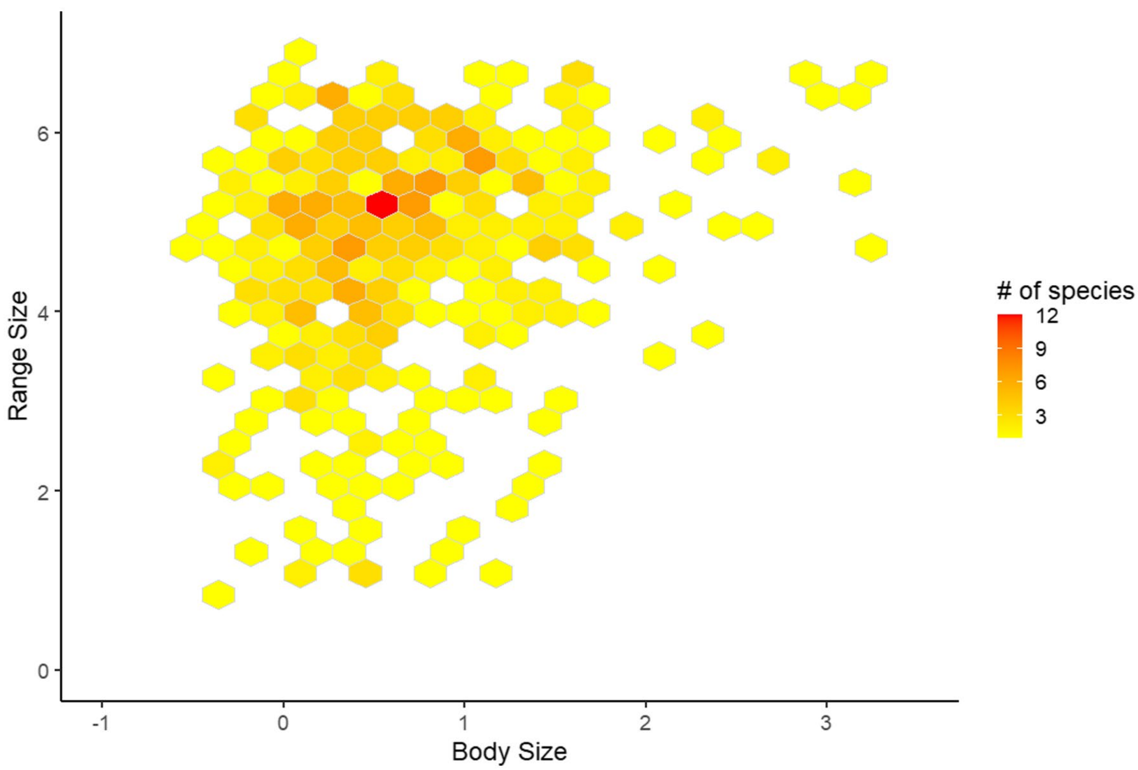

FIGURE 4 Range size versus maximum body mass in Australian skinks ($n = 438$). Colours depict the number of species (1–12) in each body/range size category. Range sizes in log(km^2), body sizes are species maxima in log grams (all logarithms to base 10)

confounding factor that prevented us from finding a real relationship as only rainfall seasonality (not temperature seasonality) emerged as a significant predictor of range size, and small-ranged (not large-ranged) species were more likely to occupy regions with high rainfall seasonality. It may be that neonate dispersal in species without parental care, such as almost all reptiles, precludes a range size versus clutch size relationship. Interestingly, one of the only clades of lizards in which parental care is frequent is the Australian near-endemic radiation of the skink subfamily Egerniinae. Nonetheless, it does not seem there is a true relationship between litter size (all Australian egerniines are viviparous) and range size even in this group. For example, among our species pairs, the narrow-ranged egernine *Liopholis slateri* has a litter size of 3.3 neonates, on average, whereas the litter size of the wide-ranged *Liopholis inornata* is 2.5.

In Australian skinks, climatic factors (including biomes) were better predictors of range size than intrinsic traits. It seems as if in determining range size where you are (geography) is more important than who you are (phylogeny) or what you are (traits). In squamates, selection on life history traits imposed by the thermal environment is likely due to differences in the duration of activity times, both on a daily and seasonal basis (Meiri et al., 2012; Sears & Angilletta, 2004). While the influence of temperature on species distribution and physiological variation has long been studied (Hoffmann & Watson, 1993; Huey, 1978; Janzen, 1967; Pither, 2003; Sunday et al., 2011), seasonality may also contribute to patterns of geographic range size (Sheldon & Tewksbury, 2014). Janzen (1967) reasoned that in more seasonal regions animals are 'automatically' adapted to a wider range of climatic conditions, which preadapts them to disperse and occupy larger ranges. Studies in mammals and amphibians have found that low seasonality in temperature and high seasonality in precipitation were linked to small range sizes (Di Marco & Santini, 2015; Whitton et al., 2012). Both these conditions are apparent in Australia's tropical regions, where temperature fluctuations are minimal (Bureau of Meteorology, 2018a) and rainfall is highly seasonal (Bureau of Meteorology, 2018b). Tropical and temperate species experience major differences in seasonality, which affects their thermal tolerance breadth (Sheldon & Tewksbury, 2014), and therefore the range of habitats species can occupy. However, we found that range size was negatively related to rainfall seasonality in our study.

We reasoned that the discrepancy between the large and continuous arid desert and the smaller, disjunct mesic areas in Australia would result in a strong tendency for wide-ranged species to occupy low rainfall regions. Precipitation was indeed the strongest correlate of range size in the congeneric species analyses, with wide-ranging species occupying more arid ranges. However, despite desert species also having large ranges in the analysis of all skink species, we found that precipitation had a positive effect on range size. Interestingly, this effect was only apparent when including a species' range position relative to the Great Dividing Range; when the GDR variable was excluded from the initial model, effects of rainfall became non-significant. This finding is likely due to the fact that regions east and north-west of the Great Dividing Range are significantly more mesic than those directly west of it. Thus, ranges are only larger in mesic regions after controlling for effects of the Great Dividing Range. The discrepancy between the results of the congeneric species analysis (in which arid regions hosted larger-ranged species), and the one based on the broader skink fauna, may be caused by the different nature of the analyses. The congeneric analyses focused on the edges of the range size distribution, whereas the analyses of all skink species focused on the more abundant centre. The congeneric analyses therefore emphasize the very small ranges of skinks in places such as those east of the Great Dividing Range or in the SW corner, whereas those of all skinks are more sensitive to variation across the arid centre and the more mesic north (Figure 3).

Ultimately, we think that neither climatic conditions nor biome distribution explains the variation in the range sizes of Australian skinks well. Large ranges occur not only in the desert but also in the Temperate Grassland and Subtropical Savannah biomes. This results in the somewhat conflicting outputs of our analyses, and failure to explain much of the variation in range size. Despite the modest height of the Great Dividing Range, it seems it is the major feature affecting range size breaks in Australian skinks, with climatic conditions in southern Victoria (SE Australia), the SW corner in Western Australia, and potentially in the Top-End (Northern Territory), also exerting significant effects.

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AUTHOR CONTRIBUTIONS

M.B., S.M. and D.G.C. conceived the ideas; M.B., L.R.B., A.D., S.M., C.T.G. and G.M.S. collected the data; M.B., S.M. and R.T. analysed the data; R.T. and S.M. produced the figures; D.G.C., R.T., S.M. and M.B. led the writing, with all authors contributing to the drafts.

DATA AVAILABILITY STATEMENT

All data are provided in the online Supporting Information, and via the Bridges online repository (https://doi.org/10.26180/16780570).

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BIOSKETCH

David Chapple leads an evolutionary ecology of environmental change research group (https://www.chapplelab.com/). His group uses a range of approaches to examine the responses of animals to both historical and contemporary (i.e., human-induced) environmental change. We investigate both species that expand their ranges (invasive species) and decline their ranges (threatened species) in response to this human-induced environmental change.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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Supplementary Material

Table S1. All mainland Australian skink species analysed and pertaining predictor and response variables.

