



## RESEARCH PAPER

# The global diversity and distribution of lizard clutch sizes

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## Abstract

**Aim:** Clutch size is a key life-history trait. In lizards, it ranges over two orders of magnitude. The global drivers of spatial and phylogenetic variation in clutch have been extensively studied in birds, but such tests in other organisms are lacking. To test the generality of latitudinal gradients in clutch size, and their putative drivers, we present the first global-scale analysis of clutch sizes across lizard taxa.

**Location:** Global.

**Time period:** Recent.

**Major taxa studied:** Lizards (Reptilia, Squamata, Sauria).

**Methods:** We analysed clutch-size data for over 3,900 lizard species, using phylogenetic generalized least-square regression to study the relationships between clutch sizes and environmental (temperature, precipitation, seasonality, primary productivity, insularity) and ecological factors (body mass, insularity, activity times, and micro-habitat use).

**Results:** Larger clutches are laid at higher latitudes and in more productive and seasonal environments. Insular taxa lay smaller clutches on average. Temperature

and precipitation per se are unrelated to clutch sizes. In Africa, patterns differ from those on other continents. Lineages laying small fixed clutches are restricted to low latitudes.

**Main conclusions:** We suggest that the constraint imposed by a short activity season, coupled with abundant resources, is the main driver of large-clutch evolution at high latitudes and in highly seasonal regions. We hypothesize that such conditions – which are unsuitable for species constrained to laying multiple small clutches – may limit the distribution of fixed-clutch taxa.

#### KEYWORDS

Ashmole's hypothesis, fecundity, fixed clutch size, geographic variation, Lack's rule, latitude, reproductive strategy, seasonality

## 1 | INTRODUCTION

Reproductive effort is a critical component of animal life histories. How reproductive effort is allocated through a single reproductive event, over a breeding season, and over an entire life span, has major fitness consequences. Clutch size, laying frequency, length of the reproductive season, and reproductive life span can vary dramatically between and within taxa (Pincheira-Donoso & Hunt, 2017; Roff, 2002). Of these components, the number of offspring within a single clutch ('clutch size') probably varies most: from one to many millions of eggs in some invertebrates and anamniote vertebrates laying oligolecithal eggs (e.g. the brown crab, *Cancer pagurus*; Ungfors, 2007; the sea hare, *Aplysia californica*; MacGinitie, 1934; the cod, *Gadus morhua*; Lambert, 2008; May, 1967; see also Sadovy, 2001). In amniotes (birds, mammals, and reptiles) laying large, yolk-laden macrolecithal eggs, clutch (and litter) size variation is narrower but clutches still range from 1 to c. 160 eggs (Vitt & Caldwell, 2013).

Among squamates (lizards and snakes), clutch sizes vary across two orders of magnitude, from 1 to over 100 eggs in some large snakes (Reed & Rodda, 2009; Vitt & Caldwell, 2013) and to over 90 eggs in some chameleons (Meiri, 2018; Tilbury, 2010; Zug, 2013). The causes underlying this enormous variation have inspired decades of research. Thus, clutch size was found to be correlated with traits such as body size, growth rates, and longevity, supporting the notion of a fast-slow continuum (Clobert, Garland, & Barbault, 1998; Dunham, Miles, & Reznick, 1988; Pincheira-Donoso & Tregenza, 2011; Scharf et al., 2015; Tinkle, Wilbur, & Tilley, 1970). Clutch size was found to be negatively correlated with egg size and clutch frequency across multiple studies (e.g. Amat, 2008; In den Bosch & Bout, 1998; King, 2000; Meiri, Brown, & Sibly, 2012). In lizards, as in most ectotherms (Shine, 1988), clutch size has been repeatedly found to increase with increasing maternal body size (e.g. Dunham et al., 1988; Scharf & Meiri, 2013; Tinkle et al., 1970) – both within and between species. An exception is lineages where females only lay one or two eggs. The evolutionary correlates of such fixed clutch sizes (e.g. small body size, but large variation in egg sizes: Kratochvil & Kubicka, 2007; Meiri, Feldman, & Kratochvil, 2015;

Schwarz & Meiri, 2017; Shine & Greer, 1991) have been widely studied. The consequences of the transition to viviparity (reviewed in Murphy & Thompson, 2011; Pincheira-Donoso, Tregenza, Witt, & Hodgson, 2013; Shine, 2005; Sites, Reeder, & Wiens, 2011) for the number of offspring per reproductive event have also been widely studied (Huang, 2010; Meiri, Feldman, Schwartz, & Shine, 2020), generally finding no relationship between reproductive mode and brood size.

Compared to the multitude of studies exploring various biological drivers of clutch size variation, studies of *geographic* signals underlying clutch-size variation in most organisms, including squamates, remain scarce. In reptiles, some studies focused on reduction of clutch sizes with insularity (e.g. Brandley, Kuriyama, & Hasegawa, 2014; Huang, 2007; Novosolov, Raia, & Meiri, 2013; Pafilis et al., 2011; Siliceo & Diaz, 2010; Slavenko, Itescu, Foufopoulos, Pafilis, & Meiri, 2015), forested habitats (e.g. Werneck, Giugliano, Colleavtti, & Colli, 2009), and saxicolous and arboreal habits (Mesquita et al., 2016; Schall, 1983; Vitt, 1981).

Few studies have addressed adaptive responses in reptile clutch size to global variation in climate. This is somewhat surprising as such climatic gradients in clutch size have been intensively studied in avian reptiles for well over a century. In fact, more than 75 years ago, Moreau (1944) wrote: 'It is over a hundred years ago since the view was first put forward that, on the whole, tropical birds tend to lay fewer eggs than birds of the temperate zones'. Birds lay larger clutches at higher latitudes and in colder, more seasonal environments (Rensch, 1938; Ricklefs, 1980). This has been shown repeatedly both within (e.g. Cody, 1966; Lack, 1947; Moreau, 1944; Rensch, 1938; Vaugoyeau, Adriaensen, Artemyev, Banbura, & Barba, 2016) and among (e.g. Boyer, Cartron, & Brown, 2010; Jetz, Sekercioglu, & Bohning-Gaese, 2008; Ricklefs, 1980; cf. Yom-Tov, Christie, & Iglesias, 1994) species and clades.

In comparison, studies of geographic gradients in clutch size (excluding island effects) of other tetrapod taxa are few and far between, never quite achieving the paradigmatic status they have for birds (Pincheira-Donoso & Hunt, 2017). Morrison and Hero (2003) found that amphibian clutches are smaller at higher latitudes once maternal body sizes are accounted for. Studies of geographic trends

in mammalian litter sizes are also uncommon (but see Bywater, Apollonio, Cappai, & Stephens, 2010; Virgos, Cabezas-Diaz, & Blanco-Aguar, 2006). When large-scale comparative studies of squamate life histories have been carried out, geographic variation in clutch size was rarely the focus (e.g. Andrews & Rand, 1974; Clobert et al., 1998; Dunham et al., 1988; Mesquita et al., 2016). Fitch (1985) found that clutch size increased with latitude within the six turtle species he studied, a result later corroborated by Iverson, Balgooyec, Byrdk, and Lyddank (1993) based on a much larger sample. Fitch (1985) nonetheless claimed that snakes, and especially lizards, show much weaker trends. Clutch size was higher at higher latitudes in half (8 of 16) the lizard species he studied, seven species showed a reverse trend, and one showed none (Fitch, 1985). The mean difference in clutch size between the high and low latitude populations was just 1%. Interspecifically, Tinkle et al. (1970) found no differences between clutch sizes of tropical and temperate lizards, but Meiri et al. (2013), and Mesquita et al. (2016), identified significant, albeit weak, negative associations between clutch size and environmental temperatures.

