RESEARCH ARTICLE

Predictors of geographic range size in Australian skinks

Mahalia Barter[1] | Luke R. Bonifacio[1] | Andressa Duran[1] | Celine T. Goulet[1] |
Reid Tingley[1] | Glenn M. Shea[2,3] | Shai Meiri[4] | David G. Chapple[1]

[1]School of Biological Sciences, Monash University, Melbourne, Victoria, Australia

[2]Sydney School of Veterinary Science, University of Sydney, Sydney, New South Wales, Australia

[3]Australian Museum Research Institute, Australian Museum, Sydney, New South Wales, Australia

[4]School of Zoology and Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

Correspondence
David G. Chapple, School of Biological Sciences, Monash University, Clayton Victoria 3800, Australia.
Email: David.Chapple@monash.edu

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

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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
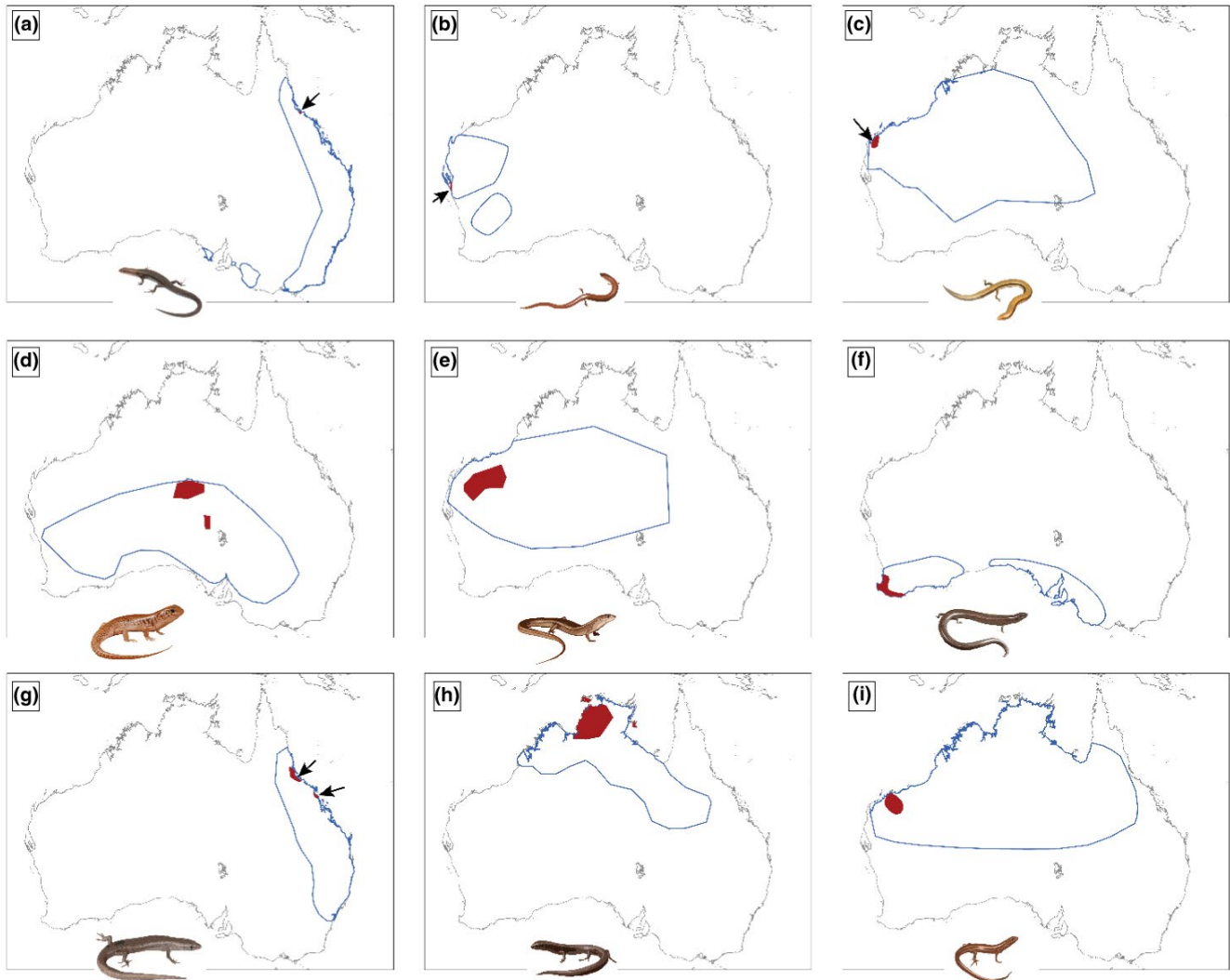
FIGURE 1 Maps of the distributions of wide-ranging (blue outline) and narrow-ranging (red fill, no outline) species pairs. Drawings are only of the wide-ranging species: (a) *Lampropholis delicata*; (b) *Lerista macropisthopus*; (c) *Lerista bipes*; (d) *Liopholis inornata*; (e) *Ctenotus helenae*; (f) *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).
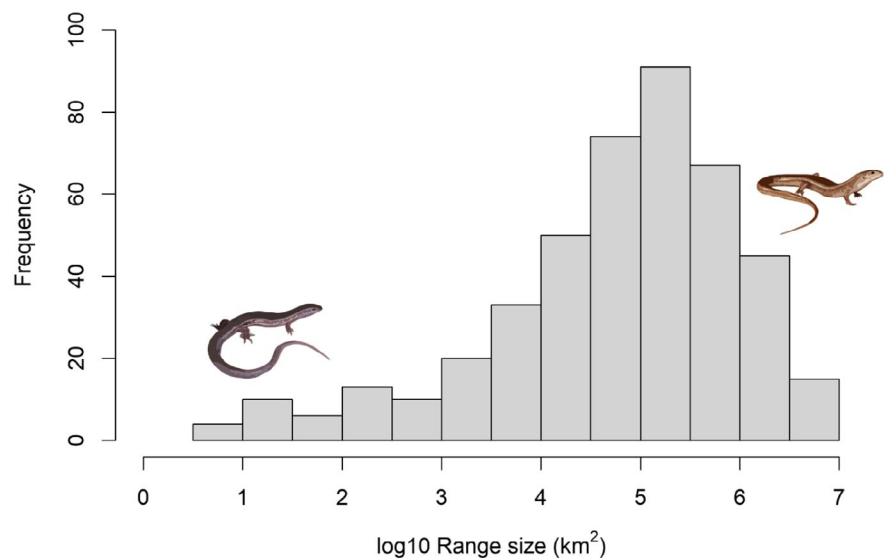