Species	name in tree	Clutch size	Temperature	Temperature seasonality	Precipitation seasonality	Precipitation	NPP	Body mass	Leg development	Range size
Acritoscincus duperreyi	*Bassiana duperreyi*	NA	13.4	776.6	24.2	3998	11.62	1.02	fully limbed	413907.2
Acritoscincus platynotus	*Bassiana platynota*	NA	14.8	807	22.8	4687	11.71	1.02	fully limbed	336962.7
Acritoscincus trilineatus	*Bassiana trilineata*	0.48	16.9	457.4	44.4	4060	11.35	1.02	fully limbed	319912.1
Anepischetosia maccoyi	*Anepischetosia maccoyi*	0.48	12.8	856.1	21.3	3950	11.69	0.62	fully limbed	179945
Anomalopus brevicollis	*Anomalopus brevicollis*	NA	22.1	723.6	58.4	4117	11.52	0.21	limbless	166576.5
Anomalopus gowi	*Anomalopus gowi*	NA	22.4	842.4	96.4	3265	11.55	0.47	limbless	92051.1
Anomalopus leuckartii	*Anomalopus leuckartii*	NA	18.9	728.2	39.4	4615	11.61	1.07	reduced	397694.6
Anomalopus mackayi	*Anomalopus mackayi*	NA	19.9	512.7	31.2	5595	11.33	0.96	reduced	65438
Anomalopus pluto	*Anomalopus pluto*	NA	25.9	1692.3	102	1090	11.72	0.12	limbless	2786.7
Anomalopus swansoni	*Anomalopus swansoni*	NA	17.1	892.2	27.3	4184	11.68	0.46	limbless	18137.7
Anomalopus verreauxii	*Anomalopus verreauxi*	NA	20.2	833.5	47.7	4155	11.61	1.4	reduced	344286.4
Austroablepharus barrylyoni	*Proablepharus barrylyoni*	0.52	23.4	806	112	3008	11.49	0.39	fully limbed	12.3
Austroablepharus kinghorni	*Proablepharus kinghorni*	0.21	23.9	432.1	71.6	5191	10.98	0.27	fully limbed	1326824.6
Austroablepharus naranjicaudus	*Proablepharus naranjicaudus*	NA	27.3	706.6	110.8	3268	11.18	0.32	fully limbed	89227.7
Bellatorias frerei	*Bellatorias frerei*	NA	22.5	1074.2	71.8	3116	11.63	2.37	fully limbed	459973.6
Bellatorias major	*Bellatorias major*	0.52	18.3	1191.8	40	3722	11.75	3.25	fully limbed	72336.8
Bellatorias obiri	*Bellatorias obiri*	NA	27.1	1460.7	107.8	2037	11.55	2.36	fully limbed	4219.5
Calyptotis lepidorostrum	*Calyptotis lepidorostrum*	NA	21.6	1073.6	56.7	3451	11.67	0.49	fully limbed	76644.6
Calyptotis ruficauda	*Calyptotis ruficauda*	NA	17.2	1249.2	40.2	3730	11.71	0.49	fully limbed	36947.7
Calyptotis scutirostrum	*Calyptotis scutirostrum*	0.72	19.5	964.1	45.5	3815	11.71	0.59	fully limbed	145320.1
Calyptotis temporalis	*Calyptotis temporalis*	0.21	22.7	1162.7	67.9	3263	11.67	0.18	fully limbed	20174.4
Calyptotis thorntonensis	*Calyptotis thorntonensis*	NA	22.2	3350.8	84.6	1880	12	-0.14	fully limbed	97.7
Carinascincus coventryi	*Niveoscincus coventryi*	NA	12.1	849.2	19.1	4232	11.78	0.47	fully limbed	133420.4
Carinascincus metallicus	*Niveoscincus metallicus*	0.7	11.5	1184.5	22.2	2989	11.64	0.85	fully limbed	96543.9
Carlia amax	*Carlia amax*	0.3	26.8	894.5	110.9	2848	11.28	0.08	fully limbed	753604.6
Carlia crypta	*NA*	NA	22.8	2068.7	91.1	2011	11.99	0.48	fully limbed	2391.2
Carlia decora	*Carlia decora*	NA	23.2	1501.2	87.4	2948	11.7	0.33	fully limbed	40731.5
Carlia dogare	*Carlia dogare*	NA	25.6	1185.3	108.7	1844	11.68	0.36	fully limbed	15243.4
Carlia gracilis	*Carlia gracilis*	0.3	27.1	1162.3	108.6	2133	11.45	0.08	fully limbed	280252.2
Carlia isostriacantha	*NA*	0.2	27	960.2	114.4	2451	11.26	0.34	fully limbed	129803.7
Carlia jarnoldae	*Carlia jarnoldae*	NA	24	1082.6	101.9	2623	11.59	0.33	fully limbed	239060.3
Carlia johnstonei	*Carlia johnstonei*	0.3	26.6	1164.2	115	2063	11.35	0.17	fully limbed	62087
Carlia longipes	*Carlia longipes*	NA	25.8	1904.8	62.5	944	11.81	0.89	fully limbed	60361.6
Carlia munda	*Carlia munda*	0.18	25.1	687.2	92.7	3920	11.23	0.18	fully limbed	2703636.6
Carlia pectoralis	*Carlia pectoralis*	0.3	21.1	769	50	4149	11.58	0.71	fully limbed	218166
Carlia rhomboidalis	*Carlia rhomboidalis*	NA	22.9	1414.1	84.1	3142	11.58	0.64	fully limbed	11001.2
Carlia rostralis	*Carlia rostralis*	0.4	23.2	1666.1	94	2344	11.78	0.83	fully limbed	41851.6
Carlia rubigo	*Carlia rubigo*	0.77	22	729.7	62.6	4241	11.47	0.19	fully limbed	332910.7
Carlia rubrigularis	*Carlia rubrigularis*	0.3	22.7	2135.9	84.8	2462	11.86	0.64	fully limbed	21870.6
Carlia rufilatus	*Carlia rufilatus*	0.6	27.2	1095.7	112.7	2344	11.39	0.12	fully limbed	299086.2
Carlia schmeltzii	*Carlia schmeltzii*	0.6	22.8	878.4	76.5	3504	11.54	0.81	fully limbed	685484.1
Carlia sexdentata	*Carlia sexdentata*	0.44	26.3	1421.5	111.2	1545	11.57	0.7	fully limbed	109427.6
Carlia storri	*Carlia storri*	NA	25.4	1723.6	94.8	1525	11.74	0.24	fully limbed	147721.7

Carlia tetradactyla	*Carlia tetradactyla*	0.3	15.5	767.3	25.6	4835	11.72	0.71	fully limbed	242171.8
Carlia triacantha	*Carlia triacantha*	0	25.8	569.8	94.3	4333	11.06	0.44	fully limbed	1878729.9
Carlia vivax	*Carlia vivax*	0.37	21.9	957.5	70.9	3449	11.59	0.36	fully limbed	745876.3
Carlia wundalthini	*Carlia wundalthini*	NA	24.5	1633	105.3	1526	11.75	0.33	fully limbed	60.2
Coeranoscincus frontalis	*Coeranoscincus frontalis*	0.48	22.4	2161.3	83.5	2566	11.87	1.46	limbless	18946.7
Coeranoscincus reticulatus	*Coeranoscincus reticulatus*	0.88	19.1	1166.7	43.2	3688	11.84	1.45	reduced	37578.3
Concinnia amplus	*Concinnia amplus*	NA	22.7	1397.1	84.5	3132	11.76	1.53	fully limbed	8152.1
Concinnia brachysoma	*Concinnia brachyosoma*	NA	22.7	824.3	73.3	3685	11.51	0.95	fully limbed	434410.3
Concinnia frerei	*Concinnia frerei*	NA	20.8	2131.4	87.1	2158	11.99	0.83	fully limbed	924.5
Concinnia martini	*Concinnia martini*	0.28	19.8	861.6	47	4065	11.65	0.85	fully limbed	281961.7
Concinnia queenslandiae	*Concinnia queenslandiae*	0.33	22.5	2347.3	81.2	2358	11.83	1.11	fully limbed	14766.3
Concinnia sokosoma	*Concinnia sokosoma*	0.55	22.6	732.4	67.6	3975	11.49	1	fully limbed	295342.9
Concinnia tenuis	*Concinnia tenuis*	0.3	18.8	920.9	44.3	4091	11.67	1.11	fully limbed	502708.5
Concinnia tigrinus	*Concinnia tigrinus*	0.3	22.3	2437.6	79.8	2344	11.9	1.11	fully limbed	11414.7
Cryptoblepharus adamsi	*Cryptoblepharus adamsi*	0.26	23.3	1024.2	96.7	2927	11.59	-0.05	fully limbed	168904.6
Cryptoblepharus australis	*Cryptoblepharus australis*	0.7	21.3	326.2	42.6	5650	10.95	0.25	fully limbed	3408710.4
Cryptoblepharus buchananii	*Cryptoblepharus buchananii*	0.3	21.5	294.2	54.8	5479	10.99	0.34	fully limbed	1126524.5
Cryptoblepharus cygnatus	*Cryptoblepharus cygnatus*	0.58	27.1	1412.4	106	1737	11.56	0.2	fully limbed	99119.8
Cryptoblepharus daedalos	*Cryptoblepharus daedalos*	NA	27.3	803.8	113.6	2864	11.25	0.08	fully limbed	4062
Cryptoblepharus exochus	*Cryptoblepharus exochus*	NA	27.8	1001.7	114.1	2402	11.29	0.08	fully limbed	11618.3
Cryptoblepharus fuhni	*Cryptoblepharus fuhni*	NA	25.4	1470	106.8	1542	11.75	0.27	fully limbed	89.8
Cryptoblepharus juno	*Cryptoblepharus juno*	0.48	27.5	784.8	113.9	2901	11.18	0.15	fully limbed	116816.5
Cryptoblepharus litoralis	*Cryptoblepharus litoralis*	NA	25.2	1657.9	89	1973	11.4	0.49	fully limbed	19990.4
Cryptoblepharus megastictus	*Cryptoblepharus megastictus*	0.3	26.8	1147.7	112.2	1993	11.36	0.07	fully limbed	22543.9
Cryptoblepharus mertensi	*Cryptoblepharus mertensi*	0.49	26.7	830.2	112.5	2765	11.32	-0.01	fully limbed	34844.6
Cryptoblepharus metallicus	*Cryptoblepharus metallicus*	0.44	25.6	768	100.3	3487	11.28	0.3	fully limbed	2091644.3
Cryptoblepharus ochrus	*Cryptoblepharus ochrus*	NA	21.9	170.1	35.1	6360	10.54	0.18	fully limbed	336894
Cryptoblepharus pannosus	*Cryptoblepharus pannosus*	0.4	21.8	478.7	53.7	5132	11.11	0.18	fully limbed	2570002.5
Cryptoblepharus plagiocephalus	*Cryptoblepharus plagiocephalus*	0.67	22.2	238.7	51.6	5763	10.88	0.27	fully limbed	508873.2
Cryptoblepharus pulcher	*Cryptoblepharus pulcher*	0.3	18.7	739.9	40.8	4065	11.51	0.21	fully limbed	756374
Cryptoblepharus ruber	*Cryptoblepharus ruber*	0.13	27.2	761.5	114.5	3099	11.21	0.28	fully limbed	497328.8
Cryptoblepharus tytthos	*Cryptoblepharus tytthos*	NA	27.8	714.5	122.3	2977	11.22	0	fully limbed	69470.1
Cryptoblepharus ustulatus	*Cryptoblepharus ustulatus*	0.28	25.8	322	88.6	5116	10.91	0.1	fully limbed	188660.4
Cryptoblepharus virgatus	*Cryptoblepharus virgatus*	0.78	25	1359.8	108.3	1971	11.64	0.08	fully limbed	188028.4
Cryptoblepharus wulbu	*Cryptoblepharus wulbu*	NA	27.6	1416	110	1483	11.6	0.01	fully limbed	12
Cryptoblepharus zoticus	*Cryptoblepharus zoticus*	NA	26.3	676.1	111.9	3551	11.16	0	fully limbed	161357.9
Ctenotus agrestis	*Ctenotus agrestis*	0.51	24.8	419.6	82.5	5020	10.95	0.93	fully limbed	78476.3
Ctenotus alacer	*Ctenotus alacer*	0.54	24.1	302.8	67.4	5945	10.86	0.78	fully limbed	722617.9
Ctenotus alleni	*Ctenotus alleni*	0.3	21.6	287.9	71.5	4757	11.15	1.23	fully limbed	13512.2
Ctenotus allotropis	*Ctenotus allotropis*	0.29	20.1	507.5	33.5	5585	11.3	0.49	fully limbed	511698.3