Mechanisms responsible for observed geographic variation in clutch size have likewise mostly been studied in birds. Moreau (1944) hypothesized that increased winter mortality selects for large clutch sizes at high latitudes. Lack (1947) suggested that high-latitude birds benefit from longer days during the breeding seasons, enabling them to obtain more food. If valid, this mechanism is likely to hold for birds, a mostly diurnal clade, but for taxa with a more varied diel activity cycle it may mean that only clutches of diurnal species will increase with latitude. If true, clutch sizes may well decrease with latitude in nocturnal taxa, because nights during the summer activity season are short at high latitudes. Ashmole (1963), and Ricklefs (1980), hypothesized that high mortality rates, caused by increased seasonality, reduce population density at the beginning of each breeding season. They reasoned that this, coupled with abundant resources in the short breeding season, increases per-individual resource availability that can be channelled towards offspring production ('Ashmole's hypothesis'). Jetz et al. (2008) and Griebeler, Caprano, and Bohning-Gaese (2010) likewise stressed the importance of juvenile and adult mortality, respectively, in selecting for a positive clutch-size/seasonality association in birds. Griebeler et al. (2010) suggested that increased predation pressure on chicks and adults at high latitudes could result in the observed pattern (but see Pincheira-Donoso & Hunt, 2017; Ricklefs, 1980). Cooper, Hochahka, Butcher, and Dhondt (2005) theorized that temperature may directly cause the observed patterns through its effect on incubation costs and survival.

Importantly, nearly all the mechanisms suggested to account for the observed geographic variation in bird clutch sizes are likely to apply more generally across other organisms. Andrews and Rand (1974) further suggested that lizards in seasonal environments lay larger clutches than in aseasonal tropical regions. In the tropics, they suggested that short-term fluctuations in rainfall will favour frequent laying of small clutches. They claimed that arboreal lizards (especially those using adhesive toe pads) are constrained to

lay small clutches because a large clutch of eggs would severely limit the climbing agility of the mother. Following a similar logic, Vitt (1981, see also Schwarzkopf, Barnes, & Goodman, 2010), and Ashton (2005), suggested that saxicolous and fossorial species, respectively, will lay smaller clutches than terrestrial species – to better allow the pregnant mother to use rock fissures and narrow burrows.

Because there are no large-scale studies of geographic variation in clutch size of non-avian vertebrates, a global test of the environmental correlates of lizard clutch size could be insightful as well as timely. Using a global dataset of clutch sizes, we test a range of predictions regarding the evolutionary mechanisms influencing this important reproductive trait. We predict that lizard clutch sizes will be (1) positively correlated with latitude, and (2) positively correlated with temperature and precipitation seasonality. These three variables are probably good proxies for the length of the reproductive and activity seasons of lizards (see below), and – because predation is likely to be weakened when animals hibernate below ground – perhaps also of mortality rates (Stark, Tamar, Itescu, Feldman, & Meiri, 2018). If day length during the reproductive season (i.e. spring and summer for non-tropical lizards) affects clutch size (Lack, 1947), we predict that (3) latitude will be positively correlated with clutch size in diurnal species but negatively associated with it in nocturnal species. We further predict (4) that in regions where resources are abundant, females will lay larger clutches because they can bear the energetic costs of doing so. We further examine the distribution of lizard lineages laying small, fixed clutches of one or two eggs relative to the distribution of lizards laying variable, usually larger, clutches. We attempt to infer (5) whether differences in their geographic distribution conform to the general relationship between clutch size and geographic distribution. Incidentally, we thus also test (6) whether clutch sizes increase with body mass (e.g. Dunham et al., 1988), (7) decrease with insularity (Novosolov et al., 2013), or (8) are lower in arboreal (Andrews & Rand, 1974), fossorial (Ashton, 2005) and saxicolous species than in terrestrial ones (Vitt, 1981).

## 2 | METHODS

### 2.1 | Lizard clutch-size data

We obtained data on lizard (Squamata exclusive of Serpentes) clutch size, body size, diurnal/nocturnal habits, and microhabitat preferences from the literature (e.g. Meiri, 2018; Slavenko, Tallowin, Itescu, Raia, & Meiri, 2016, see Supporting Information Appendix S1 for a list of sources) and our personal observations in the field, laboratory, and natural-history collections. Some of the species in our database are viviparous, but Meiri et al. (2020) found no systematic differences between clutch sizes of oviparous squamates and litter sizes of viviparous ones. We use the term 'clutch size' throughout, for simplicity, although live-bearing species are included. We used data on mean clutch sizes, and, when lacking means, we averaged the smallest and largest clutch sizes reported for a species. If multiple means were available we averaged the smallest and largest values (rather

than averaging all means, because often a single mean is reported multiple times among studies, without proper acknowledgement).

Body sizes (for testing Hypothesis 6) are mean snout-vent lengths (SVLs, in mm) of females, which we converted to masses using clade-specific allometric equations (from Feldman, Sabath, Pyron, Mayrose, & Meiri, 2016). Although within-taxon masses are highly variable (e.g. according to the time from and size of the last meal, body condition and whether a female is distended with eggs), in squamates, across squamate taxa masses better reflect size than lengths – as animals of identical length can easily vary by two orders of magnitude in mass (Meiri, 2010). Our clade-specific equations for legged, leg-reduced, and legless lizards separately take this shape variation into account and allow us to compare similar-sized taxa across the diversity in shape from long, thin pygopodids to chubby phrynosomatids (Feldman et al., 2016). As for clutch sizes, when multiple body size means were available, we averaged the smallest and largest values (Meiri, 2018). We classified lizards as either diurnal, nocturnal, or cathemeral (active during both day and night, including primarily nocturnal and primarily diurnal species) to test Hypothesis 3, and as terrestrial, fossorial, or scansorial (i.e. arboreal or saxicolous; Meiri, 2018) to test Hypothesis 8. Species that frequently occur both on trees or rocks (as adults) and on the ground were also classified as scansorial because we assume the agility of a gravid female would be most greatly constrained by any climbing activity or when trying to lodge itself in rock crevices (Schwarzkopf et al., 2010; Vitt, 1981). Semi-aquatic species ( $n = 75$ ) were classified as scansorial if they are also semi-arboreal or semi-saxicolous (Grinham & Norman, 2020), or as terrestrial otherwise. A preliminary analysis showed semi-aquatic species were not significantly different than either scansorial or terrestrial ones (not shown).

Species' geographic ranges were obtained from Roll et al. (2017) with some subsequent updates (e.g. for newly described species). We used these distributional data to find species' latitudinal centroids in ESRI ArcGIS v.10.6 (ESRI, Redlands, CA; to test Hypotheses 1 & 3) and measures of mean annual temperature (BIO1), temperature seasonality (BIO4) and precipitation seasonality (BIO15; to test Hypothesis 2). Climatic data are from CHELSA (Karger et al., 2017), and net primary productivity (NPP) data are from Imhoff et al. (2004; Hypothesis 4). We calculated a single value per species for each climatic/environmental measure by averaging the climatic data across species' distributional ranges. Insular taxa were defined as those inhabiting only landmasses equal to or smaller than New Guinea, used to test Hypothesis 7. Taxonomy follows the December 2019 version of the Reptile Database (Uetz, 2019).

## 2.2 | Analyses

To examine the relationship between clutch size and the climatic and other predictors we used species-level phylogenetic analyses. We  $\log_{10}$ -transformed clutch sizes and body masses, NPP, and temperature seasonality data to linearize relationships, improve residual normality, and reduce heteroscedasticity. We used the absolute value of

the latitudinal centroid of each species. Multicollinearity was minimal (the maximum variance inflation factor was 2.4, for temperature seasonality). Because latitude is a proxy for several climatic variables (and day length), however, we analysed latitude and climatic factors in separate models. To test whether diurnal and nocturnal species respond differently to climate (Hypothesis 3) we used two-way interactions between activity time and latitude. We then conducted a phylogenetic generalized-least squares ANCOVA (PGLS version of a Brownian-motion model of evolution; see Mesquita et al., 2016) using the *caper* R package (Orme et al., 2014), whereby the strength of the phylogenetic signal (using the  $\lambda$  parameter) is assessed using maximum likelihood, and phylogenetic distances are multiplied by  $\lambda$  before independent contrasts are calculated (Freckleton, Harvey, & Pagel, 2002).

