

# Small, rare and trendy: traits and biogeography of lizards described in the 21st century

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## Keywords

activity times; biome; description date; population decline; range size; species discovery; taxonomy; threat.

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## Abstract

The pace of new reptile species descriptions, especially of new lizard descriptions, is rapidly increasing. The number of recognized lizard species has increased by more than 30% since the turn of the century. I examined the traits of newly described lizard taxa, and compared them to those of species described earlier, to predict where new species will be found, what traits they have, and whether they are likely to be more extinction-prone than well-known species. I compiled data on the biogeography and ecology of newly described forms and examined the relationship between these traits and the date of description. As expected, new descriptions are generally of small species, predominantly with small geographic ranges. Most species have been described from the Oriental Realm, whereas few new species were described from Africa. New descriptions are disproportionately biased in favor of geckos and of nocturnal species – and, surprisingly, contain few subterranean forms. Newly described lizard species are more likely to be threatened with extinction and may be more susceptible to population decline. Although the rate of new lizard descriptions is still accelerating, this work contributes to predicting what types of species are likely to be found in the future – and where. The small ranges of such species, in regions suffering from severe habitat degradation, suggests that strong mitigation measures are needed to ensure that many of these species will not be lost shortly after being described.

## Introduction

The systematic, scientific description of animal species began over 250 years ago with Linnaeus (1758). Species description is a goal with no defined end – we do not know how many species inhabit the earth (May, 2011; Mora *et al.*, 2011; Costello, Wilson & Houlding, 2012), how many are contained within taxa, or are native to specific regions. Nonetheless, the number of described and recognized species in many groups has been increasing steadily over the last few decades (Costello, May & Stork, 2013; Fjeldsa, 2013). Rapid description and the increased numbers of recognized species are not limited only to poorly known taxa (e.g. many marine invertebrate groups; Costello *et al.*, 2012; Southeast Asian amphibians; Brown & Stuart, 2012) but also to the most charismatic of the ‘more appealing furry and feathery vertebrates’ (May, 2010) such as birds, primates and carnivores (Isaac, Mallet & Mace, 2004; Meiri & Mace, 2007; Sangster, 2009).

A similar process applies to reptiles – if anything, reptiles are currently being described very rapidly. Bird numbers, for example, have risen from 9956 to 10 425 species between the first (version 0.0, 2007, category ‘R’) and latest version (version 7) of BirdLife International (<http://www.birdlife.org/data-zone/info/taxonomy>), a 469 species increase. Over a similar time period (September 2008 to December 2015) the number of recognized reptilian species has risen from 8881 to 10 309

(<http://reptile-database.org/>) – nearly three-fold more (1428 species). Thus, reptiles will soon become the largest class of terrestrial vertebrates – perhaps they already are.

The description of new reptilian species has become more rapid than ever (Meiri, 2008; Uetz, 2010; Pincheira-Donoso *et al.*, 2013). Most of the increase in reptile species diversity (numbers are taken from successive versions of the Reptile database, Uetz, 2015, starting with the first version of 2001) has been driven by lizards (Sauria, here treated more inclusively as lizards and amphisbaenians, i.e. squamates excluding snakes). Lizard numbers have risen by c. 31% since 2001, compared to an increase of ‘only’ 22% in the number of recognized snake species, 15 and 9% increases in the numbers of turtles and crocodiles, respectively, and a 50% decrease in the number of rhynchocephalians (from two species to one: *Sphenodon guntheri* was synonymized with *S. punctatus*).

We know that description dates are correlated with some species’ traits – range size is usually by far the best predictor of the date in which a species was described, with newly described species generally having small ranges (Collen, Purvis & Gittleman, 2004; Diniz-Filho *et al.*, 2005; Brown & Stuart, 2012). Newly described species are also generally considered to be small (May, 1978; Gaston, 1991; Collen *et al.*, 2004; Diniz-Filho *et al.*, 2005), and more likely to be tropical and nocturnal than species described earlier (Collen *et al.*, 2004). Moreover, they are thought to inhabit relatively well-known,

densely populated regions (Diniz-Filho *et al.*, 2005). In reptiles, however, Reed & Boback (2002) found no relationship between description date and body size, and I (Meiri, 2008) found that lizard length was negatively correlated with description date. This correlation disappeared, however, when only species described since 1900 were considered (Meiri, 2008).