Ctenotus angusticeps	*Ctenotus angusticeps*	0.6	27.2	392.6	103.8	3425	11.02	0.91	fully limbed	27159
Ctenotus aphrodite	*Ctenotus aphrodite*	NA	25	244.5	71.8	5929	10.57	0.87	fully limbed	10
Ctenotus arcanus	*Ctenotus arcanus*	NA	19.6	959.5	45.6	3824	11.73	1.19	fully limbed	87382.2
Ctenotus ariadnae	*Ctenotus ariadnae*	NA	23.5	252.9	53	6246	10.76	0.71	fully limbed	1189934.6
Ctenotus arnhemensis	*Ctenotus arnhemensis*	NA	27.7	1560.6	105.1	1737	11.62	0.5	fully limbed	10830.3
Ctenotus astarte	*Ctenotus astarte*	0.48	24.2	227.3	62	6190	10.63	1.05	fully limbed	172871
Ctenotus astictus	*Ctenotus astictus*	NA	26.8	1181.3	104.8	1890	11.41	0.41	fully limbed	47924.7
Ctenotus atlas	*Ctenotus atlas*	0.52	19.1	254.5	26.9	5122	10.97	0.93	fully limbed	985401.3
Ctenotus australis	*Ctenotus australis*	NA	18.3	681.3	77.2	3670	11.53	1.47	fully limbed	72200.9
Ctenotus borealis	*Ctenotus borealis*	0.55	27.2	1368	106.8	1935	11.52	1.6	fully limbed	119447.3
Ctenotus brevipes	*Ctenotus brevipes*	NA	25.5	1044.3	115.7	2413	11.5	0.62	fully limbed	252251.5
Ctenotus brooksi	*Ctenotus brooksi*	0.52	23.2	288.5	55.8	5733	10.82	0.54	fully limbed	1745904.6
Ctenotus burbidgei	*Ctenotus burbidgei*	NA	26.5	1162.6	114.8	2076	11.35	0.57	fully limbed	58046.9
Ctenotus calurus	*Ctenotus calurus*	0.33	23.3	283.1	56.2	5915	10.81	0.36	fully limbed	1489502.4
Ctenotus capricorni	*Ctenotus capricorni*	NA	23.6	420.3	60.5	5384	10.99	0.73	fully limbed	45974.9
Ctenotus catenifer	*Ctenotus catenifer*	0.48	16.4	585.7	54.3	3665	11.46	0.57	fully limbed	157542.2
Ctenotus coggeri	*Ctenotus coggeri*	0.3	26.5	1274.5	108	2072	11.52	1.14	fully limbed	50859.1
Ctenotus colletti	*Ctenotus colletti*	0.51	27.7	721.8	124.4	2948	11.25	0.21	fully limbed	31414.8
Ctenotus decaneurus	*Ctenotus decaneurus*	0.48	26.7	886.2	108.2	3025	11.24	0.48	fully limbed	466656.8
Ctenotus delli	*Ctenotus delli*	NA	16.8	841.4	79	4030	11.71	0.69	fully limbed	19898.4
Ctenotus duricola	*NA*	0.3	25.9	315.1	88.6	4995	10.91	0.59	fully limbed	224988.1
Ctenotus dux	*Ctenotus dux*	0.53	23.1	260.2	50.9	6173	10.78	0.76	fully limbed	1196448.7
Ctenotus ehmanni	*Ctenotus ehmanni*	NA	26.5	1040.8	113.7	2332	11.31	0.08	fully limbed	69660.2
Ctenotus essingtonii	*Ctenotus essingtonii*	0.64	26.9	1181.8	107.7	2155	11.46	0.89	fully limbed	230173.6
Ctenotus euclae	*NA*	0.44	18	247.4	24.5	4263	10.93	0.36	fully limbed	261676.6
Ctenotus eurydice	*Ctenotus eurydice*	NA	18.1	846	41.2	4156	11.73	0.96	fully limbed	132457.1
Ctenotus eutaenius	*Ctenotus eutaenius*	0.28	22.5	846.4	95.1	3281	11.55	1.19	fully limbed	100816.1
Ctenotus gagudju	*Ctenotus gagudju*	NA	27.6	1506.2	107.9	1645	11.6	0.47	fully limbed	4592.5
Ctenotus gemmula	*Ctenotus gemmula*	0.48	16.6	469.7	44.2	3798	11.36	0.62	fully limbed	177921.7
Ctenotus grandis	*Ctenotus grandis*	0.56	24.7	319.1	71.4	5643	10.84	1.61	fully limbed	1509638.4
Ctenotus greeri	*Ctenotus greeri*	0.73	23.8	344.5	69.6	5549	10.9	0.73	fully limbed	1000822.2
Ctenotus halysis	*Ctenotus halysis*	0.78	26.5	901.6	112.8	2623	11.25	0.58	fully limbed	56545.4
Ctenotus hanloni	*Ctenotus hanloni*	0.48	24.5	293.4	67.9	5798	10.82	0.9	fully limbed	1498571.6
Ctenotus hebetior	*Ctenotus hebetior*	0.48	24.6	445.7	83.8	4912	10.99	0.62	fully limbed	577613.7
Ctenotus hilli	*Ctenotus hilli*	0.52	27.3	1444.6	105.6	1816	11.54	0.36	fully limbed	74775.9
Ctenotus iapetus	*Ctenotus iapetus*	0.3	25.2	269.4	81.3	4730	10.94	0.79	fully limbed	69457.2
Ctenotus impar	*Ctenotus impar*	0.43	17.3	442.6	48	4286	11.37	0.75	fully limbed	305525.6
Ctenotus ingrami	*Ctenotus ingrami*	NA	21.4	529.9	45.8	5311	11.26	1.09	fully limbed	449793.7
Ctenotus inornatus	*Ctenotus inornatus*	0.39	24	405.6	70.5	5192	10.95	1.26	fully limbed	4464669.4
Ctenotus joanae	*Ctenotus joanae*	NA	25	319.4	79.9	5498	10.81	1.12	fully limbed	614042.6
Ctenotus kurnbudj	*Ctenotus kurnbudj*	NA	27.8	1605.6	103.9	1650	11.67	0.52	fully limbed	3261
Ctenotus labillardieri	*Ctenotus labillardieri*	NA	16.3	644.2	55.6	3457	11.49	0.95	fully limbed	118667.9
Ctenotus lancelini	*Ctenotus lancelini*	NA	19.4	655	85	3721	11.61	1.14	fully limbed	12.1
Ctenotus lateralis	*Ctenotus lateralis*	0.24	25.1	418.1	88	5004	10.91	1.11	fully limbed	407968.8
Ctenotus leae	*Ctenotus leae*	0.27	22.2	234.8	42.8	6027	10.75	0.66	fully limbed	1951800.8
Ctenotus leonhardii	*Ctenotus leonhardii*	0.78	23.4	318.3	61.7	5514	10.86	1	fully limbed	4712066.1