We used the phylogenetic tree of squamates from Tonini, Beard, Ferreira, Jetz, and Pyron (2016) to calculate contrasts and distances. This tree is partially based on genetic data and partially inferred from taxonomy – some of which has become obsolete due to more recent genetic findings (S. Meiri, personal observation). We then ran two sets of PGLS models: one with mean female mass, insularity, microhabitat, activity time, mean annual temperature and its seasonality, mean annual precipitation and its seasonality and NPP as predictors; and another with mean female mass, insularity, microhabitat, activity time, latitude and the activity time/latitude interaction, as predictors of clutch size. Over 250 of the species in our dataset were not found in the tree of Tonini et al. (2016). Therefore, we added non-phylogenetic sensitivity analyses using an ANCOVA with the same predictors as in the PGLS. This could further allow us to assess if observed patterns result from evolutionary responses within taxa or from taxon turnover (Meiri & Thomas, 2007; Novosolov & Meiri, 2013).

We added two additional sensitivity analyses. First, our measure of body size was mean female body mass in the analyses described above. For 776 species, however, we had no data on mean female mass, whereas we had data on maximum mass of all 3,916 species. To ensure that such a loss of 20% of the data did not bias our results we repeated the analyses with data on maximum body mass of all species (taken from either sex).

Within most lizard species, clutch sizes can be highly variable (e.g. 1–41 eggs in *Elgaria multicarinata*, 1–33 eggs in *Cyclodomorphus gerrardii* and *Calotes versicolor*, 2–77 eggs in *Chamaeleo dilepis*). In the Gekkota (geckos and flap-footed lizards), Gymnophthalmidae, and Dactyloidae (anoles), however, clutches are 'fixed', nearly always comprising just one or two eggs. Because species with fixed clutch sizes cannot, by definition, increase their clutch size in response to climate, we conducted analyses only for species that have variable clutch sizes, and again for all species (regardless of whether their clutch sizes are variable or fixed). We defined laying strategy based on phylogenetic affinities rather than basing it on observed clutch sizes. We designate all members of the Gekkota, Dactyloidae, Alopoglossidae, and Gymnophthalmidae as having fixed clutches even though clutch sizes of three or more eggs have been reported for a few of them. For example, the gecko *Mediodactylus kotschy* sometimes lays three eggs, although clutches of one or two eggs are

much more common (Goldberg, 2012; Slavenko et al., 2015); nonetheless, we treated it as a fixed-clutch species. Species belonging to all other taxa were treated as having variable clutch sizes. This includes species that only lay one or two eggs. For example, the agamid *Draco bimaculatus*, the amphisbaenian *Cynisca leonina*, and the lacertid *Holaspis laevis* all have a maximum reported clutch size of two. They were treated as having variable clutch sizes because they belong to families in which most species lay larger clutches. We did this because we assume that 1–2 egg clutches in variable-clutch-sized lineages reflect ecologically induced selection pressures of the type we aim to identify here, whereas in four abovementioned fixed-clutched lineages such clutch sizes reflect constraints.

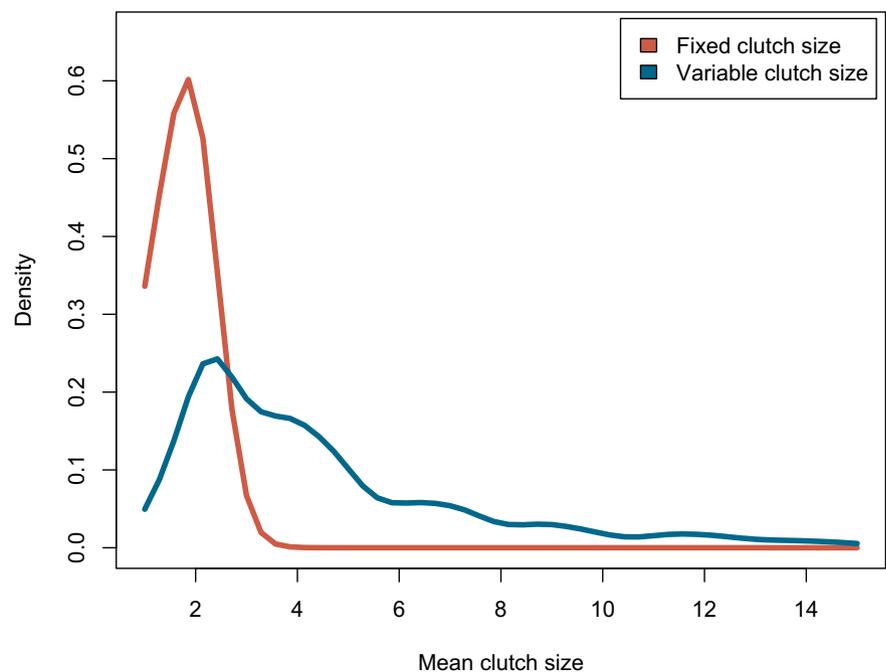
### 3 | RESULTS

We obtained clutch-size data for 3,916 lizard species. Mean clutch size per species varied between 1 (in 434 species) to 52 (in *Chamaeleo senegalensis*,  $n = 5$  individuals; Cisse & Karns, 1978), with a mode of 2 eggs (1,191 species; 1,273 with mean clutch sizes of 1.9–2.1 eggs). All 44 lizard families are represented in our dataset, which covers 56% of global lizard diversity (3,916 of 6,950 recognized species; Supporting Information Appendix S1, Figure 1).

The results of the four types of global phylogenetic models (with either all species or just lizards with variable clutch sizes, and using either average female or maximum body mass) are highly congruent (Tables 1 and 2, Supporting Information Appendix S2). Body mass is positively correlated with clutch size (Figure 2), which supports Hypothesis 6. Insular taxa lay fewer eggs, supporting Hypothesis 7; and fossorial (perhaps also scansorial) species have smaller clutch sizes than terrestrial species, supporting Hypothesis 8. Under more stringent criteria for assessing statistical significance (e.g.  $p = .005$ ,

see Benjamin et al., 2017; Johnson, 2013), differences in clutch size among microhabitats are often not significant (Tables 1 and 2). Clutch sizes increase with latitude (supporting Hypothesis 1) and, in climatic models, increase with net temperature seasonality (Hypothesis 2) and primary productivity (Hypothesis 4), under any threshold for statistical significance and across all global tests. Clutch sizes increase with increased precipitation seasonality (Hypothesis 2) in taxa with variable clutch sizes, but patterns for precipitation seasonality are inconsistent across analyses (Supporting Information Appendix S2). Mean annual precipitation and mean annual temperature, however, are not related to clutch sizes (Table 1, Supporting Information Appendix S2). Activity time was generally unrelated to clutch size (see, e.g. ANOVA tables in Supporting Information Appendix S2), but it had a significant interaction with latitude in several models. Near the equator, nocturnal species have larger clutches than diurnal species, but clutch sizes of nocturnal taxa do not increase with latitude (or seasonality), whereas those of diurnal taxa do increase poleward (Figure 3; see Hypothesis 3, above). Because of the high similarity across models we discuss below the models using maximum body mass and only taxa with variable clutch sizes, highlighting other models only when they show different patterns.

