

What geckos are – an ecological-biogeographic perspective

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Abstract Geckos are a hyper-diverse, ancient, and globally distributed group. They have diverged early from other squamates and thus can be expected to differ from them along multiple ecological, life history, and biogeographic axes. I review a wide range of gecko traits, comparing them to those of other lizard taxa, to identify the unique, and unifying, attributes of geckos among lizards, based on comprehensive databases of lizard distributions and biological attributes. Few traits completely separate geckos from other lizard taxa, yet they differ to a large degree along many axes: they are more restricted to low latitudes and altitudes, are especially diverse on islands, but relatively scarce in America. They are small lizards, that lay small, fixed clutch sizes, for which they compensate only partially by laying frequently. Because they mature at relatively similar ages and have similar lifespans to other lizards, geckos produce fewer offspring over a year, and over their lifetimes, perhaps implying that they enjoy higher survival rates. While being the only large lizard clade of predominantly nocturnal lizards a large proportion of species is active by day. Gecko body temperatures and preferred temperatures are lower than those of other lizards – even when they are compared to lizards with similar activity times. Worryingly, most geckos have small ranges that often reside completely outside of protected areas – much more frequently than in other reptile and vertebrate taxa.

Keywords activity times; body size; conservation; diet; Gekkota; life history; range size; thermal biology

Introduction

Geckos, lizards belonging to the clade Gekkota, are widespread, and species rich. They feature in the popular culture in anything from toy companies to children television series (Djeco, PJ Masks), usually depicted as the wall-clinging, broad-toed nocturnal animals that many of them really are. The Gekkota is a sister group to all other squamates, except for the enigmatic Dibamidae (e.g., Reeder et al., 2015; Harrington et al., 2016; Zheng and Wiens, 2016; Pyron, 2017). Gecko fossils are known from deposits ~100–112 million years old (Arnold and Poinar, 2008; Daza et al., 2014) and fossilized gecko eggs are reported from Valanginian-Hauterivian (~130 million years) deposits (Moreno-Azanza et al., 2016). Additionally, the Late-Jurassic lizards, *Eichstaettisaurus schroederi* and *Ardeosaurus digitatellus* are probably stem-group geckos (Simões et al., 2017), pushing gekkotan ancestry even further into the past (Kimmeridgian to the Tithonian, Simões et al., 2017; i.e., before ~145–157 million years). Geckos have therefore diverged from other groups at least some 150 million years ago, and can thus be expected to differ markedly from even their closest living kin.

The defining apomorphies of crown-group Gekkota are mostly cranial (e.g., the loss of the postorbital and supratemporal bars, non-paired frontal bone; Bauer, 2013; Daza et al., 2013). That said, there are several morphological features that usually easily allow one to tell a gecko from other lizards based on gross external morphology, even in the field. Geckos usually have large heads (Bauer, 2013) and large eyes (Boulenger, 1885; p. 4; Bauer, 2013),

especially in nocturnal species (Werner, 1969; Hall, 2008). Because geckos are a hyper-diverse, nearly cosmopolitan, and ancient group of lizards, however, attempts to define traits they all share nearly always result in failure, because some species, or clades, evolved unique features. Thus while geckos usually have no moveable eyelids, this is a defining feature of one gecko clade, the eyelid geckos, Eublepharidae. Furthermore, other lizards, such as *Ophisops*, share gecko-like transparent and immovable scale in lieu of moveable eyelids. Similarly, while most geckos are characterized by sub-digital lamellae, allowing them to cling to surfaces, this ability has been lost multiple times in gecko evolution (Gamble et al., 2012; Hagey et al., 2017) and perhaps regained multiple times (cf. Gamble et al., 2012, 2017; Harrington and Reeder, 2017). About 40% of all geckos do not have adhesive toepads (Gamble et al., 2012), and such toepads themselves are not exclusively a gekkotan trait, but are found in many anoles, and some skinks (Hagey et al., 2017).

Other traits we tend to associate with geckos, such as tail autotomy, no limb reduction, and the ability to vocalize (Bauer, 2013) are likewise not shared by all gekkotans (e.g., pygopodids, here treated as geckos, are limbless, and some geckos such as *Stenodactylus petrii* and *S. doriae* do not autotomize; Arnold 1984; Bar and Haimovitch 2018, nor does *Agamura*; Boulenger, 1885, p. 4). Nor, of course, are tail autotomy and keeping all four legs restricted to geckos (e.g., iguanians and acrodonts do not lose limbs, lacertids and skinks autotomize). Laying calcareous eggs is unique to geckos and dibamids (among lizards, Köhler, 2005).

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Females belonging to 3 of the 4 largest reptilian families: Gekkonidae, Phyllodactylidae and Sphaerodactylidae, lay such eggs, that resemble bird eggs in that they tend to lose water throughout the incubation period. Members of the other gecko families (Diplodactylidae, Eublepharidae, Carphodactylidae, and pygopodidae), however, lay the ‘usual’ parchment-shelled eggs characteristic of other squamates (which tend to take up water from the environment during at least early incubation; e.g., Henkel and Schmidt, 1995; Meiri et al., 2015). Furthermore, some diplodactylids are viviparous (Bauer 2013). A less-often discussed (and quantified) characteristic of most geckos is their usually ‘soft’ skin (Boulenger, 1885, p. 5), which is usually covered by small granules studded with larger tubercles (Henkel and Schmidt, 1995; Bauer, 2013). But this again is not ubiquitous, as some species possess larger, plate-like scales that can be shed as an anti-predatory mechanism (Boulenger, 1885; Henkel and Schmidt, 1995; Bauer, 2013; Scherz et al., 2017).