I aim to identify whether newly described species are distinct from their earlier described kin. I test for relationships between lizard traits and their year of description. For categorical traits I arbitrarily define ‘old lizards’ as those described between 1758 and 1999, and ‘new lizards’ (including amphisbaenians, henceforth ‘lizards’) as those described during the 21st century. This is merely a matter of convenience (e.g. the vast majority of 21st century descriptions contain data on the latitude and longitude of the type localities. Most of the older descriptions contain only verbal accounts, which are often vague, ambiguous or simply hard to trace). Other categorizations may be just as useful, but a ‘21st century versus earlier’ contrast is easy to conceptualize. Specifically I sought to test the hypothesis that the newly described species would differ from species described previously in several key traits related to the former being more difficult to observe (e.g. smaller, nocturnal, fossorial and with smaller ranges, see below). I predicted that: (1) ‘new lizards’ have smaller geographic ranges, making them easier to miss (Collen *et al.*, 2004; Diniz-Filho *et al.*, 2005); (2) new lizards would be found in less-studied regions, that is at lower latitudes and in tropical biomes; (3) new lizards would be more likely to be endemic to islands; (4) smaller bodied (Gaston, 1991; Collen *et al.*, 2004; Diniz-Filho *et al.*, 2005); (5) more likely to be nocturnal (Collen *et al.*, 2004); (6) more likely to be fossorial (and legless, because these traits are tightly linked), and thus more difficult to detect; and finally (7) that newly described lizards would be more likely to be threatened with extinction and to experience population decline than species described earlier – because of their small ranges or relative rarity, which may have also contributed to their being previously overlooked, and consequently, only recently identified and described.

I present the first historical analysis of lizard species discovery, examining the relationships between publication date and body size, the size and position of geographic ranges, micro-habitat preferences, activity patterns, natural history and conservation status. The results provide the first quantifiably validated data, showing that the more recently discovered lizards are smaller, inhabit increasingly smaller ranges, and are increasingly threatened with extinction – all of which have important implications for conservation in the face of habitat loss and climate change.

## Materials and methods

Data on the description year of all lizard species were downloaded from the reptile database (Uetz, 2015). Data for species described in 2014–2015 and not yet included in the March 2015 version of the database (55 new species in 5 months) were obtained from description papers. In total there are 6321 recognized lizard species, 1323 of which were described during the 21st century. Geographic data for all species were obtained

from multiple sources including the IUCN, museum databases and meta-databases such as GBIF and Vertnet, and from thousands of primary literature journal articles. Data were then thoroughly checked and amended, with special reference to changes in taxonomy, by members of the GARD working group (<http://www.gardinitiative.org/index.html>). In addition, I documented the type localities of all species described since 2000 – preferably as the coordinates given in the original descriptions. If coordinates were not reported, I found them by digitizing maps from the description papers showing the type localities, or else conducted a Google Maps search for the type locality according to its verbal description. Errors (replacing longitudes with latitudes and vice versa, typos, etc.) were rectified as appropriate. Point localities were converted to polygons using a 1.78 km radius buffer in ArcMap (giving the resultant circle a 10 km<sup>2</sup> area, IUCN 2015). Because range size estimates are highly dependent on the method used to estimate them (Jetz, Sekercioglu & Watson, 2008; Raedig & Kreft, 2011), I also compared only range sizes that were estimated based on polygonal data alone, and exclude insular endemics (which are likely to have small range sizes). Range maps are often very coarse, and range size estimates may thus be grossly imprecise. Nonetheless, range sizes vary greatly, and many species are known only from their type locality, or from islands <1 km<sup>2</sup> (e.g. *Anolis kahouannensis*, *A. chrysops*, *Uta encantadae*), whereas *Acanthodactylus boskianus*, *Zootoca vivipara* and *Varanus griseus* have ranges 7 orders of magnitude larger (all >15 million km<sup>2</sup>). Across this size variation it should be possible to identify temporal signals. Whether a species is endemic to islands (=any landmass smaller than Australia) was assessed using the available distribution data. I determined the size of the distribution of each species in the 14 WWF biomes (<https://www.worldwildlife.org/biome-categories/terrestrial-ecoregions>), and then assigned each species to the biome in which its distribution size is largest (260 ‘new’ species range across >1 biomes, but 88 of these have >90% of their range in their major biome and 133 have >80% of their distribution in the major biome). I then pooled all tropical biomes into a single ‘tropical’ category, and all three ‘temperate’ biomes into one ‘temperate’ category. I only analyzed desert, Mediterranean, montane, temperate and tropical biomes because other categories have too few species to be meaningfully examined.

Data on body size are based on maximum snout-vent lengths (mm) converted to masses using appropriate clade-specific allometric equations (e.g. Meiri 2010, Pincheira-Donoso *et al.*, 2011; Scharf *et al.*, 2015; Feldman *et al.* 2016). Species were ranked as either diurnal, nocturnal or cathemeral (active during both day and night) according to data in the primary literature (e.g. species description papers, ecological studies) and in field guides (Supporting Information Appendix S1). Using the same sources, I determined whether a species was fossorial (including semi-fossorial species), semi-aquatic or ‘surface active’ (terrestrial, saxicolous, arboreal and their combinations). The ecology of newly described species is often poorly known relative to that of species described earlier. I therefore repeated the analyses of activity times and space use (fossorial/semi-aquatic/surface active) while extrapolating

the traits of missing taxa based on phylogenetic affinities and known character states. For these sensitivity analyses I classified all amphisbaenians, dibamids and anniellids for which activity time remains unknown, as cathemeral, all gekkotans as nocturnal, and all other lizards as diurnal (although exceptions doubtlessly exist, e.g. in *Cnemaspis*, Gamble *et al.*, 2015). Activity time data were imputed for 2030 of 6319 species. I classified all amphisbaenians, dibamids, pygopodids and aconine skinks for which space use remains unknown as fossorial and all other lizards as surface active (again, an approximation as some pygopodids are surface active whereas some lygosomine skinks and gymnophthalmids burrow). Space use data were imputed for 1269 of 6319 species.