Although in global analyses clutch sizes increase with latitude, in Africa clutches are larger at low latitudes (Figure 3, Supporting Information Appendix S2). We thus explored models for different biogeographic realms individually (Supporting Information Appendix S2). In the Afrotropical realm (which excludes the Sahara and Madagascar, but includes the southern parts of the Arabian Peninsula) clutch sizes do not respond to latitude (tested in taxa with variable clutch sizes, with maximum body mass as an additional predictor. Slope =  $0.0020 \pm 0.0016$ ,  $p = .23$ ,  $n = 284$ ). Even in the Afrotropics, however, clutch sizes increase with temperature seasonality (Hypothesis 2; slope =  $0.296 \pm 0.074$ ,  $p < .0001$ ; but not



**FIGURE 1** Density plot of mean clutch sizes for the 3,916 species analysed, separated between species with fixed (red) and variable (blue) clutch sizes [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**TABLE 1** ANOVA results and parameter estimates of clutch sizes as a function of ecological and geographic predictors. For full results see Supporting Information Appendix S2. (a) ANOVA tables, all taxa, maximum body mass; a model with net primary productivity (NPP) and precipitation followed by model with latitude. (b) Parameter estimates, all taxa, maximum body mass. (c) ANOVA table, taxa with variable clutch sizes, maximum body mass. (d) Parameter estimates, taxa with variable clutch sizes, maximum body mass

Factor	d.f.	Sum of squares	Mean squares	F	p
a.					
1. ANOVA table, climatic model					
Body mass	1	0.271	0.271	774.512	< .0001
Insularity	1	0.033	0.033	93.108	< .0001
Microhabitat	2	0.004	0.002	5.411	.005
Precipitation seasonality	1	0.003	0.003	7.469	.006
Temperature seasonality	1	0.025	0.025	71.423	< .0001
NPP	1	0.013	0.013	38.149	< .0001
Residuals	3,425	1.198	0.0004		
2. ANOVA table, latitude model					
Body mass	1	0.252	0.252	693.800	< .0001
Insularity	1	0.029	0.029	78.450	< .0001
Microhabitat	2	0.005	0.002	6.318	.002
Activity time	2	0.0009	0.0004	1.177	.308
Latitude	1	0.015	0.015	40.794	< .0001
Activity time: Latitude interaction	2	0.004	0.002	5.500	.004
Residuals	3,228	1.17365	0.00036		
b. Parameter estimates, all taxa, maximum body mass					
Factor	Estimate	SE	t	p	
1. Parameter estimates, climate and NPP model					
Terrestrial	0.420	0.146	-5.651	< .0001	
Fossorial	0.392	0.147	-2.131	.0331	
Scansorial	0.405	0.147	-2.152	.0314	
Mainland	0.420	0.010	-3.337	.0009	
Insular	0.389	0.144	-5.974	< .0001	
Mass	0.176	0.006	27.943	< .0001	
Precipitation seasonality	0.0003	0.0001	2.716	.0066	
Temperature seasonality	0.119	0.012	10.041	< .0001	
NPP	0.057	0.009	6.177	< .0001	
2. Parameter estimates, latitude and activity time model					
Terrestrial	0.475	0.083	2.737	.006	
Fossorial	0.433	0.084	2.721	.0065	
Scansorial	0.456	0.083	2.581	.0099	
Mainland	0.475	0.083	2.737	.006	
Insular	0.408	0.083	1.926	.054	
Latitude (diurnal species)	0.0031	0.0004	7.179	< .0001	
Latitude (nocturnal species)	0.001	0.001	0.671	.502	

(Continues)

TABLE 1 (Continued)

Factor	d.f.	Sum of squares	Mean squares	F	p
Mass	0.170	0.007	26.142	< .0001	
c. Taxa with variable clutch sizes, maximum body mass					
Factor	d.f.	Sum of squares	Mean squares	F	p
1. ANOVA table, climatic model					
Body mass	1	0.324	0.324	654.103	< .0001
Insularity	1	0.047	0.047	94.249	< .0001
Microhabitat	2	0.004	0.002	3.811	.022
Precipitation seasonality	1	0.006	0.006	11.588	.001
Temperature seasonality	1	0.029	0.029	58.862	< .0001
NPP	1	0.025	0.025	51.457	< .0001
Residuals	2,196	1.086	0.000		
2. ANOVA table, latitude model					
Body mass	1	0.310	0.310	568.559	< .0001
Insularity	1	0.045	0.045	82.018	< .0001
Microhabitat	2	0.004	0.002	4.055	.017
Activity time	2	0.002	0.001	1.557	.211
Latitude	1	0.016	0.016	29.321	< .0001
Activity time: Latitude interaction	2	0.002	0.001	1.444	.236
Residuals	2013	1.097	0.001		
d. Taxa with variable clutch sizes, maximum body mass					
Factor	Estimate	SE	t	p	
1. Parameter estimates, climate and NPP model					
Terrestrial	0.499	0.211	-6.967	< .0001	
Fossorial	0.471	0.210	1.0645	.100	
Scansorial	0.483	0.211	1.0673	.094	
Mainland	0.499	0.211	-6.967	< .0001	
Insular	0.464	0.206	-7.319	< .0001	
Mass	0.216	0.008	25.585	< .0001	
Precipitation seasonality	0.0006	0.0001	3.846	.0001	
Temperature seasonality	0.169	0.017	9.896	< .0001	
NPP	0.096	0.013	7.173	< .0001	
2. Parameter estimates, latitude and activity time model					
Terrestrial	0.572	0.114	2.074	.038	
Fossorial	0.526	0.116	2.260	.024	
Scansorial	0.553	0.115	1.902	.057	
Mainland	0.572	0.114	2.074	.038	
Insular	0.472	0.115	1.180	.238	
Latitude (diurnal species)	0.003	0.001	5.595	< .0001	

(Continues)

TABLE 1 (Continued)

Factor	d.f.	Sum of squares	Mean squares	F	p
Latitude (nocturnal species)	0.0005	0.0008	0.648	.517	
Mass	0.212	0.009	23.565	< .0001	

Note for (b) 1:

All species, maximum body mass,  $\lambda = 0.776$ , model  $R^2 = .225$ . Mass, seasonality and NPP estimates are slopes ( $\log_{10}$  transformed except precipitation seasonality). Values (clutch sizes,  $\log_{10}$  transformed) of the categorical variables are for the means of the continuous predictors: a mass of 12.3 g (back transformed from logarithm),  $\log$  NPP = 11.37 (g C/m<sup>2</sup>/year,  $\log_{10}$  transformed), Temperature seasonality = 3.3 (standard deviation, °C\*100,  $\log_{10}$  transformed), precipitation seasonality = 66.3 (coefficient of variation of monthly values). Values for microhabitats are shown for mainland species. Values for insularity/mainland are shown for terrestrial species. Estimates are presented with their standard errors. *t* and *p* values are for differences from zero (with the continuous variables set to zero) for terrestrial and mainland species, from terrestrial species for fossorial and scansorial ones, and from insular species from mainland species. Terrestrial species have smaller clutches than both scansorial and fossorial species. There are no significant differences between scansorial and fossorial species ( $t = 0.923$ ,  $p = .356$ ).

Note for (b) 2:

All species, maximum body mass,  $\lambda = 0.794$ , model  $R^2 = .206$ . Mass ( $\log_{10}$  transformed) and latitude estimates are slopes. Values (clutch sizes,  $\log_{10}$  transformed) of the categorical variables are for the means of the continuous predictors: a mass of 12.3 g (back transformed from logarithm), latitude (absolute value): 19.55° (decimal). Values for microhabitats are shown for diurnal mainland species. Values for insularity/mainland are shown for diurnal terrestrial species. Estimates are presented with their standard errors; *t* and *p* values are for differences from zero (with mass and latitude set to zero) for terrestrial and mainland species, from terrestrial species for fossorial and scansorial ones, and from insular species from mainland species. Terrestrial species have smaller clutches than both scansorial and fossorial species but there are no significant differences between scansorial and fossorial species ( $t = 1.383$ ,  $p = .167$ ). Latitudinal slope for cathemeral species not shown.