FIGURE 2 Distribution of geographic range sizes among all Australian skinks (log10 transformed). Skink images are placed approximately above their respective range sizes (*Ctenotus lancelini*, 1.08 = 12 km^2; *Ctenotus inornatus*, 6.65 = 4,467,000 km^2)

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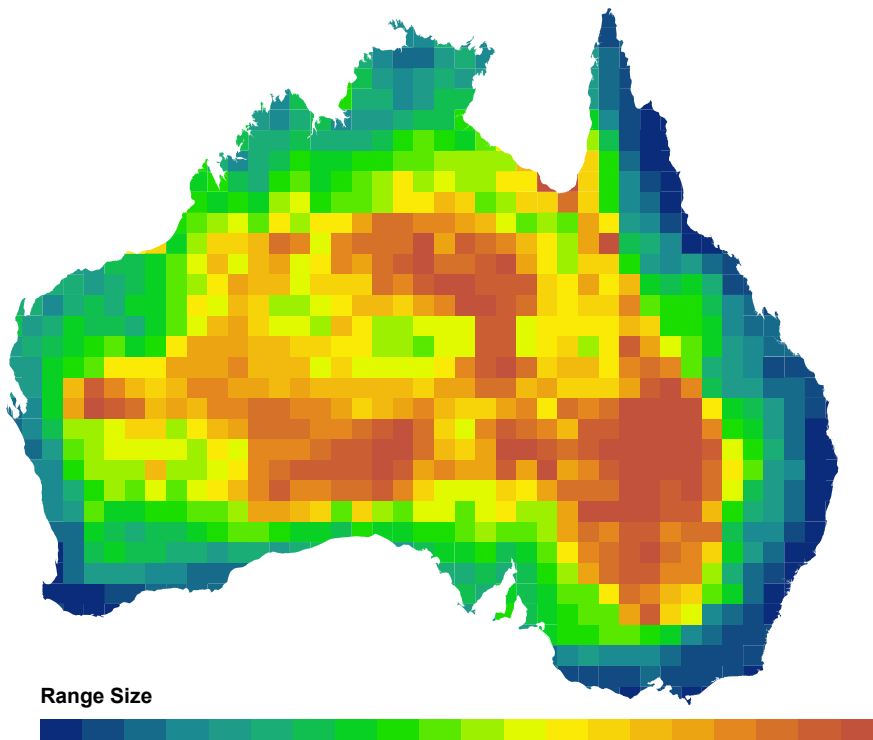
TABLE 1 Significant factors explaining range size across Australian mainland skinks ($n = 417$ species with phylogenetic data). t and p values for leg development specify differences from zero for species with fully developed limbs, and for differences from species with fully developed limbs for legless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