While few, if any, ecological and life history traits are unique to geckos, the clade nonetheless differs much from all other lizards in many such attributes. My aim here is to review and characterize such traits in geckos, and other lizards, and show which attributes of geckos generally set them apart – and to what extent. To this end I use global datasets of lizard distribution and traits, and examine whether, how, and how much, geckos differ from other lizards in important aspects their ecology, life history, distribution, physiology – and conservation status.

Specifically, I examine gecko description rates, to test whether they are increasing faster than those of other taxa (Meiri, 2016). I compare gecko distribution patterns and richness hotspots, following suggestions they show unique patterns (Powney et al., 2009; Vidan et al., 2017). I further examine gecko body size, and a suite of life history characteristics, to examine how they cope with laying small clutches of eggs (Vitt, 1986; Shine and Greer, 1991; Doughty, 1997; Rosler, 2005). Geckos are known to be predominantly nocturnal. I quantify the spread of activity time in geckos, comparing it to other lizards, and test its effect on gecko body temperatures. Diurnal activity times are also sometimes associated with the evolution of herbivory in reptiles, because high body temperatures are needed to maintain what Janzen (1973) described as “the internal compost heap” (King, 1996; Espinoza et al., 2004; Meiri et al., 2013). Lastly, I examine the threat status of geckos, as reflected in IUCN categories, to test whether their often small ranges (Meiri et al., 2018) result in them being more vulnerable to extinction than do other lizards.

Methods

Data

Four major data sources are used to compare gecko traits to those of other lizard species. For taxonomic designations, and description dates, I rely on the April 2019 version of the Reptile Database (Uetz, 2019). Data on threat and population status are from IUCN (2019, downloaded in July 2019). Distribution data, and data on overlap with

nature reserves, are from Roll et al. (2017) with subsequent updates (e.g., for species described, or split, since). Trait data are based on a large-scale review of the primary and secondary literature (Meiri, 2018). Altitudinal data are based on literature records rather than on extent of occurrence maps.

Body sizes are reported as species maxima, in grams. These are based on snout vent lengths that are converted to masses using family-specific equations (Feldman et al., 2016, for the different gecko clades: Novosolov et al., 2013, Appendix S2). Clutch (and litter) size data are means, or – if no means are reported, average of the largest and smallest reported clutch size for each species. If multiple means were reported I averaged the largest and smallest value. Reproductive frequency is calculated as the number of clutches laid in a year. Age at maturity is the average between the highest and lowest reported values and lifespans are maxima (Scharf et al., 2015; Stark et al., 2018, 2020, this issue). Annual fecundity is calculated as clutch size * clutch frequency. To calculate (maximum) lifetime fecundity I multiplied annual fecundity by ‘reproductive lifespan’ calculated as maximum longevity minus age at maturity.

Activity time was classified as either diurnal, nocturnal or cathemeral (active both at day and at night – either within the day or when diel rhythms change from nocturnal to diurnal over the seasons, etc.). Body temperatures are mean cloacal temperatures of active lizards in the field (Meiri et al., 2013). Diet is categorized into herbivory (>50% plants in diet), omnivory (10–50% plant material) and carnivory (<10% plant material in diet). Species in the IUCN categories Least Concern and Near Threatened are treated as non-threatened, those in the Vulnerable, Endangered, Critically endangered and Extinct in the Wild are threatened, and data deficient species, as well as those not yet assessed are “unclassifiable”. Areas within or outside nature reserves are from Roll et al. (2017). Insular endemics are defined as those species only occurring on landmasses smaller than Australia.

Analyses

I intentionally restrict this review to pattern descriptions and comparison, rather than evolutionary analyses aimed to uncover the drivers of such patterns and discrepancies. I am comparing two sister taxa, geckos and all other lizards (although here I treat dibamids as ‘other lizards’ and omit snakes; amphisbaenians are treated as non-gekkotan lizards). Phylogenetically ‘corrected’ methods would thus have very limited power to reject a null hypothesis (Uyeda et al., 2018). Such comparisons also treat the phylogenetically-related differences as nuisance variables to be corrected for, rather than explored as is my intention here (Westoby et al., 1995a). Mostly, I refrain from using phylogenetic analyses here because I focus on the ecological patterns and their distribution – something that may be more relevant for those interested in the occurrence, maintenance and conservation of the species and traits, rather than in the number of times they evolved and mechanisms

driving their evolution (Westoby et al., 1995b). For this reason, I also posit that omitting the highly derived snakes from analyses of all other squamates is justified, and that the fact that ‘lizards’ is a paraphyletic group is irrelevant. Paraphyletic clades, by definition, are those that include all (and only) descendants of their last common ancestor. Thus, any dataset that does not include all members of the clade is by definition paraphyletic. This means that any large-scale dataset is paraphyletic: for some species data on some character states could be missing, some taxa have not yet been described and therefore not included, and because some crown group taxa already went extinct, often many millions of years ago. The only difference here is that me omitting a clade (Serpentes) is intentional.

Results

Geckos are a species rich clade with 1896 currently recognized species (1873 in Uetz, 2019, and 23 additional species described in the 3 months since). They thus comprise 27.5% of the 6877 currently recognized lizard species (6830 in Uetz, 2019, 47 newly described). Gecko’s share of the total number of known species is steadily increasing: the value was 20% at the turn of the 20th century, and slowly increased in every decade since – except between 1950 and 1960 (where it stayed stable at 21.3%). Since 2010 44% of lizard descriptions were of geckos (see also Uetz et al., 2020, this issue).