Note for (d) 1:

Only species with variable clutch sizes, maximum body mass,  $\lambda = 0.801$ , model  $R^2 = .286$ . Mass, seasonality and NPP estimates are slopes ( $\log_{10}$  transformed except precipitation seasonality). Values (clutch sizes,  $\log_{10}$  transformed) of the categorical variables are for the means of the continuous predictors: a mass of 18.8 g (back transformed from logarithm),  $\log$  NPP = 11.36 (g C/m<sup>2</sup>/year,  $\log_{10}$  transformed), temperature seasonality = 3.35 (standard deviation, °C\*100,  $\log_{10}$  transformed), and precipitation seasonality = 65.9 (coefficient of variation of monthly values). Values for microhabitats are shown for mainland species. Values for insularity/mainland are shown for terrestrial species. Estimates are presented with their standard errors. *t* and *p* values are for differences from zero (i.e. with mass, seasonality and NPP set to zero) for terrestrial and mainland species, from terrestrial species for fossorial and scansorial ones, and from insular species from mainland species. Terrestrial species have similar clutch sizes to both scansorial and fossorial species and there are no significant differences between scansorial and fossorial species ( $t = 0.677$ ,  $p = .498$ ). The latitudinal slope for cathemeral species is not shown.

Note for (d) 2:

Only species with variable clutch sizes, maximum body mass,  $\lambda = 0.825$ , model  $R^2 = .256$ . Mass ( $\log_{10}$  transformed) and latitude estimates are slopes. Values (clutch sizes,  $\log_{10}$  transformed) of the categorical variables are for the means of the continuous predictors: a mass of 18.8 g (back transformed from logarithm), latitude (absolute value): 20.92° (decimal). Values for microhabitats are shown for diurnal mainland species. Values for insularity/mainland are shown for diurnal terrestrial species. Estimates are presented with their standard errors. *t* and *p* values are for differences from zero (with mass and latitude set to zero) for terrestrial and mainland species, from terrestrial species for fossorial and scansorial ones, and from insular species from mainland species. Terrestrial species have smaller clutches than fossorial – but not scansorial species. There are no significant differences between scansorial and fossorial species ( $t = 1.251$ ,  $p = .211$ ). The latitudinal slope for cathemeral species is not shown.

with precipitation seasonality, slope =  $0.0008 \pm 0.0005$ ,  $p = .16$ ; Supporting Information Appendix S2). We suspected that the high clutch sizes in equatorial Africa were a result of the inclusion of chameleons. Chameleons are almost exclusively confined to Africa and Madagascar and have by far the largest clutches among all lizard families (13.4 eggs on average, not many more than the New World Iguanidae with 12.0, but chameleons are much smaller animals, and include many more species: 135 vs. 24 in our analyses; the family with the third-largest clutches, the Neotropical Polychrotidae, has an average clutch size of 9.0,  $n = 7$ ). However, omitting chameleons does not change the overall conclusion that lizard clutch sizes in equatorial Africa are large compared to other equatorial regions (Supporting Information Appendix S3).

Results of the non-phylogenetic models are very similar to those of the phylogenetic models except that, in the non-phylogenetic models for taxa with variable clutch sizes, scansorial species have

similar clutch sizes to terrestrial species (Supporting Information Appendix S2e). The important factors remain body mass (positive, Hypothesis 6), insularity (negative, Hypothesis 7), latitude (positive in diurnal species; Hypotheses 1 & 3), seasonality (positive; especially temperature seasonality; Hypothesis 2), and NPP (positive; Hypothesis 4 Supporting Information Appendix S2e).

## 4 | DISCUSSION

Our global-scale evidence reveals that lizard clutch sizes are larger at higher latitudes (Hypothesis 1) and in more seasonal environments. Lizard clutch sizes thus show similar geographic patterns to those seen in birds. Africa, however, emerges as a strong anomaly in lizards (Figure 3) but not in birds (see fig. 4a in Jetz et al., 2008). Lizard clutch sizes could thus be explained by similar mechanisms as those

**TABLE 2** Summary of statistical significance of different models ( $\alpha = .05$ ). Fossorial, scansorial, and semi-aquatic species are compared to terrestrial ones. Nocturnal and cathemeral species are compared to diurnal ones (see ANOVA tables in Table 1 for overall significance of multilevel factors). Nocturnal:latitude and Cathemeral:latitude are interaction terms and depict whether, and in which direction, the latitudinal slope differs from the slope for diurnal species. See Table 1 and Supporting Information Appendix S2 for parameter estimates (contrasts and slopes).

Model	All taxa	All taxa	VCS taxa	VCS taxa
	average female size	maximum size	average female size	maximum size
a. Models with climatic and environmental predictors (seasonality and NPP)				
Lambda	0.818	0.794	0.849	0.817
<i>n</i>	2,617	3,163	1,723	1,995
Mass	+	+	+	+
Insularity	-	-	-	-
Fossorial	-	-	n.s.	-
Scansorial	-	-	n.s.	n.s.
Nocturnal	n.s.	n.s.	n.s.	n.s.
Cathemeral	n.s.	n.s.	+	+
Seasonality (precipitation)	n.s.	+	+	+
Seasonality (temperature)	+	+	+	+
NPP	+	+	+	+
$R^2$	.239	.225	.302	.288
b. Models with latitude and activity times				
Lambda	0.818	0.794	0.854	0.825
<i>n</i>	2,566	3,238	1,743	2,023
Mass	+	+	+	+
Insularity	-	-	-	-
Fossorial	-	-	-	-
Scansorial	-	-	n.s.	n.s.
Nocturnal	n.s.	+	n.s.	n.s.
Cathemeral	+	+	n.s.	+
Latitude	+	+	+	+
Nocturnal:latitude	-	-	n.s.	n.s.
Cathemeral:latitude	-	-	n.s.	n.s.
$R^2$	.216	.206	.265	.256

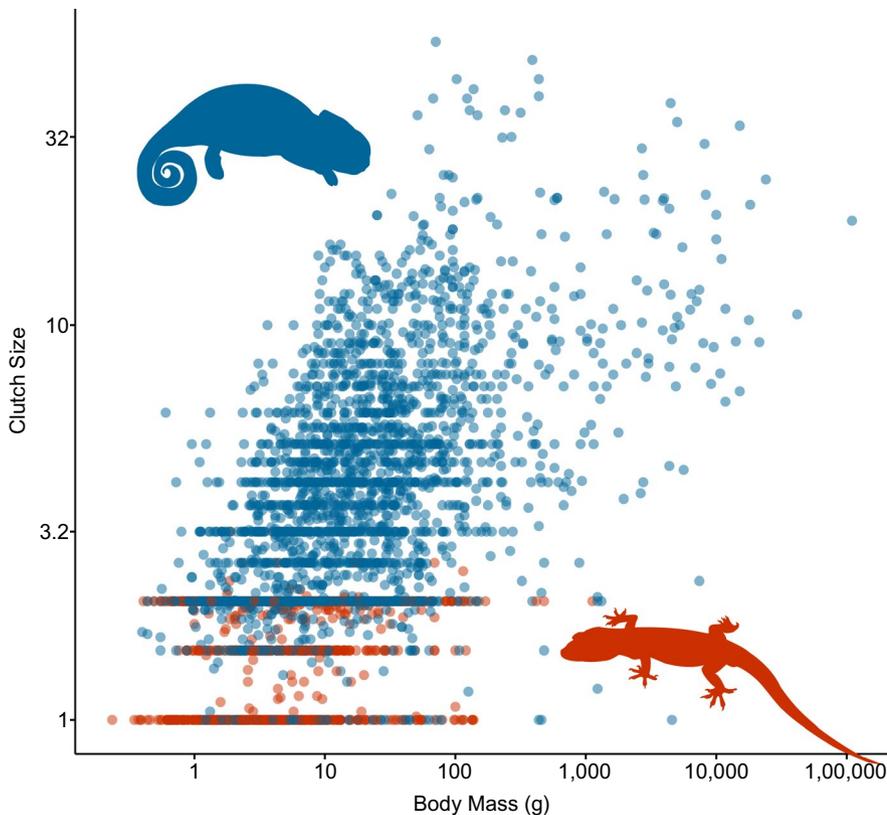
VCS = variable clutch size; NPP = net primary productivity; + = significant, positively associated with clutch size; - = significant, negatively associated with clutch size; n.s. = non-significantly associated with clutch size; *n* = number of species used in the analysis after deletion of species with missing data.

operating on birds (Jetz et al., 2008), suggesting the generality of these mechanisms beyond endotherms.