I downloaded data on conservation status and population trend from the IUCN website (IUCN 2015) and determined whether each species is extinct, data deficient, threatened (i.e. with a threat category of VU, EN or CR), non-threatened (LC and NT) or whether it has not been assessed. I also recorded whether populations were decreasing, increasing or stable – or whether population trends are unknown or have not been assessed. It should be noted, however, that IUCN assessments are only available for ~40% of lizard species, and for only 19% of the newly described species (a quarter of which are listed as DD). Population trend assessments are likewise often based on partial and subjective data.

## Statistical analyses

To compare trait frequencies from the 21st century to those of the earlier described lizards, I used simple chi-square tests of independence. To detect differences in continuous traits (e.g. body size), I used *t*-tests. No corrections were made for multiple testing (Moran, 2003; Garcia, 2004).

The question of whether one should control for phylogenetic affinities is not a trivial one. Description year does not evolve, and is not shared from a common ancestor, and thus a phylogenetic test may be inappropriate. Some traits, such as range size, are probably not shared from a common ancestor (e.g. under a peripatric cladogenetic model of speciation, and in the case of allopatric speciation in archipelagos, where the new ranges will be smaller than the ancestral range to a degree determined not by biology, but by the area of the island upon which the daughter species speciated). Such traits may nonetheless be similar in closely related species (whether range size has a phylogenetic signal is debated: cf. Diniz-Filho & Torres, 2002; Raia *et al.*, 2011; Lee, Skinner & Camacho, 2013). Other traits are shared from a common ancestor and are phylogenetically conserved (e.g. activity times: Roll, Dayan & Kronfeld-Schor, 2006; Body size: Meiri 2010).

One practical problem with using phylogenetic analyses is that only 165 species described in the 21st century are included in the currently most comprehensive, available, dated lizard phylogeny (Pyron & Burbrink, 2014). That said, many species descriptions nowadays have a phylogenetic hypothesis associated with the description, and thus topology is available for nearly half the species. I therefore created a composite phylogenetic hypothesis built upon the backbone of Pyron & Burbrink's (2014) tree, based on published phylogenies

(Supporting Information Appendix S1). I then scaled the tree to be ultrametric using FigTree (Rambaut, 2010). I used this tree to control for phylogenetic non-independence using PGLS implemented in the R package 'Caper' (Orme *et al.*, 2014) with the scaling parameter  $\lambda$  set to its maximum likelihood value. I then repeated the tests in a non-phylogenetic manner to predict what attributes newly discovered species will be likely to have regardless of phylogenetic affinities (e.g. whether they are small rather than whether newly described geckos are smaller than geckos described earlier). This also allowed for the use of much larger sample sizes by including the, generally rare and poorly known, species for which phylogenetic data are unavailable.

I repeated tests with continuous predictors (e.g. latitude, body size, and range size – the latter two log transformed) with description year rather than description in the 21st century as the response variable, to obtain a more quantitative overview of the determinants of late versus early description.