Distribution

Geckos occur in warm regions throughout the world (Fig. 1). They are especially species-rich in SW Africa, Madagascar, the southern coasts of the Arabian Peninsula, South and SE Asia, and Australia (Fig. 1). However, geckos are much less speciose in the New World: they comprise just 12% of American lizards (12% in the Neotropics, 4% in the Nearctic), but 35% of lizard species elsewhere (from 28% in Oceania and Australia to 47% in the Indo-Malay Realm; Fig. 1b). Gecko “cold spots” are generally found in cold places. Geckos are mostly absent from cold places, and do not reach the highest latitudes that lizards inhabit, such as most of the USA, parts of the Andes, the Tibetan Plateau, parts of the Caucasus and Eastern Turkey, and much of central and northern Eurasia (Fig. 1).

Geckos are more likely to be insular than other lizards: 661 of 1896 gecko species (35%) are island endemics, compared with 1419 of 4980 (28%) in other lizards ($\chi^2 = 265.3$, $p < 0.0001$). From a similar perspective, 32% of insular endemic lizards are geckos, but they comprise only 26% of non-insular endemic species. Geckos generally do not reach high altitudes. The Atlas Mountains day gecko, *Quedenfeldtia trachyblepharus*, is the gecko reaching the highest elevation of the 1160 species for which I have data (4000 m; Comas et al., 2014), but at least 81 other lizard species (of 3285 species with data) reach higher altitudes. On average, the maximum altitudinal limit of geckos is 870 m, vs. 1480 in other lizards ($t = 18.7$, $p < 0.0001$).

Body size and life history

Geckos are small lizards: the average maximum mass of gecko species, 4.7g (SD = 3.4g), is just 38% that of the average non-gekkotan lizard (12.2±5.1g; values back-transformed from logarithms; $t = 23.1$, $p < 0.0001$; Fig. 2). The largest gecko, *Hoplodactylus delcourti*, Bauer and Russell (1986), would only rank 97th in size among lizards in general. The average maximum mass among the Sphaerodactylidae is smallest across all lizard families, and those of the Gekkonidae are the third smallest (Gymnophthalmidae are second smallest).

It is therefore unsurprising that geckos lay small clutches: the average is 1.77±0.39_{SD} eggs per clutch ($n = 1123$), vs. 4.59±4.51 in other lizards ($n = 2758$; $t = 20.9$, $p < 0.0001$). Interestingly, although geckos are considered to lay fixed clutches of 1 or 2 eggs, 24 species are recorded as having maximum clutches of three (20 species), or four eggs (four species). These include members of all gecko families except the Pygopodidae (in which nearly all clutches comprise of 2 eggs, a single egg clutch is rare, and 3 or more egg clutches are unknown). To an extent, geckos compensate for their small clutch sizes by laying often. Geckos lay, on average, up to 4.2 times a year (averaging the maximum reported rates across species): more than any other lizard clade except Dactyloidae (anoles, up to 13.5 times a year; the average across all non-gekkotans is 2.4). Six of the seven gecko families are ranked among the 8 families with the highest laying rates (Corytophanidae is the only other non-gecko clade in this list, alongside Dactyloidae (anoles)). Among gekkotans all families are included in the top 8, except Pygopodidae (maximum rate up to 1.2 clutches a year).

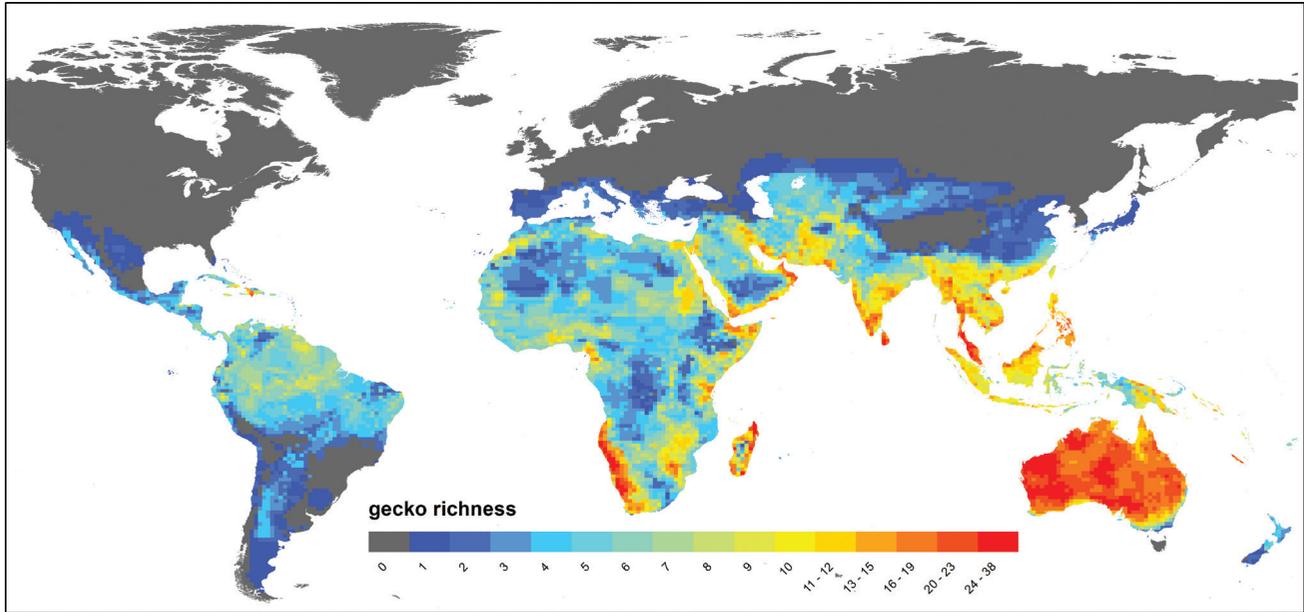
Despite being small-bodied, geckos age and survive in a similar fashion to other lizards: the mean age at maturity, across 160 gecko species is 18.0±11.9_{SD} months vs. 22.6±19.1 months in other lizards ($n = 568$ species; the difference is statistically significant, but not when mass is corrected for: $t = 1.22$, $p = 0.22$). Similarly, the maximum gekkotan longevity is 10.1±8.6_{SD} years vs. 10.5±9.9 years in other lizards (across 191 and 581 species, respectively; see also Stark et al., 2020, this volume). Thus maximum reproductive lifespan (defined here as maximum longevity minus average age at maturity) is 8.6 years in geckos and 8.7 years in other lizards.