We are unaware of large-scale data on predation intensities that would allow us to assess whether predation too is higher in seasonal environments and higher latitudes (as hypothesized for birds by, for example, Griebeler et al., 2010). The lack of temperature effects, however, leads us to conclude that seasonality (Hypothesis 2) is a stronger force than cold weather per se ('harshness', Morrongiello, Bond, Crook, & Wong, 2012), at least in lizards. In highly seasonal environments, the window of opportunity for reproduction is short. Although temperature seasonality and latitude are but proxies for the length of the activity season of lizards (and also vary with other relevant factors), we think they are good proxies (see Supporting Information Appendix S4). High latitudes are often characterized

by a high seasonal peak in environmental productivity (Geist, 1987; Huston & Wolverton, 2011), enabling lizards to produce large clutches. We posit that in such environments animals can both find sufficient resources, and are under strong selection pressure, to be as fecund as possible (Hypothesis 4).

There is another angle from which such results need to be viewed: what are the reasons that many species in stable, less-seasonal, environments do not lay large clutches? The logical converse of our proposed explanation for high clutch sizes is that lizards in less-seasonal environments do not lay large clutches because environmental productivity lacks a seasonal peak. Under these circumstances it may take more time to accrue sufficient energetic resources to produce even one or two eggs. We hypothesize that laying few eggs in a single clutch may be advantageous as long as the



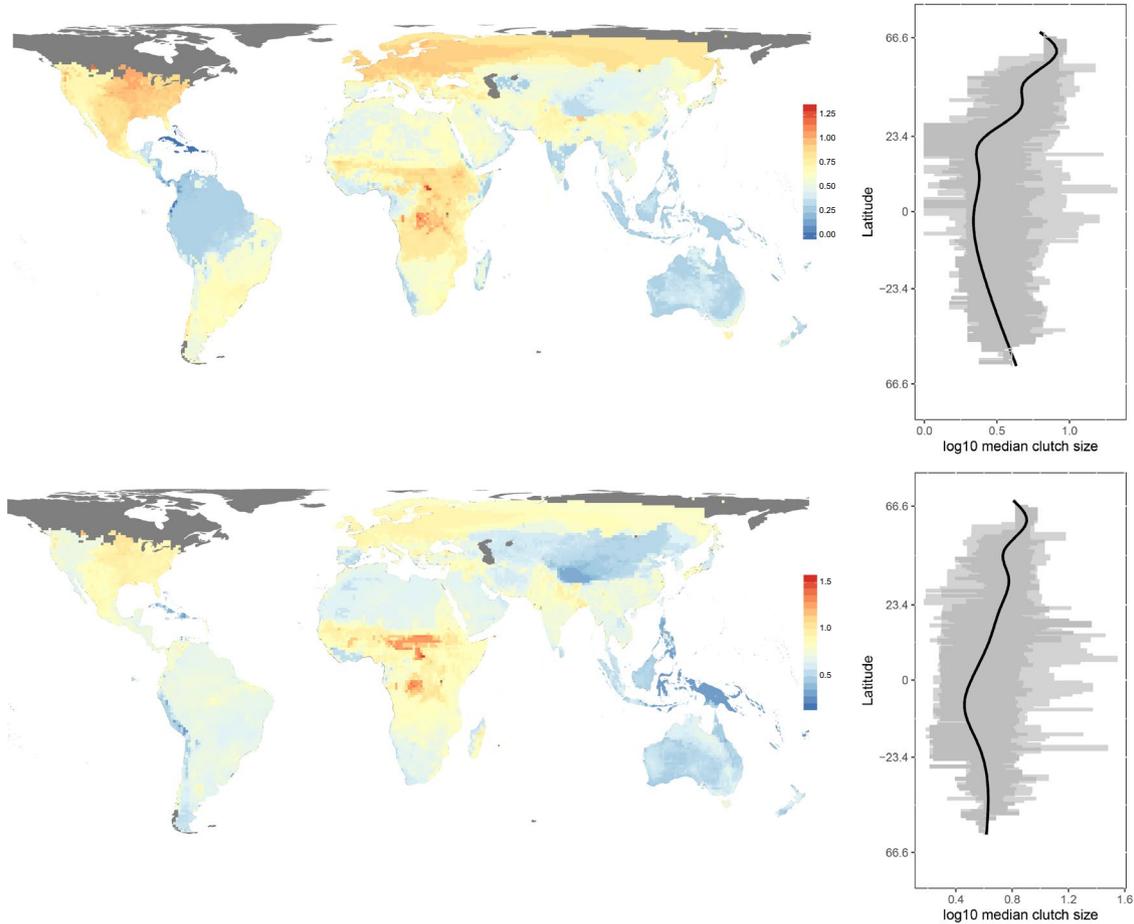
**FIGURE 2** The relationship between clutch size ( $\log_{10}$  transformed) and maximum body mass (in grams,  $\log_{10}$  transformed) in the 3,916 species in our dataset. The Ordinary Least Squares slope is  $0.241 \pm 0.005$ .  $R^2 = .334$ . Taxa with variable clutch sizes shown in blue, those with fixed clutch sizes in red [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

female can compensate for the reduced number of eggs by laying more frequently (Meiri et al., 2013) – a requirement that stable environments allow for. Laying small, frequent clutches may be a safer bet if egg or adult predation pressure is high. Furthermore, there may be a high physiological strain on mothers laying large clutches (e.g. Blazquez, Diaz-Paniagua, & Mateo, 2000; Pincheira-Donoso & Hunt, 2017): carrying many eggs in the abdominal cavity may reduce locomotory performance and thereby increase predation risk, reduce foraging success, or convey additional energetic costs associated with carrying a heavy clutch of eggs (Vitt & Congdon, 1978). In some lizard taxa, the clutch may approach the weight of the mother (e.g. Diaz-Paniagua, Cuadrado, Blazquez, & Mateo, 2002; Foster, Sharp, Greene, & Tietgen, 2019; Roitberg et al., 2013). Although this obviously also holds where seasons are short, in such regions the advantage of producing more eggs may outweigh the penalty paid for lower performance because producing multiple clutches each season is not a viable option.

The tendency of clutch sizes to be larger at higher latitudes (Hypothesis 1), and in more seasonal environments, has been known for a long time, but only in birds has it received broad attention and the status of an ecological *rule* (sensu Mayr, 1956). The mechanisms suggested to explain this pattern, however, are hardly bird specific, as the evidence we present here shows. Of the suggested mechanisms we are aware of only the supposed additional costs of nesting and nestling mortality in cold regions (Cooper et al., 2005) may be specific to birds and probably irrelevant for lizards. We note that cold temperatures per se emerged in our models as unrelated to clutch size; thus, this mechanism does not apply to lizards. Another hypothesis – that latitude

is important as it relates to day length (Lack, 1947) – suggests a difference between nocturnal and diurnal taxa. Perhaps most mammals, snakes, and owls, would show the reverse trends, though data are scant. Murray (1976) found that clutch sizes mostly increased northwards in seven species of North American owls, whereas Donazar (1990) did not find a pattern in the European eagle owl. Interestingly, Evans, Leech, Crick, Greenwood, and Gaston (2009) found that clutch size increased with day length in seven diurnal bird species in Britain, but decreased with day length (i.e. increased with night length) in the single owl in their study (*Strix aluco*). Consistent with this, we found that nocturnal and diurnal lizards differ in the relationship they show between clutch size and latitude. Diurnal lizard clutch sizes increase with latitude, whereas those of nocturnal lizards do not, as predicted by our Hypothesis 3. Thus, at high latitudes during the spring and summer reproductive seasons, longer days may enable diurnal lizards to acquire more food or shuttle more efficiently between basking and foraging activities. Nocturnal lizards do not reach the highest latitudes that some diurnal species inhabit (Vidan et al., 2017), presumably because the short summer nights at high latitudes do not allow enough time to balance energetic requirements and/or the cold night-time temperatures do not allow for activity in most lizard lineages. Thus, variation in night length is lower for nocturnal lizards, at the low latitudes they inhabit, and they can reproduce year round. Furthermore, there are few nocturnal lizards with variable clutch sizes (93 species in our dataset), and, thus, the lack of a latitudinal effect on their reproduction may reflect low statistical power.