Ctenotus maryani	*Ctenotus maryani*	0.56	25.7	281.2	83.8	4882	10.94	0.49	fully limbed	75470.6
Ctenotus mastigura	*Ctenotus mastigura*	0.37	26.6	1341.5	111.3	1865	11.43	1.15	fully limbed	6694.3
Ctenotus mesotes	*Ctenotus mesotes*	NA	27.6	1123.7	117.2	1708	11.39	0.1	fully limbed	1404
Ctenotus militaris	*Ctenotus militaris*	0.3	27.2	741.8	112.7	3157	11.21	0.73	fully limbed	311370
Ctenotus mimetes	*Ctenotus mimetes*	0.46	21.1	267.3	52.2	5786	11.06	1.05	fully limbed	181999.4
Ctenotus monticola	*Ctenotus monticola*	NA	21.8	1207.7	95.6	2388	11.7	0.73	fully limbed	2023.1
Ctenotus nasutus	*Ctenotus nasutus*	0.36	24.5	299.2	64.4	5968	10.8	0.24	fully limbed	936344.2
Ctenotus nigrilineatus	*Ctenotus nigrilineatus*	0.48	26.2	341.7	93.7	4998	10.87	0.33	fully limbed	32458
Ctenotus nullum	*Ctenotus nullum*	0.3	25.1	1285.9	106.1	1903	11.74	1	fully limbed	11115.9
Ctenotus olympicus	*Ctenotus olympicus*	0.42	20.5	204.2	27.9	6025	10.73	0.93	fully limbed	706144
Ctenotus ora	*Ctenotus ora*	NA	17.6	931.8	81.8	3098	11.74	0.62	fully limbed	1676.3
Ctenotus orientalis	*Ctenotus orientalis*	NA	17.7	343.8	25.5	5039	11.1	1.05	fully limbed	1008307.5
Ctenotus pallasotus	*NA*	0.3	25.6	345.7	90.2	4985	10.95	0.73	fully limbed	105695.6
Ctenotus pallescens	*Ctenotus pallescens*	0.56	26.8	559.3	107	4007	11.09	0.21	fully limbed	403374.7
Ctenotus pantherinus	*Ctenotus pantherinus*	0.58	23.7	368.5	66.9	5295	10.92	1.66	fully limbed	5203183.8
Ctenotus piankai	*Ctenotus piankai*	0.58	24.9	356.9	76.2	5403	10.89	0.62	fully limbed	2013053.4
Ctenotus pulchellus	*Ctenotus pulchellus*	NA	25.8	479.4	100.6	4471	11.01	1.11	fully limbed	487358
Ctenotus quattuordecimlineatus	*Ctenotus quattuordecimlineatus*	0.34	23.4	285.7	57.5	5830	10.82	0.85	fully limbed	1773968.3
Ctenotus quinkan	*Ctenotus quinkan*	0.3	24.7	1135.6	111	2002	11.72	1.04	fully limbed	5035.2
Ctenotus quirinus	*Ctenotus quirinus*	0.54	26.6	1119.1	106.7	2186	11.46	0.73	fully limbed	90611
Ctenotus rawlinsoni	*Ctenotus rawlinsoni*	0.3	25.8	1597.5	94.9	1721	11.89	1.02	fully limbed	953.9
Ctenotus regius	*Ctenotus regius*	0.6	20.8	239	31.7	5998	10.81	1.07	fully limbed	1706389.9
Ctenotus rhabdotus	*NA*	NA	27.6	530.3	111.2	4037	11.06	0.64	fully limbed	43176
Ctenotus rimacolus	*Ctenotus rimacolus*	0.36	27.5	707.5	111	3242	11.16	1.26	fully limbed	104135.2
Ctenotus robustus	*Ctenotus robustus*	0.48	21.4	665	60.6	4263	11.31	1.65	fully limbed	3394017.5
Ctenotus rosarium	*Ctenotus rosarium*	NA	23.2	544.5	78.5	4344	11.26	0.18	fully limbed	8062.8
Ctenotus rubicundus	*Ctenotus rubicundus*	0.29	25.7	316.1	87	5276	10.89	1.35	fully limbed	192672.1
Ctenotus rufescens	*Ctenotus rufescens*	NA	26.3	296.5	89.2	4134	10.94	0.21	fully limbed	49510.7
Ctenotus rutilans	*Ctenotus rutilans*	NA	25.2	313.9	84.4	5526	10.88	0.6	fully limbed	119782.9
Ctenotus schevilli	*Ctenotus schevilli*	0.48	24.8	452.8	85.2	4739	11.03	1.11	fully limbed	57308.7
Ctenotus schomburgkii	*Ctenotus schomburgkii*	0.3	22.1	276.4	51.4	5617	10.87	0.54	fully limbed	4312617.3
Ctenotus septenarius	*Ctenotus septenarius*	0.43	23.4	246.9	56.3	6191	10.75	0.87	fully limbed	651380.6
Ctenotus serotinus	*Ctenotus serotinus*	NA	24.9	252.8	73.3	5918	10.58	0.36	fully limbed	3925.8
Ctenotus serventyi	*Ctenotus serventyi*	0.85	26.8	433.7	102.3	4354	10.97	0.54	fully limbed	390514.8
Ctenotus spaldingi	*Ctenotus spaldingi*	0.34	21.1	682.5	61.7	4219	11.36	1.47	fully limbed	2888860.4
Ctenotus storri	*Ctenotus storri*	NA	27.1	1191.4	108.6	2348	11.47	0.05	fully limbed	116948.6
Ctenotus strauchii	*Ctenotus strauchii*	0.3	22	373.4	49.7	5593	11	0.69	fully limbed	2788062.9
Ctenotus striaticeps	*Ctenotus striaticeps*	0.22	26.2	713.4	111.1	3460	11.18	0.36	fully limbed	139634.2
Ctenotus stuarti	*Ctenotus stuarti*	NA	27.8	1582.5	103.9	1701	11.64	0.47	fully limbed	4745.6
Ctenotus superciliaris	*NA*	0.3	26.8	686.7	106.2	3554	11.15	1.04	fully limbed	1148466
Ctenotus taeniatus	*NA*	0.35	21.6	205.2	37.6	6128	10.72	0.52	fully limbed	813568.5
Ctenotus taeniolatus	*Ctenotus taeniolatus*	0.43	19.5	718.1	46.5	4586	11.49	1.17	fully limbed	1202821.8
Ctenotus tanamiensis	*Ctenotus tanamiensis*	0.64	25.2	385.1	80.7	5475	10.92	1.26	fully limbed	449292.2
Ctenotus tantillus	*Ctenotus tantillus*	0.41	27.2	901.4	112.7	2593	11.26	0.26	fully limbed	136991.6
Ctenotus terrareginae	*Ctenotus terrareginae*	NA	22.8	1652.1	91.3	2989	11.89	1.2	fully limbed	4514.9

Ctenotus uber	*Ctenotus uber*	0.6	23.3	261.6	60.3	5860	10.86	1.05	fully limbed	1062721.4
Ctenotus vagus	*Ctenotus vagus*	NA	27.4	794.6	112.5	2792	11.15	0.18	fully limbed	51369.7
Ctenotus vertebralis	*Ctenotus vertebralis*	NA	26.8	1114.5	107.9	2265	11.43	0.49	fully limbed	179022
Ctenotus xenopleura	*Ctenotus xenopleura*	0.48	19	271.3	30.4	5588	11.16	0.36	fully limbed	28270.7
Ctenotus youngsoni	*Ctenotus youngsoni*	NA	22	288	94	2840	10.79	1.09	fully limbed	2198
Ctenotus zastictus	*Ctenotus zastictus*	NA	22.5	229.3	77.1	4092	11.1	0.62	fully limbed	98.4
Ctenotus zebrilla	*Ctenotus zebrilla*	0.65	24.1	784.1	110.7	3109	11.45	0.05	fully limbed	82595
Cyclodomorphus branchialis	*Cyclodomorphus branchialis*	NA	20.9	317.6	64.5	5384	11.17	1.59	fully limbed	56979
Cyclodomorphus celatus	*Cyclodomorphus celatus*	0.73	20.9	389.3	79.4	4262	11.28	1.6	fully limbed	72346.8
Cyclodomorphus gerrardii	*Hemisphaeriodon gerrardii*	0.28	20.3	927.9	54.4	3835	11.63	2.65	fully limbed	419640.5
Cyclodomorphus maximus	*Cyclodomorphus maxima*	0.48	26.7	1094.9	114.6	2117	11.32	2.51	fully limbed	82496.6
Cyclodomorphus melanops	*Cyclodomorphus melanops*	0.62	22.7	284.9	54.8	5573	10.85	1.72	fully limbed	3536491.2
Cyclodomorphus michaeli	*Cyclodomorphus michaeli*	0.4	16	1018.2	24.9	3893	11.61	2.11	fully limbed	37250.1
Cyclodomorphus praealtus	*Cyclodomorphus praealtus*	0.7	10.3	1092.7	24.1	4906	11.83	1.66	fully limbed	8620.1
Cyclodomorphus venustus	*Cyclodomorphus venustus*	0.3	22.2	217.5	42.6	6168	10.67	1.35	fully limbed	576425.7
Egernia cunninghami	*Egernia cunninghami*	0.59	15	747.7	23.6	4772	11.7	2.65	fully limbed	439014.3
Egernia cygnitos	*Egernia cygnitos*	0.29	26.6	325.3	95.9	4220	10.9	1.56	fully limbed	9385
Egernia depressa	*Egernia depressa*	NA	22.5	240	52.8	6021	10.86	1.55	fully limbed	450583.6
Egernia douglasi	*Egernia douglasi*	NA	26.9	973.9	118.8	2403	11.34	2.08	fully limbed	3135.2
Egernia eos	*Egernia eos*	0.3	24.2	297.5	56.7	6101	10.81	1.47	fully limbed	196019.8
Egernia epsisolus	*Egernia epsisolus*	0.6	27	322.7	97.7	4637	10.89	1.47	fully limbed	12758.5
Egernia formosa	*Egernia formosa*	NA	22.8	267.7	55.9	5899	10.85	1.43	fully limbed	316321.2
Egernia hosmeri	*Egernia hosmeri*	0.7	24.7	647.2	103.2	3789	11.22	2.16	fully limbed	215465.3
Egernia kingii	*Egernia kingii*	0.3	16.2	687.1	60.8	3478	11.53	2.62	fully limbed	96410
Egernia mcpheei	*Egernia mcpheei*	NA	16.8	1104.3	39.8	3892	11.8	1.83	fully limbed	74857.5
Egernia napoleonis	*Egernia napoleonis*	0.63	16.7	530.4	50.8	3761	11.4	1.73	fully limbed	206542.3
Egernia pilbarensis	*Egernia pilbarensis*	NA	26.1	353.4	94.5	4783	10.91	1.6	fully limbed	64636.9
Egernia richardi	*Egernia richardi*	0.47	17.5	307.1	29.6	4240	11.15	1.4	fully limbed	235846.9
Egernia rugosa	*Egernia rugosa*	0.65	22.7	748.3	71.8	4005	11.43	2.51	fully limbed	786934.1
Egernia saxatilis	*Egernia saxatilis*	0.82	13.4	792	20.2	4451	11.72	1.75	fully limbed	250880.3
Egernia stokesii	*Egernia stokesii*	0.58	21.1	244.7	40.1	5863	10.84	2.35	fully limbed	1248788.9
Egernia striolata	*Egernia striolata*	0.51	19.5	524.2	37.7	5132	11.3	1.58	fully limbed	1971876.8
Emoia longicauda	*Emoia longicauda*	0.61	23.4	3210.3	33.1	501	11.82	1.33	fully limbed	612689.6
Eremiascincus brongersmai	*Eremiascincus brongersmai*	NA	26.7	1223.4	114.5	1947	11.37	1.3	fully limbed	48371.6
Eremiascincus douglasi	*Eremiascincus douglasi*	0.48	27	1261.8	107	1986	11.48	1.05	fully limbed	203274.8
Eremiascincus fasciolatus	*Eremiascincus fasciolatus*	0.3	22	664.9	61.9	4218	11.46	1.63	fully limbed	435110.3
Eremiascincus intermedius	*Eremiascincus intermedius*	0.28	25.4	477.1	92.9	4703	11.04	1.16	fully limbed	778320.9
Eremiascincus isolepis	*Eremiascincus isolepis*	0.3	26.7	737.9	110.2	3304	11.21	0.93	fully limbed	1415504.5
Eremiascincus musivus	*Eremiascincus musivus*	0.3	27.2	404.1	106.2	4148	10.97	0.6	fully limbed	155313.2
Eremiascincus pallidus	*Eremiascincus pallidus*	0.52	23.7	285.1	61.7	5715	10.84	0.97	fully limbed	1856896.3