Range Size

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
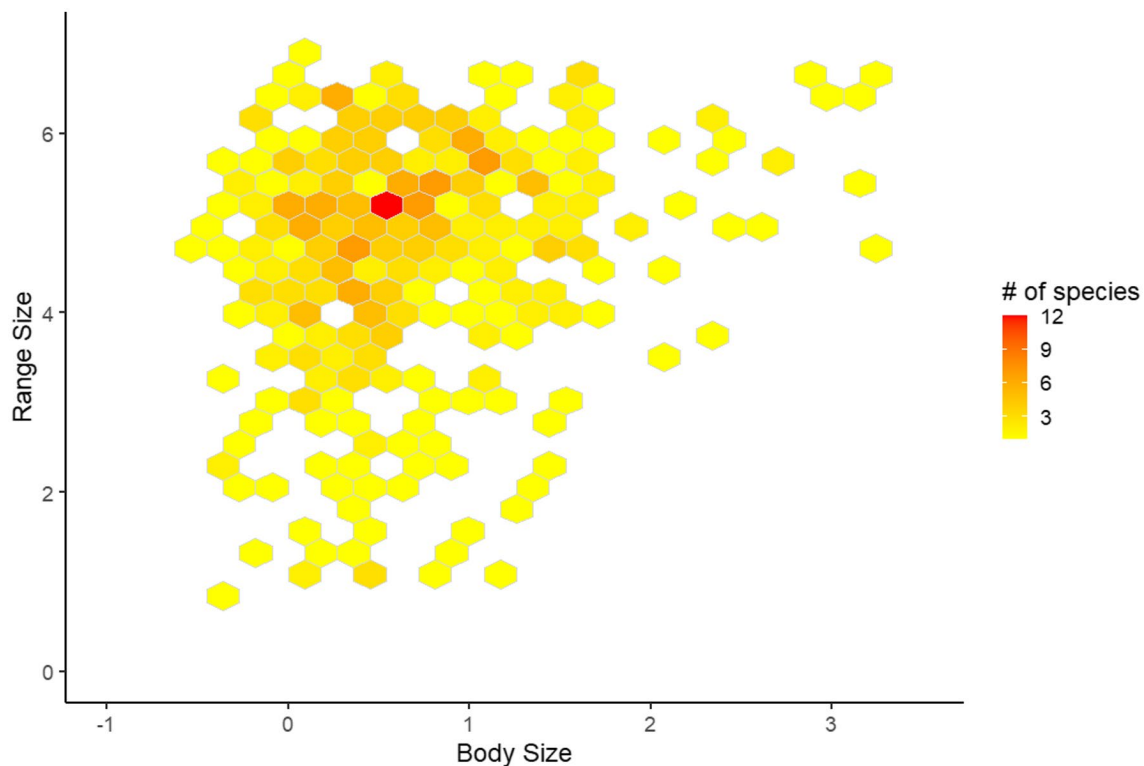

FIGURE 4 Range size versus maximum body mass in Australian skinks (*n* = 438). Colours depict the number of species (1–12) in each body/range size category. Range sizes in log(km^2), body sizes are species maxima in log grams (all logarithms to base 10)

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.

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).

ORCID

Shai Meiri https://orcid.org/0000-0003-3839-6330
David G. Chapple https://orcid.org/0000-0002-7720-6280

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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.

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