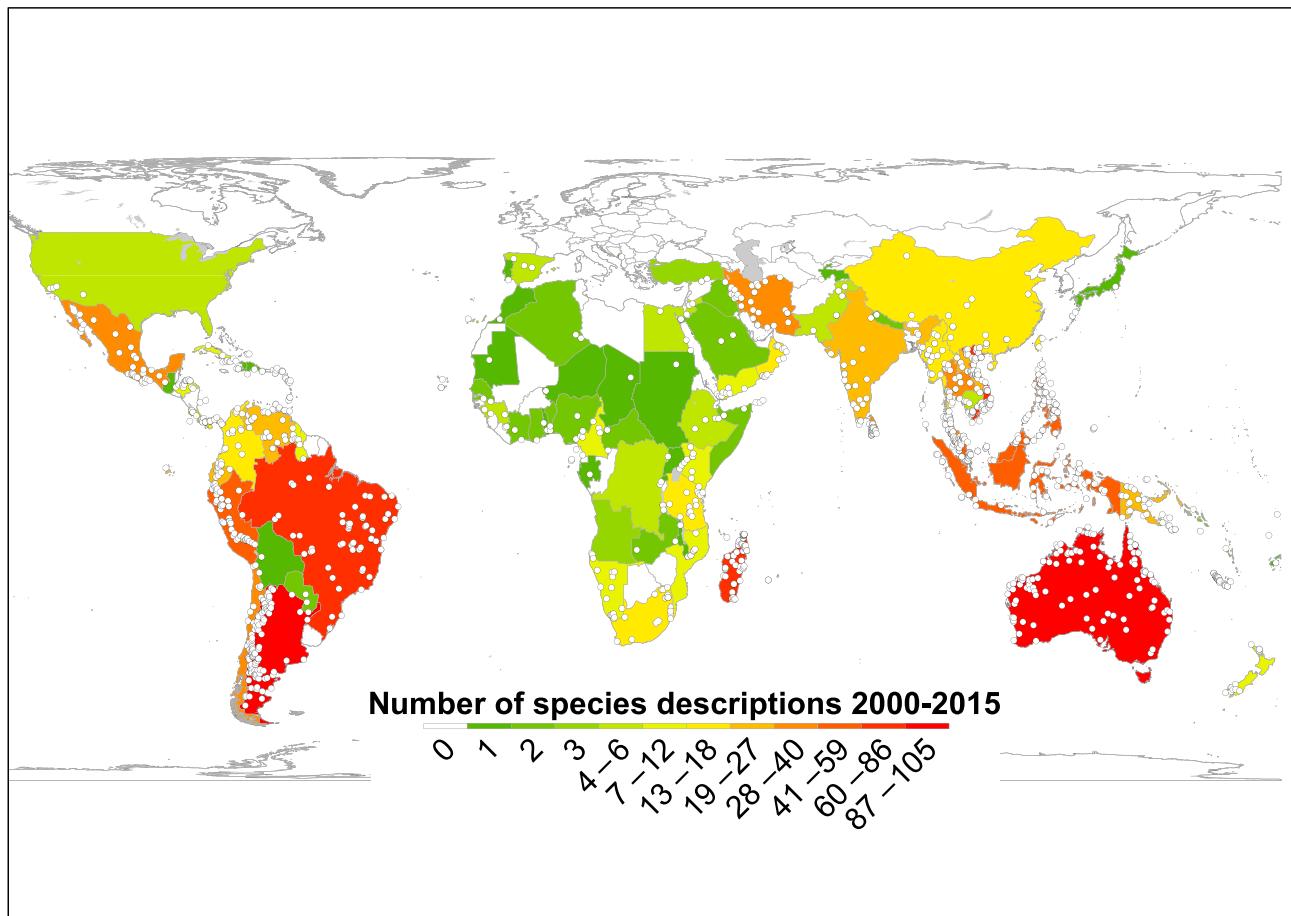
To explore the geographic focus of recent species description I digitized the type locality of all but 11 species described in the 21st century. For some of latter 11 species the descriptions of type localities were too vague. Others had none (e.g. the type of *Trachylepis dichroma*, Günther, Whiting & Bauer, 2005; was purchased from a Berlin pet shop) or were described earlier (but their name had been changed following 21st century revisions; e.g. *Acontias kgalagadi*, Lamb, Biswas & Bauer, 2010).

## Results

As of late July 2015, 1323 lizard species had been described in the 21st century. Most were geckos (516 species, 39% of all species described this century), followed by skinks (252 species), liolaemids (130), agamids (83) and gymnophthalmids (65) (for a list of species and their traits see Supporting Information Appendix S1). During the 21st century to date, lizards have been described from 96 countries (Fig. 1), mostly from Australia (105 species) and Argentina (103), followed by Vietnam (66), Brazil (64), Madagascar (60), Malaysia (58) and the Philippines (48; Fig. 1). The proportion of insular endemics described in the 21st century (31%; 414 of 1322 species) is similar to the proportion of insular endemics described earlier (30%; 1483 of 4996 species;  $\chi^2 = 1.33$ ,  $P = 0.25$ ).

The proportion of species descriptions in different biogeographic realms has changed markedly in the 21st century compared with earlier times ( $\chi^2 = 244.05$ ,  $P < 0.0001$ ). Most new lizard descriptions have been from either the Neotropic or the Oriental realms (Table 1). Although the proportion of species descriptions in the Neotropics was similar during the 21st and earlier centuries, the 21st century description proportion in the Oriental realm is more than two-fold its proportion in the past (29% of species described during the 21st century vs. 14% of species described earlier). Description proportions have dropped in most other realms, notably in Africa (9% of 21st century descriptions vs. 17% earlier) – thereby refuting my prediction #2.

On average, 21st century descriptions have taken place closer to the equator, but the magnitude of this effect is small



**Figure 1** A map of type localities of all 1312 lizard species described during the 21st century that have adequate locality data. Each dot is a point locality of one or more species (no more than 4, average 1.06). Incremental shades represent the number of species described in each country. The map is in a Behrmann equal area projection. *Emoia mokolahi* (Tonga, 18.65S, 173.98W) & *Emoia tuitarere* (Cook Islands, 21.21S, 159.78W) omitted.

( $1.80 \pm 0.34$  degrees equator-wards in the 21st century in the non-phylogenetic model,  $n = 6297$ ,  $P = 0.005$ ,  $r^2 = 0.005$ ), and a phylogenetic correction ( $\lambda = 0.966$ ) results in non-significant results (effect size  $0.28 \pm 0.22$  degrees,  $n = 4070$ ,  $P = 0.21$ ,  $r^2 = 0.0003$ ). Treating description year as a continuous variable yields similar results (non-phylogenetic model,  $-0.011 \pm 0.002$  degrees/year,  $n = 6297$ ,  $P < 0.0001$ ,  $r^2 = 0.004$ ; phylogenetic model,  $\lambda = 0.967$ ; slope =  $-0.008 \pm 0.001$  degrees/

year,  $n = 4070$ ,  $P < 0.0001$ ,  $r^2 = 0.011$ ). More species have been recently described in tropical biomes (71% of 21st century descriptions) than earlier (64%). Increased proportions, however, are also evident in temperate and montane species, whereas there are relatively fewer new descriptions of desert and Mediterranean biome species (Table 2,  $\chi^2 = 76.03$ ,  $P < 0.0001$ ).