From the above one could calculate annual and lifetime egg (or neonate) production in geckos and other lizard taxa, assuming that mean laying rates and maximum longevities scale isometrically with maximum laying rates and longevities. The fast laying rates of geckos, under these assumptions, do not compensate for the small clutches they lay: the annual rate (1.77 eggs laid 4.2 times a year) is 7.4 eggs vs. 11 eggs a year (4.59*2.4) in other taxa. Similarly, across a maximum lifetime, geckos will lay 63.9 eggs, under these assumptions, vs. 95.8 eggs, on average, laid by other lizards.

Activity times and thermal biology

One of the hallmarks of geckos is that they are nocturnal. Indeed, some 73% of geckos I have data for are strictly

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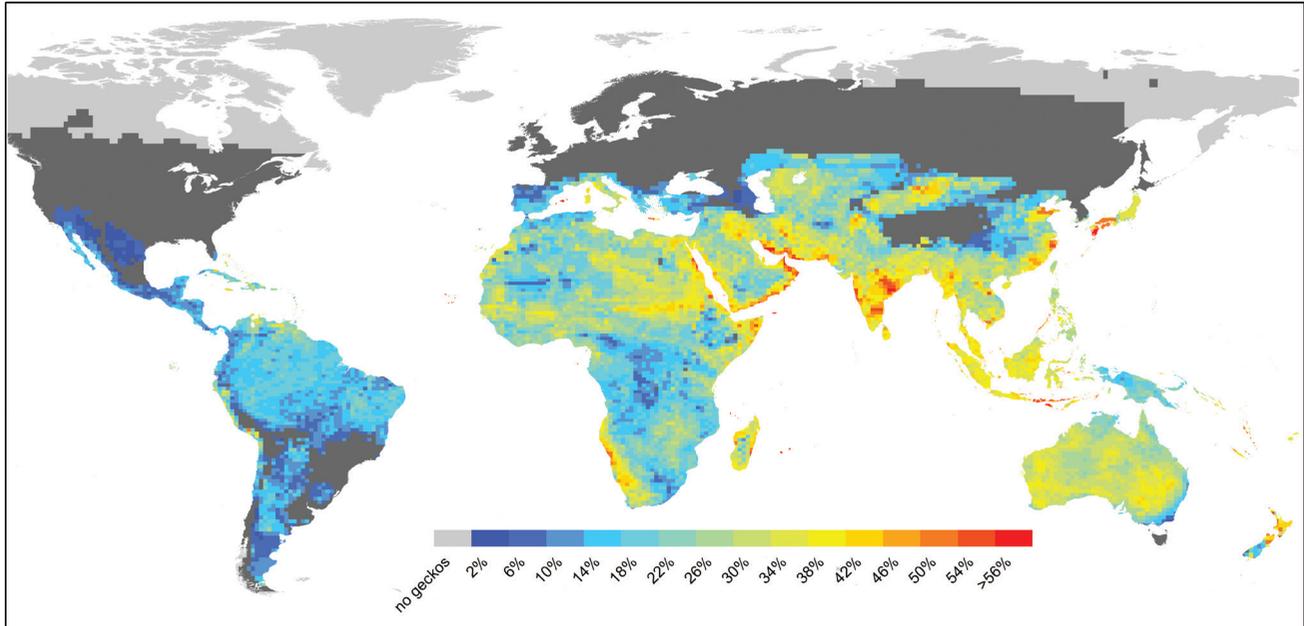


Figure 1. A. gecko species richness in 96*96 km grid cells (Behrmann projection). B. the proportion of geckos out of all lizards within a grid cell; dark gray: regions without geckos but with other lizards; light gray: regions with no lizards at all.

nocturnal (or nearly so), while only 4.4% of other lizard species are. Indeed, only ten other lizard families (three of them are amphisbaenid families) even have nocturnal species. The only non-gekkotan family containing more than 50% nocturnal species is the Lanthanotidae, comprised of a single species, the earless monitor, *Lanthanotus borneensis*. The amphisbaenid families Amphisbaenidae (9 of 18 species with known activity times nocturnal, 183 species in the family), and Trogonophidae (1 of two species with known data nocturnal, 6 species in the family as a whole), have 50% nocturnal species, but data are scant. Even the “night lizards” (Xantusiidae) are in-fact, less than 50% strictly nocturnal. Though the vast majority are active at night (18 species, vs. 3 diurnal) I classify nine of them

as cathemeral and nine as nocturnal. That said, geckos are far from being only nocturnal: Some 8.7% of species (145 of 1673 species with data) are cathemeral and 18.4% (307 species) are diurnal. Across gekkotan families the Carphodactylidae and Eublepharidae are entirely nocturnal (100% of species), while Sphaerodactylidae is predominantly diurnal (66% of species, 23% nocturnal), and the Pygopodidae is predominantly cathemeral (49% of species, 32% nocturnal). The Gekkonidae (76% nocturnal, 16% diurnal), Phyllodactylidae (85% nocturnal, 14% cathemeral), and Diplodactylidae (89% nocturnal, 7% diurnal) take up intermediate positions.