Eremiascincus pardalis	*Eremiascincus pardalis*	NA	25.5	1232.4	113.1	2046	11.57	0.93	fully limbed	226359.6
Eremiascincus phantasmus	*Eremiascincus phantasmus*	0.53	22.4	214	42.2	6305	10.69	1.26	fully limbed	948555.2
Eremiascincus richardsonii	*Eremiascincus richardsonii*	0.71	22.4	319.3	54.2	5557	10.92	1.67	fully limbed	5310041.9
Eremiascincus rubiginosus	*NA*	NA	24.4	401.9	91.7	5303	11	1.05	fully limbed	2085.7
Eroticoscincus graciloides	*Eroticoscincus graciloides*	0.3	20.6	1131.1	46	3587	11.75	-0.14	fully limbed	26729.7
Eugongylus rufescens	*Eugongylus rufescens*	0.3	25	3092.2	31.1	459	11.82	2.07	fully limbed	830809.9
Eulamprus heatwolei	*Eulamprus heatwolei*	0.48	13.7	843.4	23.2	4430	11.75	1.35	fully limbed	283849
Eulamprus kosciuskoi	*Eulamprus kosciuskoi*	0.48	12.4	1011.9	31.8	4370	11.89	1.11	fully limbed	34693.1
Eulamprus leuraensis	*Eulamprus leuraensis*	NA	12.2	1027.5	26	4416	11.89	1.11	fully limbed	1217.1
Eulamprus quoyii	*Eulamprus quoyii*	0.18	18.4	689.1	34.9	4688	11.5	1.67	fully limbed	1000547.4
Eulamprus tympanum	*Eulamprus tympanum*	0.3	13.1	802.4	22.9	4104	11.7	1.33	fully limbed	244013.9
Glaphyromorphus clandestinus	*Glaphyromorphus clandestinus*	0.3	22.2	1183.1	98.3	2987	11.7	0.87	fully limbed	257
Glaphyromorphus cracens	*Glaphyromorphus cracens*	0.48	22.3	953.3	100.4	2827	11.6	0.57	fully limbed	43804.9
Glaphyromorphus crassicaudus	*Glaphyromorphus crassicaudus*	0.36	25.4	1377.2	104.6	1752	11.62	0.49	fully limbed	176669.7
Glaphyromorphus darwiniensis	*Glaphyromorphus darwiniensis*	NA	27.2	1391.8	106.8	1820	11.54	0.59	fully limbed	130544.5
Glaphyromorphus fuscicaudis	*Glaphyromorphus fuscicaudis*	0.48	22.6	2241.7	83.3	2509	11.86	1.2	fully limbed	18802.8
Glaphyromorphus mjobergi	*Glaphyromorphus mjobergi*	NA	22	2187	82.2	2401	11.9	1.29	fully limbed	9666.5
Glaphyromorphus nigricaudis	*Glaphyromorphus nigricaudis*	NA	25.4	1805.1	83.8	1411	11.7	1.19	fully limbed	238893.8
Glaphyromorphus nyanchupinta	*Glaphyromorphus nyanchupinta*	NA	23.1	1668	113	1505	11.97	0.46	fully limbed	247.8
Glaphyromorphus othelarrni	*Glaphyromorphus othelarrni*	NA	24.6	1654.3	105	1526	11.75	1.23	fully limbed	68.8
Glaphyromorphus pumilus	*Glaphyromorphus pumilus*	NA	25.2	1392.3	109	1798	11.66	0.49	fully limbed	137255.6
Glaphyromorphus punctulatus	*Glaphyromorphus punctulatus*	0.4	22.9	782.7	70.1	3742	11.52	0.83	fully limbed	201903.8
Harrisoniascincus zia	*Harrisoniascincus zia*	0.48	16.5	1211.7	43.6	3833	11.94	0.59	fully limbed	13692.9
Hemiergis decresiensis	*Hemiergis decresiensis*	NA	16.3	374.4	28.4	4626	11.24	0.48	reduced	141971.2
Hemiergis gracilipes	*Hemiergis gracilipes*	NA	15.9	956.9	68.8	2988	11.66	1.17	fully limbed	30507.6
Hemiergis initialis	*Hemiergis initialis*	0.72	17.5	349.8	34.2	4256	11.19	-0.01	reduced	418702.7
Hemiergis millewae	*Hemiergis millewae*	NA	17.8	266.4	24.6	4954	11.04	0.57	fully limbed	279034.3
Hemiergis peronii	*Hemiergis peronii*	0.3	16.7	405.6	35.6	4155	11.28	1	fully limbed	643823.6
Hemiergis quadrilineata	*Hemiergis quadrilineata*	NA	17.9	887.2	83.1	3560	11.69	0.43	reduced	12529.7
Hemiergis talbingoensis	*Hemiergis talbingoensis*	0.54	14.2	840.7	24.2	4644	11.76	0.27	reduced	282958.7
Lampropholis adonis	*Lampropholis adonis*	NA	21.2	943.3	51.5	3571	11.7	0.44	fully limbed	43491.4
Lampropholis amicula	*Lampropholis amicula*	NA	19	1090.9	43.7	3724	11.75	-0.14	fully limbed	105352.5
Lampropholis bellendenkerensis	*NA*	NA	20.9	2582.5	71.7	2370	11.99	0.29	fully limbed	1759
Lampropholis caligula	*Lampropholis caligula*	NA	13.8	879.3	24.4	4588	11.82	0.47	fully limbed	3501

Lampropholis coggeri	*Lampropholis coggeri*	NA	22.8	1921	91.7	2114	11.63	0.27	fully limbed	5207
Lampropholis colossus	*Lampropholis colossus*	NA	15.8	951	45	4087	11.72	0.52	fully limbed	10
Lampropholis couperi	*Lampropholis couperi*	0.3	20.4	1041.1	49.8	3635	11.84	0.33	fully limbed	21874.6
Lampropholis delicata	*Lampropholis delicata*	0.46	17.8	865.7	44	3811	11.64	0.49	fully limbed	937657.5
Lampropholis elliotensis	*NA*	0.48	21.5	1322	100	2944	11.74	0.06	fully limbed	30.3
Lampropholis elongata	*Lampropholis elongata*	NA	11	1036.6	24.9	4319	11.91	0.44	fully limbed	121
Lampropholis guichenoti	*Lampropholis guichenoti*	0.3	15.1	714.8	25.8	4441	11.61	0.42	fully limbed	688423.7
Lampropholis mirabilis	*Lampropholis mirabilis*	0.7	22.4	971.6	97.8	3026	11.79	0.42	fully limbed	10
Lampropholis robertsi	*Lampropholis robertsi*	NA	21.8	2240.4	80.3	2311	11.81	0.49	fully limbed	5902.8
Lampropholis similis	*NA*	NA	22.8	2590	77.1	2690	11.96	0.12	fully limbed	7955.1
Lerista aericeps	*Lerista aericeps*	0.22	23.1	225.6	51.9	6192	10.7	0.07	reduced	540613.2
Lerista alia	*NA*	NA	25.4	845.5	117.5	2804	11.62	0.4	reduced	43.5
Lerista allanae	*Lerista allanae*	NA	22.3	612	59.8	4177	11.42	0.65	reduced	597.1
Lerista allochira	*Lerista allochira*	NA	24.3	258.7	77.4	3241	10.95	-0.25	reduced	312.6
Lerista ameles	*Lerista ameles*	0.36	23.4	805.9	111.1	3012	11.47	-0.01	limbless	1116.1
Lerista amicorum	*Lerista amicorum*	0.38	26	288.9	83.7	5647	10.84	-0.03	reduced	5887.5
Lerista anyara	*NA*	NA	25.5	1243	114	1994	11.45	0.24	limbless	16.6
Lerista apoda	*Lerista apoda*	NA	27.3	801.7	125.3	2391	11.45	0.14	limbless	161.3
Lerista arenicola	*Lerista arenicola*	NA	17.6	314	36.9	3250	10.99	0.75	fully limbed	27987.6
Lerista axillaris	*Lerista axillaris*	NA	20.4	395.3	87.6	3833	11.13	0.59	reduced	260.8
Lerista baynesi	*Lerista baynesi*	NA	17.8	294.3	23.5	3142	11.13	0.63	reduced	230.8
Lerista bipes	*Lerista bipes*	0.78	23.7	306.8	61.1	5861	10.82	0.31	reduced	1375254.1
Lerista borealis	*Lerista borealis*	NA	27.3	787.7	110.7	2987	11.22	0.24	reduced	34070.9
Lerista bougainvillii	*Lerista bougainvillii*	0.45	15.6	544.6	23.3	4752	11.47	0.93	fully limbed	694518.2
Lerista bunglebungle	*Lerista bunglebungle*	0.3	27.3	598	109	3698	11.09	0.31	reduced	26.8
Lerista carpentariae	*Lerista carpentariae*	NA	26.6	1015.1	113.6	2549	11.28	0.35	reduced	7719.3
Lerista chalybura	*Lerista zietzi*	0.54	24.7	358.8	86.5	5583	10.93	0.07	reduced	19360.8
Lerista chordae	*Lerista chordae*	0.69	23.8	509.6	76.4	4459	11.15	-0.12	reduced	8647.8
Lerista christinae	*Lerista christinae*	NA	18.9	539.1	77.5	4636	11.48	-0.25	reduced	14329.7
Lerista cinerea	*Lerista cinerea*	NA	23.4	667.5	82.3	3595	11.44	0.38	reduced	9924.8
Lerista clara	*Lerista clara*	0.3	25.7	308.2	86.8	4989	10.92	-0.03	reduced	251821.8
Lerista colliveri	*Lerista colliveri*	0.43	22.8	622.8	88.4	3792	11.43	0.62	reduced	25979.2
Lerista connivens	*Lerista connivens*	0.78	23.3	247.3	75.8	4353	11.03	0.57	reduced	54227.7
Lerista desertorum	*Lerista desertorum*	0.36	21.7	226.5	39.2	6021	10.75	0.67	reduced	1491474.2
Lerista distinguenda	*Lerista distinguenda*	0.48	17.4	429.4	45.9	4261	11.33	0.01	reduced	405701.1
Lerista dorsalis	*Lerista dorsalis*	0.3	17.7	291.2	25.5	4222	11.04	0.37	reduced	457453.3
Lerista edwardsae	*Lerista edwardsae*	NA	17.7	289.2	30.6	4444	11.06	0.68	reduced	174843.5
Lerista elegans	*Lerista elegans*	NA	22.5	349.3	76.1	4673	11.14	-0.12	reduced	199093.9
Lerista elongata	*Lerista elongata*	0.3	19.7	182.3	23.1	5592	10.71	0.19	reduced	117950.1
Lerista emmotti	*Lerista emmotti*	0.47	24.7	377.5	79.6	5291	10.87	0.77	reduced	259455.5
Lerista eupoda	*Lerista eupoda*	0.3	22.5	206	50.7	6413	10.79	0.62	reduced	4716.6
Lerista flammicauda	*Lerista flammicauda*	NA	25.3	356	90.1	5269	10.93	0.12	reduced	81841.4
Lerista fragilis	*Lerista fragilis*	NA	22.1	664.2	60.8	4373	11.41	0.19	reduced	520308.5
Lerista frosti	*Lerista frosti*	0.3	22.2	304.7	54.5	6104	10.9	0.32	reduced	65897.1
Lerista gascoynensis	*Lerista gascoynensis*	NA	23.9	225.2	66.6	5353	10.92	0.35	reduced	36711.8
Lerista gerrardii	*Lerista gerrardii*	0.48	20.5	289.2	52.1	5817	11.1	0.63	reduced	174869.8

