

Traits of lizards of the world: Variation around a successful evolutionary design

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Abstract

Motivation: over the last 12 years I have been collecting trait and geographic data on lizards. These data could be useful for scientists studying this remarkable reptilian radiation. Furthermore, as published data for some of the less well known species are scarce, I hope this study can initiate a community effort to fill in data gaps. I present geographical, morphological, ecological, physiological and life history data for the 6,657 known species of lizards. I further indicate whether there are phylogenetic data associated with them, and their threat assessment, if they have one. I present descriptive statistics regarding these traits and point to avenues for future research using the dataset.

Main types of variable contained: body size, ecological, thermal biology, geographic, phylogenetic and life history data.

Spatial location: Global.

Time period: data are for species known from living, or recently extinct species. Most underlying data were collected during the 20th and 21st centuries.

Major taxa: Reptilia, Sauria (Squamata, including Amphisbaenia but excluding Serpentes).

Level of measurement: species.

Software format: csv.

KEYWORDS

distribution, ecology, life history, morphology, natural history, Sauria, thermal biology, traits

1 | INTRODUCTION

Lizards form a remarkable radiation of land vertebrates. The basic tetrapod design, of a four-legged sprawling-postured ectothermic animal, has been highly successful ever since vertebrates first moved to land. Together with the amniote adaptations for fully terrestrial lives it has set crown group squamates on a path to ecological and evolutionary success since they evolved over 200 million years ago (Evans, 2003; Zheng & Wiens, 2016). Over this time period lizards have diversified into all terrestrial habitats except the coldest ones (but see Berman, Bulakhova, Alfimov, & Meshcheryakova, 2016), filling multiple ecological niches, and showing a remarkable array of adaptations. Lizards have repeatedly evolved legless forms (e.g.,

Brandley, Huelsenbeck, & Wiens, 2008; Gans, 1975), including the hugely successful and highly derived, group of snakes - comprising over a third of the total diversity of squamates (Uetz, 2018). Even without snakes, over 6,650 species of lizards (here including the amphisbaenians) are nowadays recognized (Uetz, 2018), and about 120 new forms are added to the list yearly (Meiri, 2016). This makes lizards more species rich than all of the Mammalia (6,369 species, with 83 species on average, added per year since 2005; Burgin, Colella, Kahn, & Upham, 2018).

This extraordinary radiation has made lizards a highly studied model system for evolutionary (e.g., Gamble, Greenbaum, Jackman, Russell, & Bauer, 2016; Losos, 2009; Losos, Jackman, Larson, Queiroz, & Rodriguez-Schettino, 2009; Rabosky, Donnellan, Talaba,

& Lovette, 2007; Vitt & Pianka, 2005), life history (e.g., Clobert, Garland, & Barbault, 1998; Dunham, Miles, & Reznick, 1988; Fitch, 1970; Meiri, Brown, & Sibly, 2012; Mesquita et al., 2016; Scharf et al., 2015; Tinkle, Wilbur, & Tilley, 1970) ecological (e.g., Novosolov et al., 2017; Olesen & Valido, 2003; Pianka & Vitt, 2003; Pianka, Vitt, Pelegrin, Fitzgerald, & Winemiller, 2017; Vidan et al., 2017) and conservation biology (Böhm et al., 2013; Roll et al., 2017; Sinervo et al., 2010) studies.

Increasingly, macroecological and macroevolutionary studies – that have been traditionally based on geographic ranges and phylogenetic affinities, incorporate a wide array of physiological, ecological, morphological and life history traits to study animal ecology and evolution. Supermatrices now exist that map the phylogenetic relationships of over half of the known squamates (Pyron, Burbrink, & Wiens, 2013; Tonini, Beard, Ferreira, Jetz, & Pyron, 2016), with PASTIS trees (Thomas, Tallwin, Itescu, Raia, & Meiri, 2016) available for nearly all species (Tonini et al., 2016). Distribution data are also now compiled for virtually all reptiles (Roll et al., 2017). Adding trait data to these datasets could greatly facilitate future studies of lizard diversity, ecology, evolution and conservation.

Over the last 12 years I have been assembling a dataset of lizard traits (e.g., Meiri, 2008, 2010, 2016 ; Meiri et al., 2012; Meiri et al., 2018). Using the continuously evolving Reptile Database (Uetz, 2018, February 2018 version) as the taxonomic backbone, I have strived to map important and commonly studied traits of all lizard species. I do not consider snakes as their derived body plan, and jaws, makes them highly distinct. While the Sauria is paraphyletic, scientists aptly continue to use the term “lizard,” as the fact that a particular group of them set on a distinct evolutionary trajectory did not diminish the cohesiveness of the parental group.