Given the much higher incidence of nocturnality in geckos it is unsurprising that they tend to have much lower

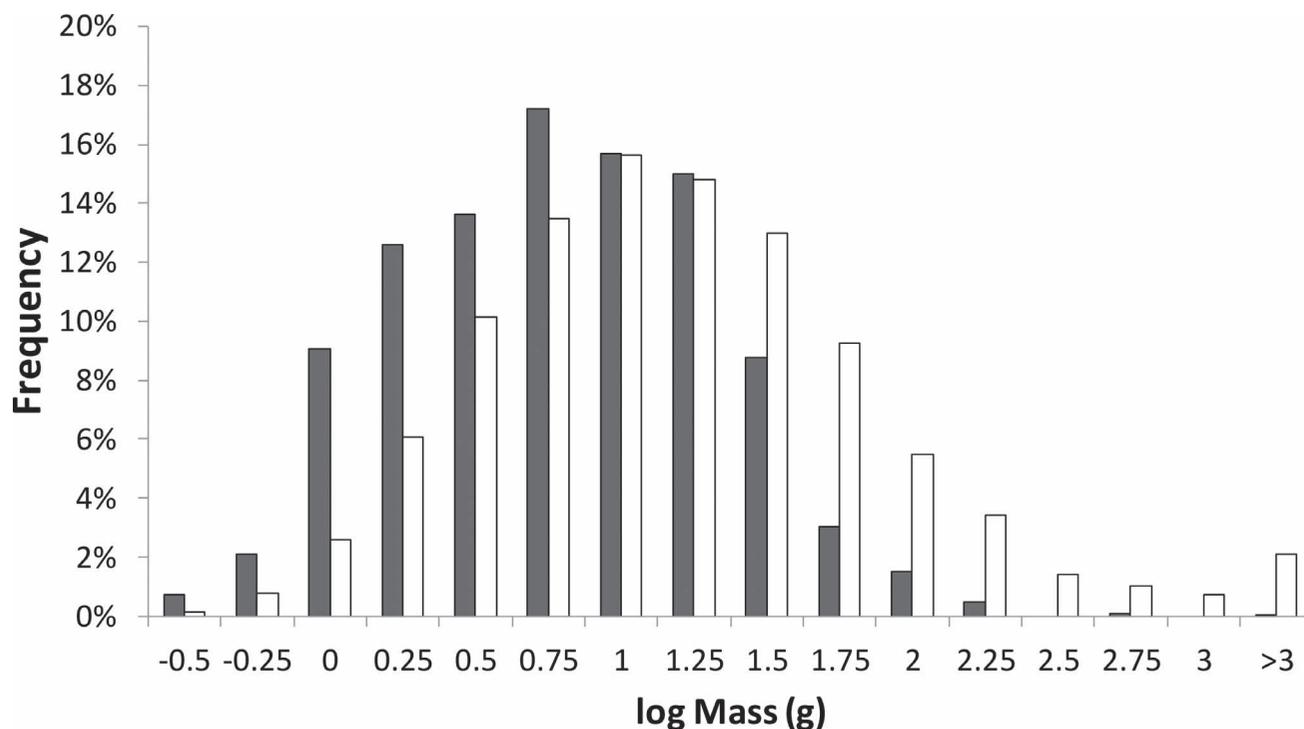


Figure 2. Frequency distribution of maximum body masses of geckos (gray) and other lizards (white); masses are calculated from maximum SVLs. Data are proportions out of values for 1894 species of geckos and 4955 species of other lizards.

body temperatures than other lizards. The average body temperature of active individuals across gekkotan species is 26.6°C, fully 5.3 degrees colder than the 31.9°C for other taxa ($n = 137$ and 952 species, standard deviations: 4.9 and 4.5°C, respectively, $t = 12.7$, $p < 0.0001$) (Fig. 3). Geckos are not just active at lower temperature in nature, they actually like it this way: the mean preferred temperature of geckos in thermal gradient experiments is 28.4 ± 4.0 °C, while other lizards prefer, on average, temperatures of 32.8 ± 3.7 °C ($n = 51$ and 430 species, respectively, $t = 7.9$, $p < 0.0001$).

Surprisingly, however, activity times are not the only factors that lies behind these differences, because activity body temperatures of nocturnal geckos (mean 25.3°C) are lower than those of nocturnal other lizards (27.8°C), and so are those of diurnal gecko species (29.4°C vs. 32.3°C in other diurnal lizards; Fig. 3b).