Lerista greeri	*Lerista greeri*	NA	27.7	650.5	114.9	3448	11.13	0.27	reduced	158370.6
Lerista griffini	*Lerista griffini*	0.3	27.2	807.3	115.6	2878	11.27	0.31	reduced	175115.7
Lerista haroldi	*Lerista haroldi*	NA	24.3	242.1	77.4	4189	10.93	-0.25	reduced	12054.6
Lerista hobsoni	*NA*	0.74	22.1	672.1	90.3	3763	11.5	0.32	reduced	13941.7
Lerista humphriesi	*Lerista humphriesi*	0.48	21.6	314	86	4048	11.3	-0.04	limbless	3354.4
Lerista ingrami	*Lerista ingrami*	0.48	25.9	1632	93.3	1694	11.09	-0.36	reduced	237.1
Lerista ips	*Lerista ips*	0.59	26.1	322.2	78.5	5641	10.81	0.38	reduced	434664.2
Lerista jacksoni	*Lerista jacksoni*	0.65	25.9	337.3	91.7	4958	10.91	-0.1	reduced	132247.3
Lerista kalumburu	*Lerista kalumburu*	NA	26.9	1189.1	111.8	1950	11.38	0.24	reduced	14077.8
Lerista karlschmidti	*Lerista karlschmidti*	NA	26.7	1209.6	106.9	2022	11.48	0.37	reduced	125271.6
Lerista kendricki	*Lerista kendricki*	NA	21.9	293.9	88.3	3746	11.24	0.31	reduced	2250.6
Lerista kennedyensis	*Lerista kennedyensis*	0.43	23.7	226.8	73.5	5346	10.92	0.15	reduced	1289.1
Lerista kingi	*Lerista kingi*	1.34	20.5	262.2	42	5777	10.99	-0.1	reduced	427958.5
Lerista labialis	*Lerista labialis*	0.28	22.6	264.2	49.9	5864	10.79	0.19	reduced	2261135.1
Lerista lineata	*Lerista lineata*	0.3	21.2	387.8	81.8	4060	11.26	0.22	reduced	25103.6
Lerista lineopunctulata	*Lerista lineopunctulata*	NA	21.4	374.1	79.2	4194	11.25	0.87	reduced	75800.9
Lerista macropisthopus	*Lerista macropisthopus*	NA	22.9	263	61.6	5748	10.93	0.74	reduced	632412.9
Lerista maculosa	*Lerista maculosa*	NA	22.7	227	71	4575	10.92	-0.22	reduced	20
Lerista micra	*Lerista micra*	NA	23	243.3	72.2	4729	11.05	-0.1	reduced	56656.9
Lerista microtis	*Lerista microtis*	NA	16.3	617.4	54.2	3253	11.4	0.64	fully limbed	102848.3
Lerista miopus	*NA*	0.6	20.5	446.8	85.1	3935	11.35	0.8	reduced	26772
Lerista muelleri	*Lerista muelleri*	0.3	20.6	342.6	38.8	5608	11.04	-0.01	reduced	2180207.9
Lerista neander	*Lerista neander*	0.48	24.9	259	71.1	6114	10.78	0.64	reduced	51189.5
Lerista nevinae	*Lerista nevinae*	0.57	27	292.6	90.8	3453	11.87	-0.2	reduced	139.2
Lerista nichollsi	*Lerista nichollsi*	0.59	22.4	230.6	53.9	6118	10.89	0.32	reduced	76208.9
Lerista occulta	*Lerista occulta*	NA	23	254.2	71.6	4810	11.06	-0.28	reduced	56586.2
Lerista onsloviana	*Lerista onsloviana*	0.38	26	292.7	85	4377	11	0.36	reduced	10074.9
Lerista orientalis	*Lerista orientalis*	0.3	26.8	864	110.4	2980	11.29	-0.03	reduced	613473.4
Lerista parameles	*NA*	0.63	23.4	899	110.5	2737	11.5	0.37	reduced	213.7
Lerista petersoni	*Lerista petersoni*	NA	25	259.3	78.7	5205	10.92	0.37	reduced	53512.1
Lerista picturata	*Lerista picturata*	NA	18.4	264.6	23.8	4708	11.09	0.65	reduced	172738.8
Lerista planiventralis	*Lerista planiventralis*	NA	22.9	299.8	78.5	4450	11.11	0.38	reduced	111772.5
Lerista praepedita	*Lerista praepedita*	NA	21.4	362.3	76.1	4454	11.22	-0.02	limbless	106473.5
Lerista punctatovittata	*Lerista punctatovittata*	0.7	20.3	399	35.2	5589	11.12	0.79	reduced	1426405.4
Lerista puncticauda	*Lerista puncticauda*	NA	19.2	221.5	27.4	5185	10.8	0.57	reduced	9735
Lerista quadrivincula	*Lerista quadrivincula*	NA	26.8	279.8	94.1	3912	10.85	0.03	reduced	1015.2
Lerista robusta	*Lerista robusta*	0.61	28.3	491.3	117.5	3959	11.13	0.26	reduced	3239.2
Lerista rochfordensis	*Lerista rochfordensis*	NA	23.6	678.9	80.1	3502	10.87	0.52	reduced	363.9
Lerista rolfei	*Lerista rolfei*	NA	24.9	254.3	75.2	5643	10.88	-0.05	reduced	106156.1
Lerista separanda	*Lerista separanda*	NA	27.5	681.7	122.2	2958	11.2	-0.49	reduced	52679.9
Lerista simillima	*Lerista simillima*	0.3	28.4	613.5	121.2	3346	11.16	0.09	reduced	15039.8
Lerista speciosa	*Lerista speciosa*	0.3	19.9	285	41.2	6289	10.8	0.01	reduced	3678.1
Lerista stictopleura	*Lerista stictopleura*	NA	24.5	249.2	76.1	6007	10.93	0.15	reduced	1470.6
Lerista storri	*Lerista storri*	0.3	24.4	855.1	114.1	2796	11.46	0.4	reduced	14805.6
Lerista stylis	*Lerista stylis*	NA	27	1359.7	104.4	2072	11.42	0.12	limbless	11150.2
Lerista taeniata	*Lerista taeniata*	0.18	22.2	278.8	47.6	5686	10.82	-0.1	reduced	1565451.8