I gathered data from field guides and books on lizard biology and husbandry, and from the primary and secondary literature, as well as from my personal experience in the field. Some data were gleaned from the internet (although I tried to keep this to the bare minimum), and other data were communicated to me by fellow herpetologists (mostly members of the global assessment of reptile distribution working group: see <https://www.gardinitiative.org/>, and collaborators such as Panagiotis Pafilis and Dave Chapple). I largely refrained from using data from some recent compilations (e.g., Bars-Closel, Kohlsdorf, Moen, & Wiens, 2017; Myhrvold, 1944) that seemed to me to sometimes use generic means and imputation based on close relatives, without always adequately acknowledging them as such. I also refrained from imputing missing data from data on relatives, and only did this when overarching statements (e.g., “all members of this genus are diurnal”) were made for genera of fewer than six species. Even that I did only rarely, and never for taxonomic ranks above the genus level. I never imputed numeric data. Recently it seems that the rate at which I can add new data for known species is lower than the rate of description of new ones. As we have also recently compiled range data for virtually all currently recognized lizard species (Roll et al., 2017) it seems to me that making this dataset widely available can benefit the scientific and herpetological communities, and generate

fascinating new research. I also hope that making the data available will expose both the gaps – and the errors, that are inevitably made when compiling a dataset of this size.

2 | THE DATASET

Data are presented in easily analysed tabular format (Supporting Information Appendix S1). I try to present each type of data in a column, or set of columns, that can be instantly used for analyses as well as in another descriptive column where I present some data sources, conflicts between sources, and the basis for my decision on the final use of a datum in the preceding column.

Where data are numeric I give either means or both means and ranges. When more than one datum is known for a given species I average the smallest and highest reported means. When means are unavailable I average the minimum and maximum reported values. I prefer this to averaging all reported means because the different data points may be non-independent, either in the true statistical sense (taken from the same individuals or when many authors report data from the same primary sources) or geographically (e.g., more means are likely to be reported for Iranian populations than for Iraqi ones because more herpetological research is conducted in Iran).

The dataset contains the following fields (see Supporting Information Appendix S2 for full metadata including % completion for each field):

1. Species – the binomial as spelled in the Reptile Database (Uetz, 2018), followed by genus and epithet.
2. Valid – whether the species is listed in the February 2018 version of the database, or is a new species described hence.
3. Year of description.
4. Country described from: The country (according to 2018 political boundaries) each species was described from.
5. Main biogeographic realm: The realm (according to the WWF, 2006) a species' range resides in (in cases of a species inhabiting more than one realm: the one where the largest portion of the range reside in).
6. Geographic range – a short verbal description of the range (mostly countries inhabited). Range maps are available in Roll et al. (2017).
7. Known only from the only type? Whether the species maximum linear distribution extent is higher than 10 km (“wide ranging”), or not. Species with smaller ranges are divided into those known only from the description paper (“description”), or only from the holotype (“specimen”), or whether they were observed after they were first described (“locality”; Meiri et al., 2018).
8. Latitude and longitude centroids (from Roll et al., 2017 and newer data; in decimal degrees, rounded to 2 decimal points).
9. Insular endemic - whether species reside only on landmasses smaller than Australia - or not.
10. SVL: Three values: The maximum known snout-vent length (SVL, all in mm) of the species, the mean female SVL (midpoints between the minimum and maximum values where means are not reported), and midpoint of hatchling or neonate SVL.

11. Leg development – whether the species has four functioning legs (“four-legged”), reduced pair or two pairs of legs (“leg reduced”, usually meaning either that the species has fewer than 20 fingers or very short limbs relative to the expectation given its body length. I acknowledge the latter is sometimes arbitrary), only forelimbs or hind-limbs, or no limbs at all.
12. Mass equations – the best equation I have for converting the species (log₁₀) SVL (in mm) into (log₁₀) mass (in grams; Feldman et al., 2016; Meiri, 2008). Data are the intercept and slope.
13. Activity time: Whether a species is diurnal, nocturnal, or cathemeral.
14. Substrate: Whether a species is arboreal, fossorial or cryptic (i.e. almost always only found under objects such as rocks or logs, e.g., the skink *Chalcides ocellatus*), saxicolous, semi-aquatic, terrestrial– or a combination of some of those.
15. Diet: Whether a species is herbivorous (consumes mostly plants: >50% if quantitative data are available), carnivorous (eats only, or nearly only, animal matter, >90% if quantitative data are available), or omnivorous (eats mostly animal matter but with considerable percentage of plants: i.e., 10%–50% plant matter, if quantitative data exist).
16. Foraging mode: Whether the species is reported to be an ambush predator (“sit and wait”), an active forager (“Active foraging”), or uses a mixed strategy (“mixed”).
17. Reproductive mode: Whether a species is oviparous or viviparous, or whether there are reports on both parity modes (“mixed”). Ovoviviparous species are considered viviparous because the mother carries the young in her abdomen until parturition.
18. Clutch size: Minima, maxima and means (highest and lowest reported means) of clutch or litter sizes.
19. Breeding age: The youngest and oldest reported ages (in months) of first breeding (of females if data are given separately for males and females).
20. Body temperature: The highest and lowest reported mean body temperatures of active lizards recorded in the field (in °C).
21. Family – according to the taxonomy of the reptile database (or slightly more conservative).
22. Phylogeny: Whether there are published accounts of the phylogeny of the species (and hence, likely, GenBank records), and the genes used to infer it.
23. IUCN red-list assessment and population trends, as of January 2018. Data were converted to the Reptile Database taxonomy when needed (3,021 species are missing assessments [“NE”]; and an additional 453 species are listed as data deficient; population trend is not assessed for 3,097 species, and is unknown for 1620 more).
24. Extant/Extinct: Whether the species is known or strongly suspected to be extinct (43 species; Slavenko et al., 2016), or whether (to the best of our knowledge, but see Meiri et al., 2018) it is still extant. Two species are considered extinct in the wild (EW: *Lepidodactylus listeri* and *Cryptoblepharus egeriae*). Note that of the species I consider extinct 17 are considered critically endangered or data deficient by the IUCN, and 12 are not assessed.
25. Remarks – other interesting natural history attributes.