Africa emerges as a strong anomaly for the latitudinal clines we identify. Australia likewise seems to have lizards with relatively



**FIGURE 3** Median log-transformed clutch size in 96 km × 96 km grid cells globally. Top: all lizards; bottom: only lizards with variable clutch sizes. Note that the colour scale differs between the maps. To the right of each map is a curve showing a generalized additive model of the mapped variable (in black), the 95% confidence intervals of the mapped variable per 96-km latitudinal band (shaded dark grey), and the range of values of the mapped variable per 96-km latitudinal band (shaded light grey). For similar maps where residuals from a phylogenetic clutch-size on body-size analysis are portrayed see Supporting Information Figures S1–S2. Equal area Behrmann projection, 96 km × 96 km resolution [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

small clutch sizes for its latitudinal range and seasonality, and little within-continent variation (Figure 3, but see Supporting Information Figure S1). We cannot readily explain these unexpected anomalies – although the presence of many fossorial species in deserts of both continents could explain some of these patterns. We hypothesized that the mostly tropical, African-endemic, radiation of chameleons, with their huge clutches, could explain the large clutch sizes of tropical African lizards. We further reasoned that much of the pattern will disappear once body mass is accounted for, because variation in clutch size seemed to mirror body-mass variation in Africa (compare Figure 3 with fig. 1c in Slavenko et al., 2019). Removing chameleons from the analyses and accounting for body mass, however, still leaves us with an anomaly in Africa (Supporting Information Appendix S2, Figure S2). More research is needed to identify why this is so, and we note that our models still leave much unexplained variation (as do many models in ecology and evolution; Møller & Jennions, 2002; Peek, Leffler, Flint, & Ryel, 2003). For Australia, it may be that poor soils and low primary productivity (Hypothesis 4) constrain lizards to lay relatively small clutches. We note that, although clutch sizes in

African lizards do increase with temperature seasonality, no factor except body mass (Hypothesis 6) emerged as related to lizard clutch size within Australia (Supporting Information Appendix S2). It may be that clutch size data for a larger proportion of African lizards are missing than for other regions (see also Tingley, Meiri, & Chapple, 2016; Tolley, Alexander, Branch, Bowles, & Maritz, 2016). The lack of data is always a worry, though we have little reason to think these missing data would create systematic biases.

Birds and mammals are much better studied than reptiles generally (Bonnet, Shine, & Lourdis, 2002; Donaldson et al., 2016; Meiri & Chapple, 2016; Troudet, Grandcolas, Blin, Vignes-Lebbe, & Legendre, 2017). It is, therefore, unsurprising that latitudinal variation in bird clutch sizes has been much more intensively studied than in reptiles. Interestingly, studies of geographic variation in litter sizes of mammals are few (but see Bywater et al., 2010; Virgos et al., 2006). Thus, words written over 80 years ago – ‘A corresponding rule of the litter-size of mammals is not yet sufficiently founded’ (Rensch, 1938) – still ring true. Nonetheless, our study demonstrates that insights from the study of reptiles are not just interesting in

their own right, but could inform more pervasive patterns. That patterns shown by birds and lizards are broadly similar suggests a wider generality across more taxa and perhaps similar mechanisms.

#### 4.1 | Additional factors potentially affecting clutch sizes

Our results support key predictions regarding other factors that affect clutch sizes. Clutch size increases with body mass (supporting Hypothesis 6) – most steeply when average female mass of taxa with variable clutch sizes is considered (Appendix 2b; the only analysis where the 95% CI of the slope includes the canonical 0.25 slope). Clutches are smaller on islands (Hypothesis 7), as expected under the predictions of the island syndrome (Adler & Levins, 1994; Covas, 2012; Novosolov et al., 2013; Pafilis et al., 2011), whereby life history is assumed to ‘slow down’ on islands. This pattern is consistent across phylogenetic and non-phylogenetic models and remains true when fixed-clutched taxa are excluded. Thus, we posit that this reflects, at least in part, an evolutionary response of insular lizards to the ecological settings they encounter (Hypothesis 7) rather than simply a matter of taxon turnover related to the greater propensity of geckos and anoles to colonize islands (Novosolov & Meiri, 2013). Strong intraspecific competition on islands (Adler & Levins, 1994; Itescu, Schwarz, Meiri, & Pafilis, 2017; Judd & Ross, 1978; Melton, 1982; Novosolov et al., 2016), in the face of lower predation and interspecific competition pressures, has been suggested to drive this. Interestingly, however, within insular taxa there does not seem to be an association between clutch size and island area (examining the largest island inhabited by a species; results not shown).

Microhabitat preferences were related to clutch size in many models (though not always significantly so, especially at  $\alpha < .005$ ; see Supporting Information Appendix S2). Scansorial species seem to lay smaller clutches than terrestrial species of similar sizes that inhabit similar regions. This agrees with Hypothesis 8 that carrying a large clutch of eggs can be a disadvantage to arboreal species, limiting the female's ability to climb (Andrews & Rand, 1974; Kratochvil & Kubicka, 2007; Shine, Keogh, Doughty, & Giragossyan, 1998). It also agrees with Vitt (1981), who found that some crevice-living species have small clutches, and who hypothesized that evolving large clutch sizes may prevent females from entering their retreats. Schwarzkopf et al. (2010) have shown experimentally that gravid females with larger clutch sizes had wider mid-bodies and required larger crevices.

We note, however, that most chameleons are arboreal, yet have the largest clutches of all lizards. Distinguishing between arboreal taxa that respond to predators by fleeing (as most lizards do), rather than by camouflage (as most chameleons do), may prove illuminating. The prehensile tail of chameleons may also facilitate their ability to climb while gravid with large clutches. In our main analyses we designated all lizards that often climb rocks or vegetation as scansorial. We did not distinguish between strictly arboreal, strictly saxicolous, arboreal and saxicolous or even arboreal and terrestrial or terrestrial and saxicolous species, reasoning that climbing constrains the

clutch sizes of all such species. In further analyses we found no significant differences between strictly terrestrial and strictly arboreal species, whereas species classified as both arboreal and saxicolous had slightly larger clutches than strictly arboreal ones (Supporting Information Appendix S5; see also table 5 in Mesquita et al., 2016, showing that semi-arboreal species have larger clutches than either saxicolous or arboreal ones).

Fossorial taxa emerged as having smaller clutches than terrestrial species in some models (Table 2, Supporting Information Appendix S2). Overall, our results add some evidence to support Ashton's (2005) claim that because the fossorial *Plestiodon reynoldsi* lays small clutches it is ‘similar to those of other fossorial lizards’. We further note that within skinks (the only lizard clade with variable clutch sizes and multiple transitions to a fossorial lifestyle) fossoriality is indeed associated with small clutches (see Supporting Information Appendix S2 for within-clade models). We suspect this may be caused by increased energetic demand on burrowing for gravid females. Overall our results generally support the hypothesis that scansorial and fossorial lizards have smaller clutches than terrestrial ones, but effect sizes are generally small, and support varied across models.