Species described more recently have small range sizes. This holds true regardless of whether the predictor is description year or whether dichotomous 21st century/earlier categories are used, and regardless of whether all ranges are included or only those that are based on polygonal data alone (Table 3).

Newly described species differ in many morphological traits from their earlier described kin. In line with my prediction #4, they are smaller animals (a 21st century lizard weighs, on average, 0.14 log units less, or 73% of a lizard described earlier; Table 4), although there is considerable scatter ( $R^2$  values: 7–8%). There is, however, no difference between the masses of lizards described in the 20th or 21st century ( $0.025 \pm 0.021$  log units,  $P = 0.24$ ). Treating year as a continuous variable the

**Table 1** Species descriptions according to biogeographic realms

	18th–20th centuries	21st century
Afrotropic	838	124
Australia	638	111
Madagascar	228	64
Nearctic	175	14
Neotropic	1558	419
Oceania	390	117
Oriental	682	389
Palearctic	489	84

**Table 2** Species descriptions according to biome

Biome	18th–20th centuries	21st century
Desert	958	158
Mediterranean	259	22
Montane	160	66
Temperate	371	120
Tropical	3129	881

slope is  $-0.00035 \pm 0.00028$ ,  $P = 0.21$ ). Lizards described in the 21st century are less likely to be legless or leg reduced (107 of species described in the 21st century, 545 earlier, vs. 1216 and 4453 species, respectively,  $\chi^2 = 8.97$ ,  $P = 0.003$ ), contradicting my prediction #6.

Interestingly, lizards described in the 21st century are much more likely to be nocturnal (37% of described species with real data, 34% if I extrapolate by familial affiliation, vs. 21 and 20%, respectively, for earlier descriptions, Table 5;  $\chi^2 = 93.14$  and 123.59, respectively,  $P < 0.0001$  in both cases; prediction #5). Newly described lizards, however, are less likely to be fossorial (7% of later descriptions both with and without extrapolation, vs. 11 and 10% of earlier descriptions, respectively,  $\chi^2 = 11.87$  and 17.70, respectively,  $P = 0.003$  and 0.001, respectively; Table 5; contradicting prediction #6).

Lastly, lizards described during the 21st century are, unfortunately, more likely to be threatened with extinction than those described earlier (Table 6): 55% of the more recently assessed species are either threatened (91 species) or already extinct (10 species), versus 27% of earlier described forms ( $\chi^2$  for threatened vs. non-threatened, excluding extinct, DD and NE species: 76.03,  $P < 0.0001$ ). They are also much less likely to have been assessed (19% of the species, vs. 42% of those described earlier) – although the proportion of DD species is similar (5 vs. 6%). Although this is probably the result of their smaller ranges (which feature heavily in the IUCN assessments), it is probably not the only cause: their populations are also often assessed as decreasing. The proportion of species described as ‘decreasing’ by the IUCN out of species with an assessment other than ‘unknown’ is much higher in species described during the 21st century (47% vs. 37% of species described between 1758 and 1999), although this finding is

**Table 3** Range sizes and description dates

Predictor	Effect size	SE	t	R <sup>2</sup>	n	λ	Ranges
Dichotomic	-1.964	0.052	-37.92	0.186	6283	na	All
Continuous	-0.014	0.000	-44.16	0.237	6283	na	All
Dichotomic	-0.650	0.113	-5.75	0.020	1582	na	mainland, polygons
Continuous	-0.006	0.000	-14.07	0.111	1582	na	mainland, polygons
Dichotomic	-1.843	0.060	-30.87	0.190	4062	0.697	All
Continuous	-0.012	0.000	-39.73	0.280	4062	0.713	All
Dichotomic	-0.904	0.137	-6.59	0.036	1181	0.673	mainland, polygons
Continuous	-0.007	0.000	-18.56	0.226	1181	0.740	mainland, polygons

Models for range sizes (in km<sup>2</sup>, log transformed) as functions of description dates. Continuous: the predictor of range size is the year of description. Dichotomic: the predictor of range size is 21st century or earlier description. Effect size is the slope (for year as a predictor) or mean difference (for early vs. late description). Ranges are either of all species, or of mainland species (i.e. not island endemics, but part of their distribution can be on islands) where ranges are based on polygonal data only. All  $P$  values  $<0.0001$ .

n, number of species; λ, na: non-phylogenetic model.