Diet

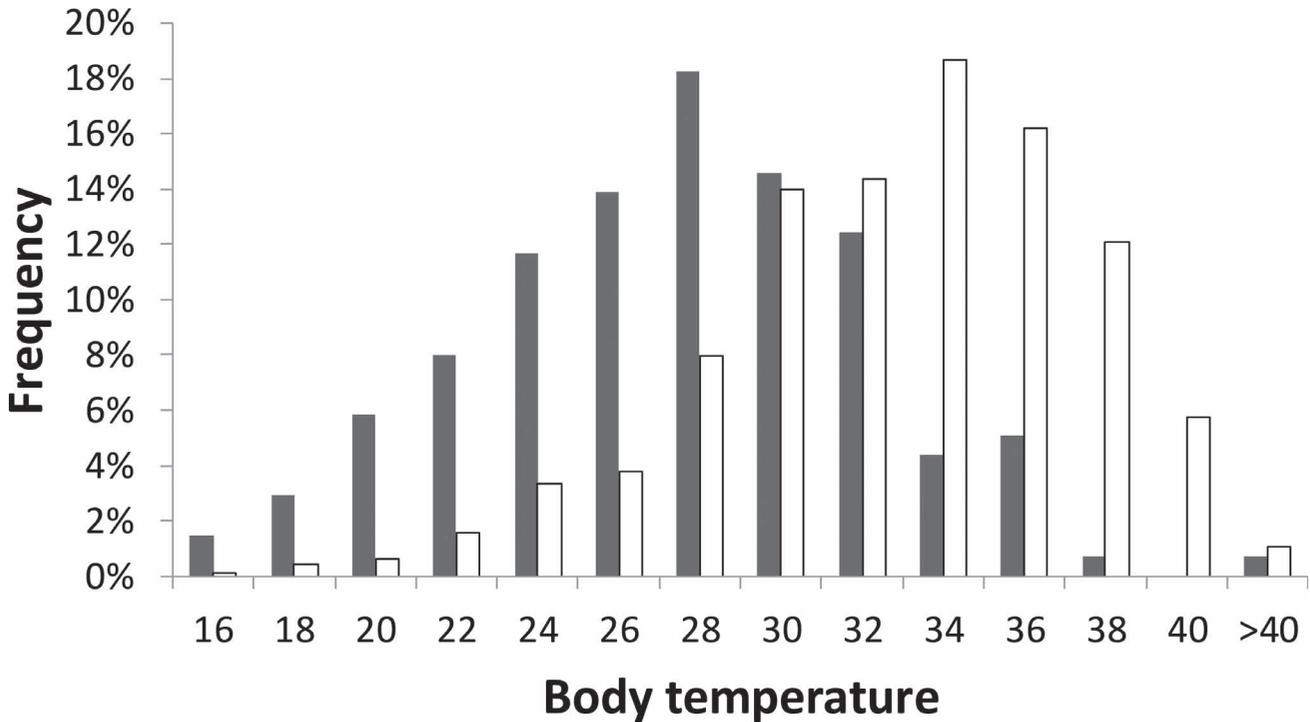
Most lizards are predominantly carnivorous, but many are either herbivorous or omnivorous. Geckos are no exception: in fact, the incidence of omnivory is similar across geckos and other lizards (15.3 and 15.3%, 130 and 398 species, respectively). Herbivory, even under my liberal definition of species feeding mostly on plant matter, occurs in other lizard taxa (6% of species, 155 of 2766 species with data) – but is nearly absent in geckos. I categorize only three species: *Ailuronyx trachygaster*, *Gehyra vorax*, and *Strophurus assimilis* as predominantly herbivorous (mostly feeding on fruit and sap), and this is based on limited data. Interestingly, most of the 133 species of plant-eating geckos (130 omnivorous, 3 herbivorous) are either diurnal (71 species) or cathemeral (13 species) – just 44 are nocturnal (and for the other four I have no data on activity times).

Threat

On the face of it, geckos are as threatened as the next lizards. Thirteen percent of gecko species are listed by the IUCN as threatened (251 species in categories VU, EN, CR and EW), similar to the 12% proportion of other lizards. Similarly, in both groups, 8% of species are listed as data-deficient, and while 44% of geckos are non-threatened (classified as LC or NT) and 34% are left to be evaluated by the ICUN, the corresponding figures for other lizard taxa are very close at 45% and 35%, respectively. Thus, for both groups, species with helpful, classifiable categories form 57% of the total number of species whereas non-classifiable taxa (data deficient or non-evaluated) form 43%. The population trends are also broadly similar across geckos and other lizards: 12.2% of gecko species are listed as decreasing, 0.7% as increasing, and 38.2% of the species are classified as ‘stable’. For other lizards these numbers are 14.8, 0.3 and 39.9%. I note, however, that for nearly half the species (49% of geckos, 45% of other taxa) the population status is unknown. Five gecko species (*Phelsuma edwardnewtoni*, *P. gigas*, *Hoplodactylus delcourti*, *Tarentola albertschwartzi* and *Nactus soniae*) have gone extinct in the last few centuries. *Lepidodactylus listeri* is extinct in the wild.

The B criteria (range sizes) predominate among those by which threat is assessed by the IUCN – 738 species (73%) were classified at least in part based on the B criteria, and 720 species were assessed as threatened based on B criteria alone. We would therefore expect geckos have similar range sizes to those of other lizards – but this is not the case. The average range sizes of geckos, 2844 km² (log-transformed, averaged, then back-transformed) are only 40% the size of other lizard range sizes (6998 km²). This

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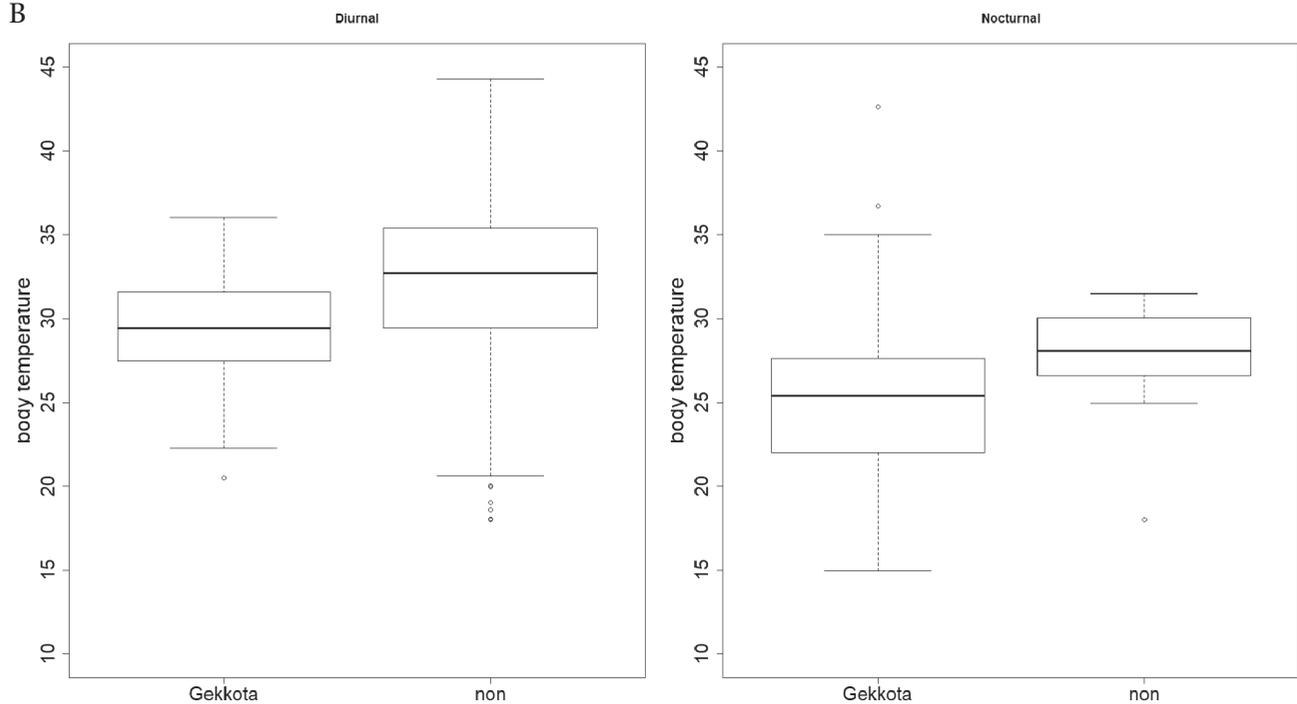