#### 4.2 | The geographic distribution of lizards with fixed and variable clutches

We have found that lizard clutches are generally larger in higher latitudes and in seasonal regions even when only taxa with variable clutch sizes are considered and when phylogenetic non-independence is accounted for (Figure 3). We note that the distribution of lizards with fixed clutch sizes would only serve to strengthen the generality of these patterns. Although taxa in which females lay only one or two eggs are, of course, not expected to show geographic variation in this parameter, they can nonetheless inform us about the relationship between clutch size and the environment. With the exception of a few gecko taxa (e.g. the New Zealand radiation, Cree & Hare, 2016; Nielsen, Bauer, Jackman, Hitchmough, & Daugherty, 2011; the South American *Homonota darwini*; Ibaranguoytia & Casalins, 2007; Weeks & Espinoza, 2013), the distribution of fixed-clutch lizards is mostly limited to tropical, subtropical, and desert regions (geckos) or tropical and subtropical regions alone (anoles, gymnophthalmids; Roll et al., 2017). One could easily come up with hypotheses relating to the distribution of each of these three taxa. Gymnophthalmids, being mostly leaf-litter inhabitants, and anoles, being predominately scansorial (mostly arboreal, but with many leaf-litter species; for example, Losos, 2009; Vitt & Caldwell, 2013), could perhaps not penetrate temperate desert belts and migrate further north. This, however, would not necessarily explain their absence from more temperate, higher latitudes south of the equator in South America. Geckos, being predominately nocturnal (Bauer, 2013; Gamble, Greenbaum, Jackman, & Bauer, 2015), may be restricted largely to low latitudes by their inability to tolerate the cold nights prevailing at higher latitudes. Indeed Vidan et al. (2017)

identified a sharp distinction between the distributions of Eurasian diurnal lizards, some of which range above the Arctic Circle, and nocturnal taxa (mostly geckos), which do not reach anywhere near this far north. However, geckos have another trick up their sleeve: some of them evolved diurnal activity in colder regions, or bask during the day and forage at night (e.g. New Zealand *Naultinus*, *Tarentola mauritanica* in southern Europe, *Ptyodactylus puiuseuxi* in northern Israel, and *Quedenfeldtia* in the Atlas Mountains; see, for example, Gamble et al., 2015; Hare & Cree, 2016).

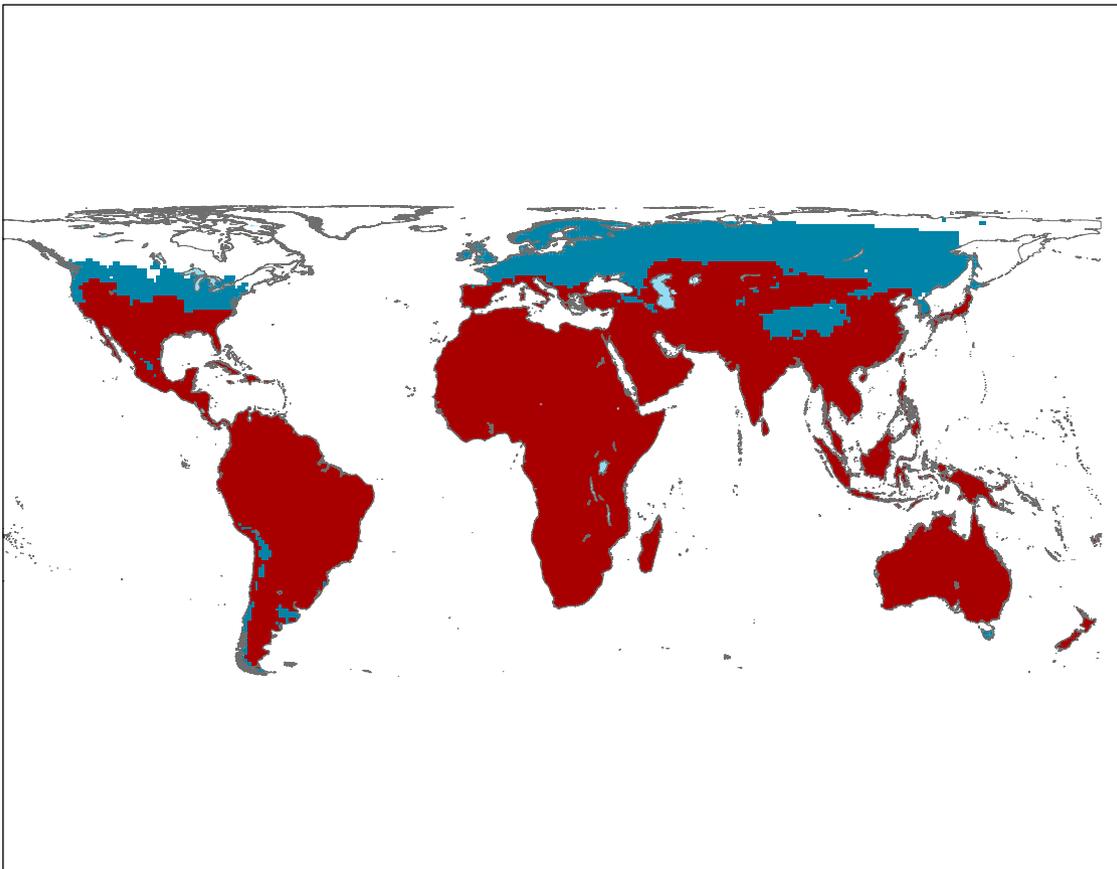
In the light of our findings, we tentatively suggest an alternative mechanism (Hypothesis 5): it may be that such taxa are restricted to low latitudes because their reproductive strategy – laying few eggs frequently – is simply not viable at higher latitudes (Figure 4). At high latitudes, and in other highly seasonal environments, the reproductive season is short, and laying multiple clutches is thus not viable. It could be that fixed-clutch species are excluded from high latitudes and highly seasonal regions not because of cold climates but because the short activity seasons in those regions do not allow them to produce enough offspring to ensure population replacement. If this hypothesis is true it would suggest that evolving a fixed clutch size has implications beyond its immediate effects on reproduction. What are the proximal mechanisms constraining species to

this strategy, and which ultimate mechanisms allow fixed-clutched lizards to thrive, are fascinating questions for future research.

In summary, lizard clutches are highly attuned to geographic cues, whether in the form of insularity or climatic clines. It seems though, that rather than climate per se, lizard clutch sizes respond to the degree of seasonality through its effect on the number of opportunities for reproduction within a year and perhaps through seasonal effects on food abundance, mortality rates, and foraging opportunities.

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**FIGURE 4** Distribution of lizards with fixed clutch sizes (red). Note that in the northernmost (North America, northern Eurasia) and southernmost distribution of lizards (South America; Australia, Tasmania, and New Zealand), and cold regions (e.g. Central Asia, the Caucasus and the Andes), fixed clutched taxa are generally absent. Lizards with variable clutch sizes inhabit all regions (both red and blue) that lizards occur in. White regions have no lizards. Equal area Behrmann projection, 96 km × 96 km resolution [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## DATA AVAILABILITY STATEMENT

Meiri, Shai et al. (2020), Data from: The global diversity and distribution of lizard clutch sizes, v4, Dryad, Dataset, <https://doi.org/10.5061/dryad.gf1vhhmkv>, [https://datadryad.org/stash/share/yrBYmta30PyavKaRXdJOfhkLhpj4e0\\_x\\_erKouUgj48](https://datadryad.org/stash/share/yrBYmta30PyavKaRXdJOfhkLhpj4e0_x_erKouUgj48). All data used in the analyses are available as Supporting Information Appendix S1.

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## BIOSKETCH

Shai Meiri is interested in the evolution of traits, and its relationship with geography.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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