**Table 4** Body size and description dates

Predictor	Slope	SE	t	R <sup>2</sup>	n	λ
Dichotomic	-0.137	0.022	-6.31	0.006	6301	na
Continuous	-0.003	0.0001	-22.18	0.072	6301	na
Dichotomic	-0.137	0.015	-9.10	0.020	4068	0.953
Continuous	-0.002	0.0001	-19.63	0.087	4068	0.954

Maximum body size (log grams, derived from maximum SVL using taxon-specific equations) as functions of description dates. Continuous: the predictor of range size is the year of description. Dichotomic: the predictor of range size is 21st century or earlier description. Effect size is the slope (for year as a predictor) or mean difference (for early vs. late description). All  $P$  values  $<0.0001$ .

n, number of species; λ, na: non-phylogenetic model.

marginally non-significant (decreasing vs. increasing;  $\chi^2 = 3.65$ ,  $P = 0.056$ ; Table 6).

## Discussion

Newly described lizard species are certainly different animals than those described earlier: they have distinct morphologies, ecologies and biogeography. Such distinction, however, did not always meet my *a priori* predictions. The newly described species inhabit lower latitudes (but this effect is weak), and are more likely to inhabit tropical biomes, especially in the Oriental biogeographic realm. They also have much smaller ranges than lizards described earlier, regardless of the method used for mapping. This may derive from the shorter time available for observations beyond the type locality to accumulate. I nonetheless think that this mostly represents a true pattern, because of the strong relationship between range sizes and description dates. The newly described lizards are also small (although my use of maxima as measures of size may bias the results against newly described species because of nearly ubiquitous small sample sizes; Meiri, 2007), more likely to be nocturnal (and disproportionately have turned out to be geckos), and (probably at least partially related to this phylogenetic bias) less likely to be leg-reduced and fossorial.

**Table 5** Activity times and substrates of lizards described in the 21st century or earlier

	18th–20th centuries	21st century
Time (real)		
Cathemeral	193	37
Diurnal	2551	483
Nocturnal	723	303
Time (extrapolated)		
Cathemeral	350	75
Diurnal	3663	796
Nocturnal	985	451
Element (real)		
Air	3543	908
Earth	414	68
Water	99	19
Element (extrapolated)		
Air	4361	1209
Earth	538	94
Water	99	19

Values are the number of species in each category. 'Real': based only on species-level data I obtained. 'Extrapolated': missing values assigned to activity times and substrates according to familial affiliation as outlined in the Methods section. The classical elements, air, earth and water refer to above surface activity (including terrestrial, arboreal and saxicolous forms), fossorial and semi-fossorial lifestyle, and aquatic and semi-aquatic activity. There are, to my knowledge, no fire-bound lizards.

**Table 6** Description dates and conservation status

	18th–20th centuries	21st century
a		
DD	298	65
EX	26	10
Non-threatened	1304	82
Threatened	453	91
Not assessed	2917	1074
b		
decreasing	366	40
increasing	15	1
stable	621	44

Numbers of a. threatened (VU, EN and CR) and non-threatened (LC, LR/Lc, NT and LR/Nt) lizard species. b. species with decreasing, increasing, or stable populations according to the century of description. The EX category includes species not officially assessed by the IUCN (subfossil species and some of the new Caribbean skinks described by Hedges & Conn, 2012).

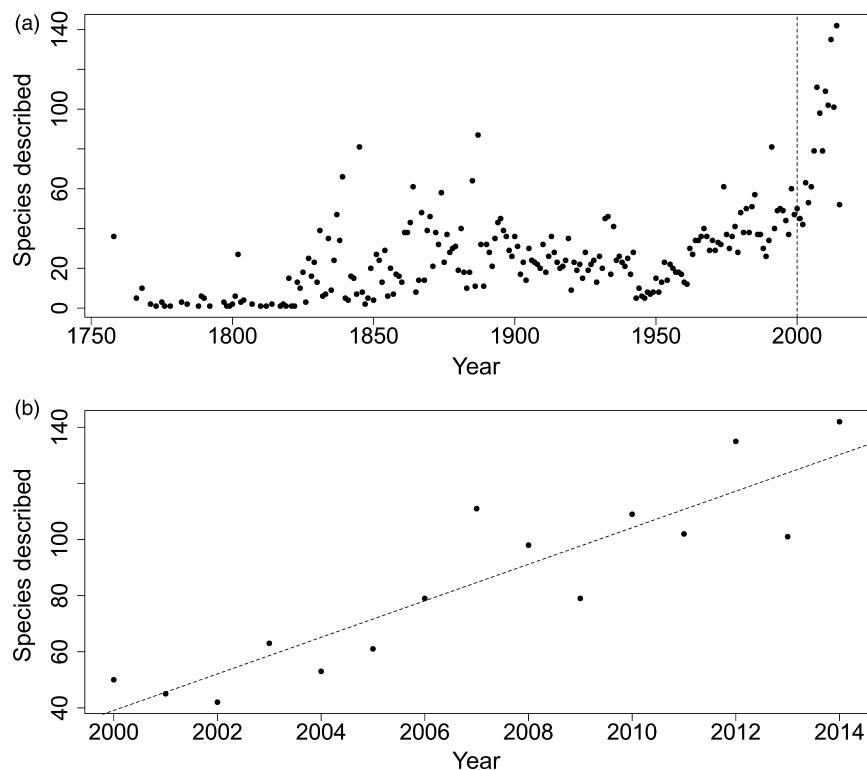
Identified biases all have exceptions: Australia, which saw its share of descriptions shrink from an early 13% to 8% of the species in the 21st century, still has more species described this century than any other country (and by a large margin of any country except Argentina, Fig. 1). Some of the largest lizards in the world (e.g. *Varanus palawanensis*, Koch, Gaulke & Bohme, 2010 and *Varanus bitatawa*, Welton *et al.*, 2010; see Feldman *et al.*, 2016) were only recently described. Newly described lizards, however, never have very large ranges: the largest-ranged species described in the 21st century, *Trapelus*

*boehmei* (Wagner *et al.*, 2011), has only the 218th largest range of all lizards.