Figure 3. A. frequency distribution of gecko (gray) and other lizard (white) body temperatures (in °C) during activity. B. The same temperatures for geckos and other lizards (“non”), across diurnal and nocturnal species (catemeral species and those with unknown activity times omitted).

discrepancy is not simply related to the positive relationship between body size and range size (e.g., Brown et al., 2016; Camacho et al., 2016): ranges of geckos are smaller by 76% (0.245 ± 0.049 log units, $t = 5.01$, $p < 0.0001$), on average, than those of other lizards, even after the effects of body size (slope of the log-log relationship: 0.368 ± 0.031 ; assuming a common slope) are controlled for. Furthermore, the percentage of gecko species that do not have any part of their range in the better-kind of protected area (IUCN reserve categories I–IV), 39.6%, is much higher

than that of other lizards (27.7%). Even more worryingly, fully 24% of gecko species ranges are completely outside any nature reserve, almost double the proportion of other lizards (12.5%).

Discussion

Geckos are a large, ancient, diverse, and widely distributed group of lizards. As such it is unsurprising that at least some gecko species occupy almost all corners of the

'lizard' niche. We can find small and large (though not huge) ones, legged and legless (Pygopodidae) ones, but interestingly no intermediate reduced-leg forms. There are viviparous geckos (only in the Diplodactylidae), and (few) herbivorous ones, there are terrestrial, arboreal, and saxicolous ones (and gliding forms to boot), and all their combinations – although the only fossorial gekkotans are pygopodids and no gecko is semi-aquatic. Geckos can also be found along the length of the slow to fast life history continuum, can be active at any time along the diel cycle, and feed on either vertebrates (e.g., *Hoplodactylus duvaucelii*, Hare et al., 2016; *Tarentola annularis*, Crochet and Renault, 2008), invertebrates (most species), or the richer part of plants (e.g., sap, fruit, berries, but none are true folivores; Daza et al., 2009).

Nonetheless, geckos have clear modes across most traits I examined here: they generally inhabit relatively warm regions, are absent from high latitudes and altitudes, and are over-represented on islands. They are small lizards that lay fixed clutched eggs (only 1.8% of species with known reproductive modes are viviparous, $n = 21$) at high frequencies. Despite that they mature, and age, at similar rates to other lizards (see above and Stark et al., 2020, this issue). They are predominantly nocturnal though a substantial minority of species are diurnal or cathemeral. They have lower body temperatures, and prefer lower body temperatures than other lizards. This can be a phylogenetic constraint (my analyses are not phylogenetically corrected), but it persists despite substantial variation. They are predominantly carnivorous though a substantial minority are omnivores. Thus while popular notions of what traits geckos possess are, to a large degree, correct, much variation does occur.

That geckos are restricted to lower altitudes and latitudes than other lizards (Vidan et al., 2017 and see above) is unsurprising, given that they are predominantly nocturnal. Night temperatures are lower than day temperatures and even the ability of geckos to function, indeed to prefer such temperatures (see above), cannot compensate for that. Some gecko taxa inhabiting high altitudes and latitudes (e.g., New Zealand *Naultinus* species; Tingley et al., 2013; van Winkel et al., 2019) evolved diurnal activity and it is unsurprising that several of the species reaching the highest altitudes (e.g., *Pristurus popovi*, *Quedenfeldtia trachyblepharus*) belong to the predominantly diurnal Sphaerodactylidae. The presence of many gecko species on islands could be explained by their unique (among lizards), highly calcified eggshells (of Gekkonidae, Phylloactylidae and Sphaerodactylidae members), which may enhance their ability to survive exposure to sea water, and by the tendency of females in many gecko species to glue their eggs to the substrate, which may facilitate overwater rafting. Novosolov and Meiri (2013) suggested that the small, frequent, clutches laid by geckos may predispose them to be successful island colonizers, in keeping with the notion that selection pressures on islands act to reduce brood sizes (the 'island syndrome': Adler and Levins, 1994; Pafilis et al., 2011; Novosolov et al., 2013). Meiri et al. (in press) recently suggested that these small clutches may prevent geckos from inhabiting highly seasonal, high

latitude regions where laying multiple clutches across the short reproductive season is impossible. Another factor that promotes gecko colonization of islands (mostly in the Pacific Ocean) is the evolution of parthenogenesis. Obviating the need for males is an excellent strategy for taxa to disperse across biogeographic barriers such as sea water. A single female, or even a single egg (see above) can easily facilitate successful colonization. *Hemiphyllodactylus typus*, *Hemidactylus garnotii*, *Nactus pelagicus* and *Lepidodactylus lugubris*, have evolved parthenogenesis – which most likely was a major factor allowing them to colonize islands over thousands of kilometers in the Indo-Pacific. That said, parthenogenesis is rare in geckos overall, only a handful of other species evolved it, and it does not seem to be the main driver of the high gecko diversity on islands.