Lerista talpina	*Lerista talpina*	0.48	25.1	277	77	3926	11.74	-0.36	reduced	10
Lerista terdigitata	*Lerista terdigitata*	NA	17.4	315	34	4317	11.16	0.35	reduced	104465.9
Lerista timida	*NA*	0.42	21	313.8	40.9	5704	10.97	0.05	reduced	3880712.8
Lerista tridactyla	*Lerista tridactyla*	0.59	17.8	272.8	20.3	4305	11.24	0.21	reduced	38757.5
Lerista uniduo	*Lerista uniduo*	0.48	24	242.4	72.2	5049	10.95	0.2	reduced	137381
Lerista vanderduysi	*NA*	NA	22.5	741.2	106.3	3430	11.5	0.31	reduced	3976.6
Lerista varia	*Lerista varia*	NA	22.5	260	86.6	3290	10.9	0.56	reduced	8001.8
Lerista verhmens	*Lerista verhmens*	0.54	26.1	337.6	92.5	4821	10.93	-0.01	reduced	145990.6
Lerista vermicularis	*Lerista vermicularis*	0.72	26.7	381.6	90.2	5122	10.87	-0.2	reduced	338305.8
Lerista viduata	*Lerista viduata*	0.41	16.3	395.8	24.2	3548	11.36	0.21	fully limbed	548
Lerista vittata	*Lerista vittata*	0.78	23.6	724.4	75.6	3601	11.48	0.44	reduced	518.3
Lerista walkeri	*Lerista walkeri*	0.48	26.6	1326.6	117.5	1855	11.36	0.34	reduced	23436.7
Lerista wilkinsi	*Lerista wilkinsi*	NA	22.9	603.1	86	4077	11.37	0.43	reduced	8726.2
Lerista xanthura	*Lerista xanthura*	NA	25.4	296.7	68.3	6027	10.78	0.15	reduced	491755.2
Lerista yuna	*Lerista yuna*	NA	20.8	335.5	70.2	5169	11.33	0.29	reduced	2191.1
Lerista zonulata	*Lerista zonulata*	0.3	23.7	770.1	101.2	3274	11.46	0	reduced	178448.1
Liburnascincus artemis	*NA*	NA	25.5	1195.7	113.7	1843	11.63	0.56	fully limbed	2529.8
Liburnascincus coensis	*Liburnascincus coensis*	NA	25	1440.5	109	1453	11.87	0.82	fully limbed	7030.7
Liburnascincus mundivensis	*Liburnascincus mundivensis*	NA	22.8	918.5	85	3347	11.56	0.62	fully limbed	194851.8
Liburnascincus scirtetis	*Liburnascincus scirtetis*	NA	25.4	1597	98	1876	11.66	0.83	fully limbed	26
Liopholis guthega	*Liopholis guthega*	NA	6.8	1285.8	22.4	4763	11.85	1.51	fully limbed	1108.2
Liopholis inornata	*Liopholis inornata*	0.7	20.9	240.7	35	5921	10.84	1.11	fully limbed	2541547.1
Liopholis kintorei	*Liopholis kintorei*	NA	24.2	334.8	66.9	5602	10.85	2.35	fully limbed	1336754.1
Liopholis margaretae	*Liopholis margaretae*	NA	22.3	299.9	52.5	6172	10.88	1.54	fully limbed	166363
Liopholis modesta	*Liopholis modesta*	0.3	18.4	720.5	36	4792	11.6	1.49	fully limbed	299217.7
Liopholis montana	*Liopholis montana*	NA	10.5	1002.1	21.2	4575	11.82	1.48	fully limbed	40858.2
Liopholis multiscutata	*Liopholis multiscutata*	NA	17.3	343	33.6	4348	11.21	1.28	fully limbed	568850.2
Liopholis personata	*NA*	0.36	18.4	248.2	20.6	5698	10.93	1.43	fully limbed	66520.8
Liopholis pulchra	*Liopholis pulchra*	NA	16.6	733.7	67.2	3582	11.6	1.47	fully limbed	82245.5
Liopholis slateri	*Liopholis slateri*	0.58	22.2	283.4	50	6215	10.84	1.29	fully limbed	73309.2
Liopholis striata	*Liopholis striata*	0.3	24	314.9	66.1	5627	10.86	1.55	fully limbed	2261381.9
Liopholis whitii	*Liopholis whitii*	0.52	15	711.3	25	4432	11.59	1.5	fully limbed	832101
Lissolepis coventryi	*Lissolepis coventryi*	0.36	13.2	823.4	22.5	3587	11.66	1.9	fully limbed	109274.5
Lissolepis luctuosa	*Lissolepis luctuosa*	0.3	16.1	889	68.6	3190	11.71	1.7	fully limbed	42083.2
Lygisaurus abscondita	*Lygisaurus abscondita*	NA	25.2	909.2	117.8	2748	11.71	-0.36	fully limbed	170.5
Lygisaurus aeratus	*Lygisaurus aeratus*	0.3	25.3	1355.8	110.4	1725	11.66	0.01	fully limbed	122772.7
Lygisaurus foliorum	*Lygisaurus foliorum*	0.46	20.4	779	53.3	4291	11.54	0.18	fully limbed	842593
Lygisaurus laevis	*Lygisaurus laevis*	0.34	22.4	2437.7	79.5	2298	11.8	-0.06	fully limbed	11367.4
Lygisaurus macfarlani	*Lygisaurus macfarlani*	0.32	26.1	1704.5	87.6	1135	11.66	0.03	fully limbed	94490
Lygisaurus malleolus	*Lygisaurus malleolus*	NA	23.9	1219.4	105.8	2160	11.67	-0.26	fully limbed	36639.8
Lygisaurus parrhasius	*Lygisaurus parrhasius*	0.7	25.8	1611.1	102.8	1212	11.75	-0.14	fully limbed	769.6
Lygisaurus rimula	*Carlia rimula*	0.38	25.3	1439.8	109.3	1440	11.74	0.01	fully limbed	11980.6
Lygisaurus rococo	*Lygisaurus rococo*	NA	22.7	812.4	109.3	2869	11.57	0.21	fully limbed	950.6
Lygisaurus sesbrauna	*Lygisaurus sesbrauna*	NA	25.7	1373.6	108.4	1553	11.68	-0.18	fully limbed	44260.6
Lygisaurus tanneri	*Lygisaurus tanneri*	0.3	25.2	1691.6	96.6	1789	11.88	-0.06	fully limbed	3356.7

Lygisaurus zuma	*Lygisaurus zuma*	0.3	22.7	1400.9	90.3	3069	11.78	-0.15	fully limbed	14785
Menetia alanae	*Menetia alanae*	0.36	27.2	1281.8	107.9	2094	11.49	-0.36	fully limbed	137935.2
Menetia concinna	*Menetia concinna*	NA	27.7	1533.2	106.8	1773	11.61	-0.31	fully limbed	2356.3
Menetia greyii	*Menetia greyii*	0.7	22.4	419.6	60	5069	11.03	0.05	fully limbed	7074448.3
Menetia maini	*Menetia maini*	0.57	26.3	684	103.8	3688	11.14	-0.26	fully limbed	1319453.7
Menetia surda	*Menetia surda*	NA	25.2	301.4	85	5004	10.94	-0.26	fully limbed	342735.6
Morethia adelaidensis	*Morethia adelaidensis*	0.44	19.8	239.9	29	5518	10.86	0.62	fully limbed	1707089.6
Morethia boulengeri	*Morethia boulengeri*	0.31	20.7	381.6	39.9	5576	11.04	0.54	fully limbed	3302069.4
Morethia butleri	*Morethia butleri*	0.64	20	245.3	34.1	5385	10.91	0.54	fully limbed	1275921.1
Morethia lineoocellata	*Morethia lineoocellata*	0.48	20.9	415.7	73.7	4559	11.25	0.54	fully limbed	259510.7
Morethia obscura	*Morethia obscura*	NA	18.5	306	32.9	4927	11.08	0.52	fully limbed	1568655
Morethia ruficauda	*Morethia ruficauda*	0.78	25.3	457.7	83.1	4937	10.96	0.24	fully limbed	3133775.4
Morethia storri	*Morethia storri*	0.29	26.9	835	111.6	3015	11.26	-0.02	fully limbed	910498.8
Morethia taeniopleura	*Morethia taeniopleura*	0.3	23	876.2	78.1	3500	11.51	0.18	fully limbed	736535.7
Nangura spinosa	*Nangura spinosa*	NA	19.5	982.8	49.5	3813	12	1.26	fully limbed	110
Notoscincus butleri	*Notoscincus butleri*	NA	25.4	372.5	94.1	4750	10.96	0.12	fully limbed	40112.7
Notoscincus ornatus	*Notoscincus ornatus*	0.43	25.4	488.9	87.2	4751	11	0.07	fully limbed	3561379.5
Ophioscincus cooloolensis	*Ophioscincus cooloolensis*	0.4	21.6	1061.1	51.3	3327	11.6	0.04	limbless	18329.2
Ophioscincus ophioscincus	*Ophioscincus ophioscincus*	0.6	20.3	978.5	47.3	3728	11.78	0.36	limbless	41104.7
Ophioscincus truncatus	*Ophioscincus truncatus*	0.52	18.6	1263.6	42.5	3627	11.74	0.16	limbless	37027.5
Proablepharus reginae	*Proablepharus reginae*	0.45	24.5	375	72.7	5260	10.89	0.08	fully limbed	2311039.4
Proablepharus tenuis	*Proablepharus tenuis*	0.6	25.9	779.6	104.2	3348	11.27	-0.26	fully limbed	1533991.1
Pseudemoia baudini	*Pseudemoia baudini*	0.3	17.5	301.6	33	3530	11.02	0.44	fully limbed	89650.8
Pseudemoia cryodroma	*Pseudemoia cryodroma*	0.3	10.4	1061.2	22.9	4467	11.82	0.62	fully limbed	22939.7
Pseudemoia entrecasteauxii	*Pseudemoia entrecasteauxii*	0.6	14.1	712.9	23.6	4236	11.58	0.73	fully limbed	583234.3
Pseudemoia pagenstecheri	*Pseudemoia pagenstecheri*	0.46	12.8	842.4	23	4102	11.73	0.81	fully limbed	250687
Pseudemoia rawlinsoni	*Pseudemoia rawlinsoni*	0.65	12.5	873.3	22.4	3872	11.71	0.69	fully limbed	144656.6
Pseudemoia spenceri	*Pseudemoia spenceri*	NA	12.9	840.2	19.5	4275	11.72	0.73	fully limbed	191793.5
Pygmaeascincus koshlandae	*Pygmaeascincus koshlandae*	NA	24.8	1184.9	109.9	2020	11.65	-0.45	fully limbed	75717.5
Pygmaeascincus timlowi	*Pygmaeascincus timlowi*	0.3	21.9	756.1	64.1	4083	11.5	-0.4	fully limbed	530273.3
Saiphos equalis	*Saiphos equalis*	0.52	16.9	898.5	34.2	4279	11.72	0.65	reduced	245723.8
Saproscincus basiliscus	*Saproscincus basiliscus*	NA	22.6	2044.7	85	2587	11.84	0.36	fully limbed	22505.2
Saproscincus challengeri	*Saproscincus challengeri*	NA	18.5	1156.3	42.4	3698	11.89	0.59	fully limbed	19136.4
Saproscincus czechurai	*Saproscincus czechurai*	NA	22.3	2242.2	82.1	2345	11.89	0.05	fully limbed	13187.3
Saproscincus eungellensis	*Saproscincus eungellensis*	NA	20.6	1630.8	81.3	3201	11.99	0.77	fully limbed	391.7
Saproscincus hannahae	*Saproscincus hannahae*	0.54	22.7	1397.5	84.3	3142	11.73	0.13	fully limbed	10833.2
Saproscincus lewisi	*Saproscincus lewisi*	NA	24.6	2084.9	93.2	1860	11.94	0.15	fully limbed	1565.7
Saproscincus mustelinus	*Saproscincus mustelinus*	0.4	13.9	922.4	24	4080	11.73	0.71	fully limbed	212849.6
Saproscincus oriarus	*Saproscincus oriarus*	NA	19.3	1459.4	34.9	3268	10.78	0.15	fully limbed	4911
Saproscincus rosei	*Saproscincus rosei*	NA	17.2	1106.7	42.1	3894	11.85	0.73	fully limbed	65674.2
Saproscincus saltus	*Saproscincus saltus*	NA	23.5	1705	106	1501	11.41	0.15	fully limbed	10.7
Saproscincus spectabilis	*Saproscincus spectabilis*	NA	17.2	1162.2	39.2	3793	11.76	0.62	fully limbed	66672.6