Some findings ran counter to my predictions. I anticipated the proportions of descriptions in Africa, in desert regions, and of fossorial and/or legless species such as amphisbaenids and dibamids to increase, whereas in fact they all decreased, some considerably so. I hypothesize that this is because new regions have become logically and legally more accessible to European and US taxonomists, as they can now more conveniently travel to these regions, work in collaboration with, and train, local herpetologists (e.g. in Malaysia, the Philippines, Vietnam, Madagascar). Description by people working in their own countries has also become more prevalent in some countries (e.g. Brazil, Argentina, Vietnam, the Philippines) which have seen general increases in the availability of higher education (e.g. [https://en.wikipedia.org/wiki/Education\\_in\\_Argentina](https://en.wikipedia.org/wiki/Education_in_Argentina)). Other regions remain poorly studied, notably much of Africa, as well as some politically unstable regions. I doubt, for example that Iran, a local power house of new species descriptions (28 new species described), really had that many more unknown species than adjacent Iraq (2 new species), or Afghanistan (none). I think that species are being described mostly in low-latitude countries that are scientifically strong, or those which allow and welcome foreign scientists to work and collect specimens in, and are not torn by civil war.

It seems that herpetologists nowadays may be more likely to venture out at night (or at least to specialize in geckos), but that with current field methods fossorial species (and perhaps also canopy-top species) are still very hard to detect. Hence, I predict that much of their diversity remains to be described. I thus fully anticipate that legless and fossorial species, especially dibamids and amphisbaenids, will be described at relatively higher rates in the future. Indeed, the decline in the relative description rates of legless and fossorial species is also evident in relatively well-studied regions such as Australia (but not in the USA where *Xantusia bezyi*, Papenfuss, Macey & Schulte, 2001, is the only surface active species described in the 21st century, and all four other descriptions are of fossorial species of *Anniella*).

This description of four *Anniella* species (Papenfuss & Parham, 2013) leads to the difficult subject of what kinds of descriptions exist. The most obvious kind is that of genuine descriptions of new forms which clearly no one has ever seen before (e.g. *Cnemaspis psychedelica*, Grismer, Tri & Grismer, 2010). Another kind is the splitting of a formerly recognized species (e.g. Papenfuss & Parham, 2013 splitting of *Anniella pulchra*, Gray 1852, into five species). The last, and hardest to distinguish kind is the finding of a form that only merits specific status when the standards used to distinguish species are lowered (sometimes therefore referred to as 'taxonomic inflation'; Isaac *et al.*, 2004; Harris & Froufe, 2005; Meiri & Mace, 2007). I hypothesize that the new species discoveries are mostly being made in formerly poorly surveyed regions. Splitting, on the other hand, probably affects well-studied regions. Taxonomic inflation (be it perfectly justified or not) can happen anywhere (because scientific paradigms are shared and European and USA scientists do much of the species descriptions in tropical Asia and Africa).



**Figure 2** Lizard species described per year and considered valid (by Uetz, 2015) since (a). the beginning of modern animal taxonomy in 1758; (b). the 21st century (year 2000). The regression line has a slope of 6.5 (additional species per year) from an intercept of 38.6 in 2000;  $R^2 = 0.817$ .

How are modern taxonomic practices reflected in the traits studied here? Splitting recognized forms often result in very similar old and new species. So too will treating new populations as specifically distinct where they would have been considered mere varieties under older taxonomic practices (e.g. van Cleave, 1933; Mayr, 1942 p. 7 and pp. 125–127). Subspecies elevated to specific rank are treated here as ‘old’ – because they have been assigned the date of the subspecies description. Only 67 subspecies of lizards (in 50 species) have been described in the 21st century so far (Uetz, 2015), just ~4.5% the number of species descriptions. Interestingly, nine of these subspecies are European, but only one (*Liolaeus pictus codoceae* Pincheira-Donoso & Nunez, 2005), is from South America. Taxonomic inflation will make it harder to distinguish new species from old ones in terms of their traits and biogeographic ranges (e.g. they will inhabit similar biomes in similar realms and latitudes, share activity times, substrate, body size, etc. Isaac *et al.*, 2004). Indeed taxonomic inflation, if biased toward charismatic, large and deadly species (as seems to be the case in mammals, e.g. Meiri & Mace, 2007; Heller *et al.*, 2013; Roll *et al.*, 2016), may actually result in new species being larger.