26. References – the sources used to obtain the data in #2–24 above (and sometimes other data; e.g., longevity data: Scharf et al., 2015) regarding a species. My personal observations and personal communications are often reported in the appropriate fields rather than here. References are listed for the biological data (all columns except those dealing with SVL and phylogenies; for 168 species there are no sources listed), and for SVLs of unsexed individuals (including hatchlings or neonates), females, and males separately. Although I do not report values for males here I include all three categories as the maximum SVL can be of a male, a female, or an unsexed individual. The list of sources for all data is provided as Supporting Information Appendix S3.

3 | PRELIMINARY ANALYSES AND DIRECTIONS FOR FUTURE RESEARCH

The data presented here can be used to study lizard evolution and ecology along multiple axes. I present some examples below. Phylogenetic and geographic data (Roll et al., 2017; Tonini et al., 2016) will be needed for more compelling and informative studies, but some directions can be glimpsed at, to suggest which future research avenues are likely to prove fruitful.

Most lizards seem to be diurnal (70%, 3,578 of 5,093 species with data), but substantial percentages are active at night (1,247 species, 24%), and 5% (268 species) are cathemeral. Similarly, most (80%) lizard species are strict carnivores (2,685 of 3,361 species with data, 80%), 15% of species (515) with known diet are omnivorous, and 5% are herbivores (159 species), although I suspect that of the species with unknown diet the proportion of carnivores is even higher. In terms of microhabitat use, terrestrial is the most common category (1,750 species fully terrestrial, 31%), whilst arboreal and saxicolous species are also common (19% of species fully arboreal, 15% fully saxicolous, and 5% combine both modes). The terrestrial/scansorial mode is also common (933 species, 16.5%), whilst fossorial and cryptic species are relatively rare (612 species at least partially fossorial or cryptic, 11%).

Looking at combinations of these characters, herbivorous and omnivorous diets are highly associated with diurnal activity (88% of species, only four herbivores are nocturnal), while nocturnal species tend towards carnivory (92%). Nocturnal species also tend to be saxicolous (255 species), arboreal (236 species) or both (127 species), more than they are terrestrial (223 species), whilst diurnal species tend to be terrestrial (1,219 species) rather than arboreal (687) and, especially, saxicolous (432 species). Semi-aquatic species are nearly always diurnal (only four nocturnal species, 11 cathemeral).

The data suggest that the allometry of clutch size (calculated as the mean of the smallest and largest mean clutches per species, and lacking those, the midpoint, log transformed) on mean female body size has a slope close to the commonly assumed 0.25 (0.276 ± 0.008 , $n = 2,866$, $R^2 = 0.32$). Treating taxonomic family as a fixed effect, the overall slope declines to 0.194 ± 0.007 ($R^2 = 0.66$, as much

variation is explained by taxonomy). The allometric slope of age at first reproduction (calculated as the mean of the smallest and largest values, per species, log transformed) against maximum mass is shallower (0.150 ± 0.012 , $n = 701$, $R^2 = 0.18$, correcting for family: slope 0.155 ± 0.016 , $R^2 = 0.47$).

As expected, insularity (Covas, 2012; Novosolov, Raia, & Meiri, 2013; Schwarz & Meiri, 2017; Siliceo & Diaz, 2010) has a negative effect on clutch size: and insular species lay clutches that are 78% the size of continental species (with female mass and family as covariates). Age at sexual maturity (log transformed) is not significantly different on islands than on the mainland (log transformed, corrected for family and species' mass; insular species have a 5.9% higher intercept: 0.025 ± 0.024 , $p = 0.28$).

Clutch size is further positively associated with latitude (Cody, 1966; Griebeler & Bohning-Gaese, 2004; Jetz, Sekercioglu, & Bohning-Gaese, 2008; Meiri et al., 2013; Moreau, 1944) (with female mass, insularity, and family as covariates, the absolute value of latitude has a slope of 0.0025 ± 0.0004). Age at sexual maturity (log transformed, with maximum mass and family as covariates) likewise increase with latitude (slope 0.0094 ± 0.0008).

I hope the dataset provided here will prove useful to those aiming to study such evolutionary, biogeographical and ecological questions in lizards, reptiles, and animals in general.

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DATA ACCESSIBILITY

Data are available on the Global Ecology and Biogeography webpage and on Dryad: <https://doi.org/10.5061/dryad.f6t39kj>. Questions regarding the metadata, terms etc., as well as reporting values currently missing and correcting errors could be addressed directly to the author.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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