Saproscincus tetradactylus	*Saproscincus tetradactylus*	0.5	22.5	2299.3	81.4	2556	11.85	-0.22	fully limbed	14781.5
Silvascincus murrayi	*Silvascincus murrayi*	0.3	17.2	1171.3	41	3803	11.81	1.44	fully limbed	75207.1
Silvascincus tryoni	*Silvascincus tryoni*	0.36	16.9	1615	43.1	3409	11.95	1.39	fully limbed	629.1
Techmarscincus jigurru	*Techmarscincus jigurru*	NA	17.7	4749	61.5	2196	10.74	1.02	fully limbed	30.3
Tiliqua adelaidensis	*Tiliqua adelaidensis*	NA	15.3	441.6	36.9	4418	11.5	1.43	fully limbed	11850.6
Tiliqua multifasciata	*Tiliqua multifasciata*	1.04	24.8	376.5	75.8	5283	10.88	2.87	fully limbed	3512580.5
Tiliqua nigrolutea	*Tiliqua nigrolutea*	0.9	13	899.9	22.6	3919	11.68	3.16	fully limbed	363007.2
Tiliqua occipitalis	*Tiliqua occipitalis*	0.3	20	270	37.3	5406	10.94	2.96	fully limbed	2511015.1
Tiliqua rugosa	*Tiliqua rugosa*	0.3	19.1	382.4	33.8	5256	11.11	3.09	fully limbed	3236351
Tiliqua scincoides	*Tiliqua scincoides*	0.28	21.5	666.5	61.8	4263	11.32	3.21	fully limbed	3476649.9
Tumbunascincus luteilateralis	*Tumbunascincus luteilateralis*	NA	19.3	1728.2	83.5	3064	11.92	1.49	fully limbed	180

Species refers to the species name in the August 2020 version of the Reptile database (Uetz et al. 2020). Name is tree is the equivalent name in the phylogenetic tree of Tonini et al. (2016). Temperature is mean annual temperature (in ºC, BIO1, Temperature seasonality: BIO4), Precipitation (BIO12, precipitation seasonality BIO15) is in mm. NPP (g carbon per m2, per year) and body mass (in g) values are log 10 transformed. Body masses are species maxima. Range size is in km^2.

Table S3. List of measurements taken for each specimen of skink. All measurements were taken with the specimen ventral side up and from the left side of the body where possible.

Measurement	Abbreviation	Method
Snout-Vent Length	SVL	Specimen was positioned flat on a steel ruler and measured from tip of nose to vent.
Snout-Axilla Length	SAL	Measured from tip of the snout to midpoint of juncture between the front-limb and body.
Inter-limb Length	ILL	Specimen was placed ventral side up with limbs held perpendicular to body. Measurement taken along the midline of the body, from level of crease of the front-limb to level of crease of hind-limb.
Body Width	BW	Midpoint of ILL from one lateral side to the other.
Body Height	BH	Measured using same midpoint used for BW, with calipers positioned on dorsal and ventral sides of the specimen. Specimen was squeezed slightly to reduce bulge.
Pelvic Width	PW	Measurement taken at midpoints of hind-limbs from crease of left limb to crease of right limb.
Pelvic Height	PH	Taken from same point used for PW, with calipers placed on dorsal and ventral surfaces of specimen. Specimen was squeezed slightly to reduce bulge.
Head Width	HW	Measured across widest part of head from one dorsolateral edge to the other.

Measurement	Abbreviation	Method
Head Length	HL	Taken from anterior edge of the ear (or dimple for earless species) to tip of snout.
Head Depth	HD	With the calipers placed on the dorsal surface and ventral surface of the head, measured at tallest part of head. Calipers were slightly squeezed to flatten any soft-tissue bulge of the jaw.
Front-limb Length	FLL	Measured from crease of limb to the longest toe with limb stretched out perpendicular to body.
Hind-limb Length	HLL	Measured from crease of limb to the longest toe with limb stretched out perpendicular to body.
Tail Width	TW	Measured at base of vent from one dorsolateral edge to the other.

Table S4. Effects of biome on geographic range size of all Australian mainland skinks. Means and sd values back-transformed from logarithms.

biome	**# species**	**mean range size (km^2)**	**sd**
Deserts & xeric shrublands	127	198,461.1	15.8
Mediterranean forests, woodlands & scrub	48	35,158.7	10.5
Montane grasslands & savannas	1	1,108.2	NA
Temperate broadleaf mixed forests	61	62,497.7	9.7
Temperate grasslands, savannas & shrublands	3	362,823.8	4.8
Tropical & subtropical grasslands, savannas & shrublands	168	34,938.2	19.3
Tropical & subtropical moist broadleaf forest	30	5,344.9	10.6

Table S5. Results of phylogenetic mixed models investigating effects of environmental covariates on geographic range size in 9 paired sets of Australian skinks. SVL was a covariate in all models except those noted with an asterisk.

Parameter	Estimate (median)	2.5% Credible Interval	97.5% Credible Interval
SVL*	7.768938e-08	-7.283716e-05	7.293002e-05
SAL	6.668399e-07	-4.339920e-04	4.347795e-04
ILL	-5.236725e-07	-3.370119e-04	-3.370119e-04
BW	-4.692737e-07	-4.270348e-04	4.269470e-04
PW	-1.822625e-06	-9.842860e-04	9.858558e-04
PH	-2.055695e-06	-7.528487e-04	7.437990e-04
HW	-3.388030e-06	-9.402136e-04	9.354000e-04
HL	-3.928108e-07	-7.406764 e-04	7.344181e-04
HD	1.406934e-06	-9.103468e-04	9.093580e-04
TW	1.253710e-06	-7.797952e-04	7.785853e-04
FLL	-7.614903e-07	-4.673851e-04	4.673028e-04
HLL	-3.489804e-07	3.184006e-04	3.186304e-04
Clutch size	-6.190107e-01	-1.091266e+01	5.516162e+00
Annual rainfall*	-3.544198e+00	-5.796652e+00	-1.274022e+00

Mean annual temperature*	-2.798991e-01	-5.759805e-01	1.795408e-02

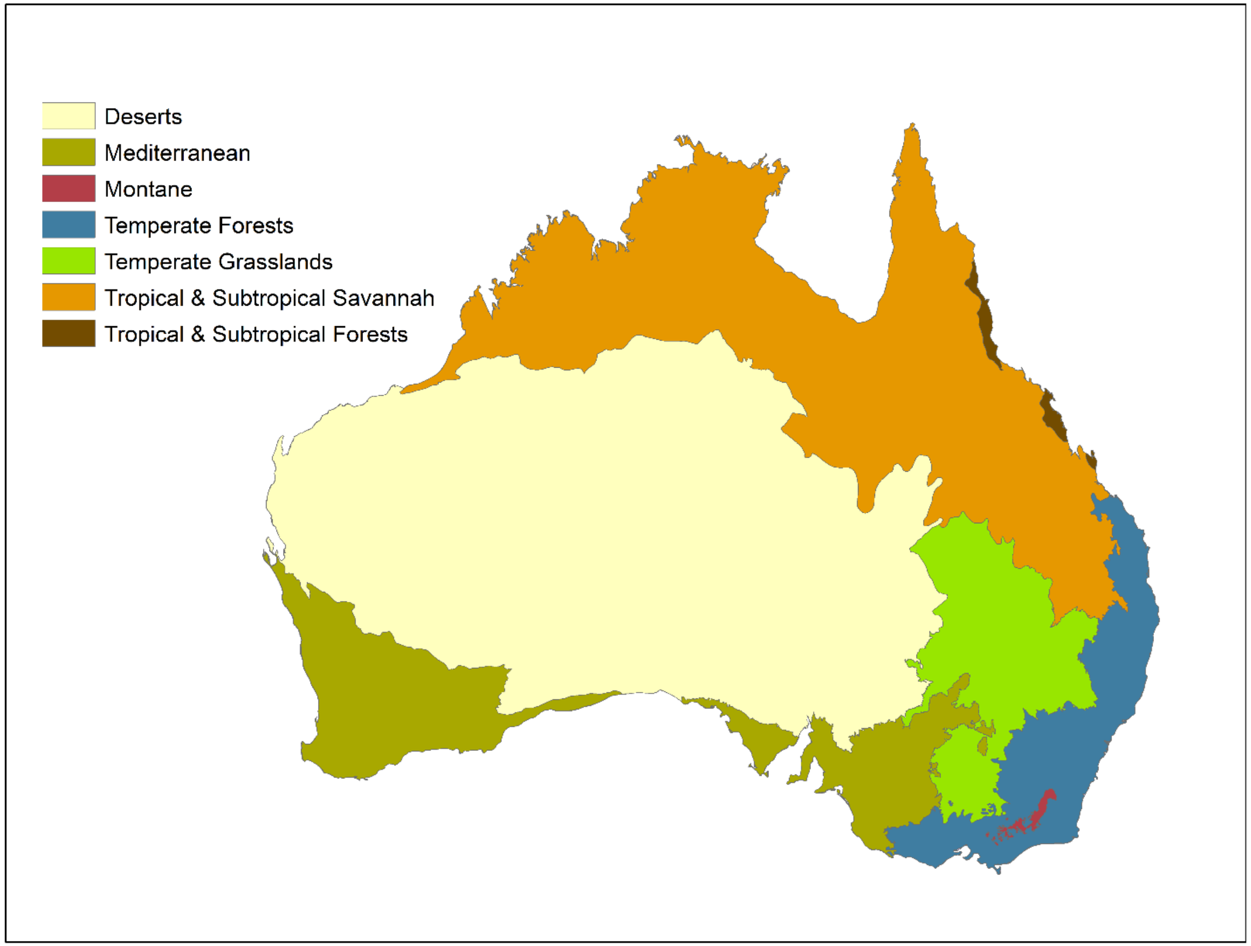

Fig. S1. Biomes in Australia; from Olson et al. (2001).