Species descriptions are not abating. In fact they continue at a record pace (Abdala, Quinteros & Espinoza, 2008; Meiri, 2008; Shea *et al.*, 2011; Uetz, 2010; Pincheira-Donoso *et al.*, 2013; Fig. 2). The seven years with the most lizard

descriptions are those between 2008 and 2014 (except 2009, which is ranked 11th overall), while 2014 was the year with the most reptile species description in history. The data presented here, however, do seem to suggest that the days of description of species north of the 40th parallel are almost over (5 species, none of which are from Russia and Canada or even from the USA except southern California). This is not true for descriptions below latitude 40°S: 45 species were described this century further poleward: in Chile, Argentina and New Zealand (Supporting Information Appendix S1). We do not know how many reptile species currently exist. An informal survey among reptile taxonomists had a modal expectation of around 15 000 species (Meiri, unpublished), but this is mostly guesswork. I fully predict that Africa will be a hotspot of future species descriptions – but this will probably first require greater economic prosperity, better infrastructure and more political stability. Alfred Russel Wallace (1859) claimed that South America is ‘absolutely as free as Europe to the research of naturalists’ and its (bird) fauna is therefore much better known than those of tropical Africa and Asia, in much of which ‘the naturalist only penetrates at the risk of his life’, and with much greater difficulties. It seems that matters have drastically changed for the better in the Oriental region lately, but apparently less so in Africa.

Because fossorial habits entail much greater energetic costs of locomotion (e.g. Wu *et al.*, 2015) fossorial animals are

expected to be dispersal limited (although they may be more likely to disperse by rafting, Townsend, Leavitt & Reeder, 2011), and to have small ranges. These conditions should be ideal for allopatric speciation, and I thus predict that their actual taxic diversity is relatively higher than current numbers suggest, and indeed current description trends reveal. Why relatively fewer amphisbaenians, leg reduced and fossorial lizards have recently been described is a question I cannot answer, except by suggesting the weakest of mechanisms – ascribing it to the research preferences of individual scientists or scientific teams. Some individuals have certainly made great inroads into species descriptions in poorly studied taxa, and the 21st century has seen many such scientists (e.g. Aaron Bauer, Lee Grismer, Rafe Brown, Gunther Kohler. See, e.g. Jacobsen *et al.*, 2014; Grismer *et al.*, 2014; Linkem & Brown, 2013; Kohler *et al.*, 2014). Since Carl Gans, however, who last described species in 1987 (Gans, 1987) only a few amphisbaenian specialists have published much taxonomic work (but see, e.g. Vanzolini, 1991). Perhaps, the description of six amphisbaenians in 2014 (Supporting Information Appendix S1) marks the start of a renaissance in amphisbaenian taxonomy?

Unfortunately, it seems that many of the newly described species will only have an ephemeral existence as living organisms known to science, as so many of them are threatened with extinction – because of their small range sizes and their rarity they may become coveted trophies for the pet trade (Stuart *et al.*, 2006; Yang & Chan, 2015). Some of the species described during this century are already lost – probably prey to invasive species in Reunion (Arnold & Bour, 2008), the Caribbean (Hedges & Conn, 2012) and Fiji (Pregill & Worthy, 2003; Pregill & Steadman, 2004; the species described therein, *Lapitiguana impensa* and *Brachylophus gibbonsi* are not represented in Uetz, 2015 and thus not used in the analyses conducted herein). Indeed, nearly half of the species described in the last 15 years for which population trends are known seem to be decreasing, although the very act of description may either harm (Stuart *et al.*, 2006) or help conserve the newly described forms (Morrison *et al.*, 2009). The small range size of newly described lizards, and the fact that many are found in regions that are undergoing rapid and intensive land use changes may spell doom for many of them (Newbold *et al.*, 2015).

Yet lizards, new or old, are seldom highlighted in conservation initiatives. For example no lizards feature in the WWF's highlighted species list ([http://wwf.panda.org/about\\_our\\_earth/species/](http://wwf.panda.org/about_our_earth/species/)), they cannot be adopted as part of the Durrell Wildlife Conservation Trust (<http://www.durrell.org/adopt/#animals> – despite Gerald Durrell's fascination with them and efforts to conserve some species, e.g. Durrell, 1977), and no reptiles feature in the Zoological Society of London's 'Edge' initiative (<http://www.edgeofexistence.org/species/default.php>, perhaps because of the lack of a complete phylogeny). This also seems to be the case locally – in my country, for example (Israel, where the last lizard description was in 1999 – of the small, endemic, critically endangered and declining, desert lacertid *Acanthodactylus beershebensis*; Moravec *et al.*, 1999), no reptiles except turtles enjoy any special conservation efforts, whereas many mammals and birds do.

We may well be losing species in many regions even before they are formally described. Strong mitigation measures must be implemented if we want to prevent these new and fascinating reptiles from going the way of the Dodo, or of the largest gecko known (Bauer & Russell, 1986), the extinct New Zealand Kawekawau *Hoplodactylus delcourti*.

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## Supporting Information

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

**Appendix S1.** Traits and biogeography of lizards described during the 21st century.