The scarcity of New World geckos is puzzling. Gamble et al. (2011) estimated that geckos colonized the new world on 8 separate natural events, dating as far back as ~98 and 67 million years ago in the predominantly new world clades Sphaerodactylidae and Phylloactylidae, respectively. Two other families: the Gekkonidae and Eublepharidae also inhabit America. Thus geckos had ample time to diversify in the New World. They have also spread widely across it: from *Coleonyx eublepharids* reaching latitude 37.5°N in Nevada, United States to *Homonota darwinii*, the southernmost gecko in the world, reaching ~51.3°S in Patagonia, Argentina (e.g., Conrad and Bradley, 2009; Daza et al., 2017; Roll et al., 2017). They also diversified in size there, ranging from the smallest geckos, indeed the smallest lizards, reptiles, and amniotes in general, *Sphaerodactylus elasmorhynchus*, *S. ariasae* and *S. parthenopion* (estimated masses of 0.12–0.15 g; Feldman et al., 2016) to about 80 g in recently extirpated populations of *Aristelliger lar* ('*H. titan*', Hecht, 1951). American geckos further include diurnal, nocturnal, and cathemeral forms, carnivores and omnivores, and both arboreal, saxicolous and terrestrial species (Meiri, 2018; Vidan, 2019). Thus they are morphologically, biogeographically, phylogenetically and ecologically diverse. Furthermore, there are few non-gekkonid nocturnal lizard taxa in the New World that could potentially competitively exclude them. *Heloderma* is quite unlike any gecko. Night lizards (Xantusiidae) a small, geographically and ecologically restricted taxon, inhabiting parts of Central America to SW USA, are unlikely to have restricted gecko diversification. While arboreal lizards such as anoles may likely be competing with geckos, and could potentially be a factor in their scarcity, separating the niche along the time axis often allows potential competitors to coexist (Schoener, 1974; Kronfeld-Schor and Dayan, 2003; Gordon et al., 2010; Giulia et al., 2019; see also Toft, 1985). Furthermore, while ~24% of geckos with known activity time in Africa, Eurasia, Australia and Oceania are diurnal or cathemeral (352 of 1466 species), the respective figure for the Americas is 48% (100 of 207 species). It is thus the scarcity of nocturnal geckos that is most surprising. Duellman and Pianka (1990) suggested that competition with frogs may have prevented geckos from increasing in diversity in the Neotropics, but admitted that "Evidence for or against the existence of competition between frogs and gekkonoids for resources is

hardly compelling". Further research is definitely needed to follow up on this hypothesis.

The evolution of fixed clutch size in lizards may well have been coupled with the evolution of small body size. Today, however, it is a constraint, and even the largest geckos only lay two eggs at most per clutch. While there are reports of larger clutches in a number of species, I suspect at least some of them are artefacts of some methods of estimating clutch size. Specifically, because geckos often have a semi-transparent abdominal peritoneum (e.g., Khan and Tasnim, 1990; Doughty, 1997; and my personal observations), and large eggs (e.g., Doughty, 1997; Kratochvil and Kubicka, 2007), their eggs are often counted by observing them through the female body wall. This, however, is often difficult, as determining whether a large white blob is an egg or not is not always straightforward. Furthermore, abdominal eggs may be re-absorbed, or laid in different clutches. Thus in working on *Mediodactylus kotchyi*, we have sometimes estimated abdominal number of eggs as 3 (Slavenko et al., 2015), but bringing these geckos later to the lab, we never observed more than 2 eggs laid in a clutch (Schwarz et al., 2020). Defining what constitute a single clutch, in species laying frequent, small clutches of eggs, is also challenging (Rachel Schwarz, pers. comm.). The tendency of many geckos for communal laying (e.g., Doody et al., 2009; Godoy and Pincheira-Donoso, 2009; Dayananda et al., 2016; Ngo et al., 2018; Aaron Bauer, pers. comm.; and my personal observations) likewise makes inferring clutch sizes tricky.

The small number of eggs, coupled to the overall similarity in age at maturity between geckos and other lizards, means that geckos lay fewer eggs per unit time, and have lower lifetime reproductive output in terms of overall number of offspring produced. Yet geckos persist and thrive. This could be coupled to their abundance in, and mostly restriction to, low latitudes and to islands – two types of habitats that are often associated with K selection and the production of few, large sized offspring. The large hatchlings of geckos may have better survival than the relatively smaller young of other lizard taxa. I have no data to test this hypothesis.

As a predominantly nocturnal clade, it is unsurprising that geckos needed to develop adaptations enabling them to be active at night. Such adaptations include large eyes (Boulenger, 1885; Werner, 1969), olfactory prey discrimination (although diurnal lizards in other clades use vomerolfaction that is likely as effective; Vitt and Pianka, 2005), and an ability to be active at low environmental temperatures (Meiri et al., 2013 and see above). Of course such adaptations may have been already present in the common ancestor of the Gekkota (Gamble et al., 2015), if not of all squamates (Sites et al., 2011). It is therefore hardly surprising that geckos are active at lower body temperatures than other lizards. In this light I hypothesize that, when geckos evolved diurnal activity (which they did multiple times; Gamble et al., 2015), their thermal physiology remained, to an extent, more conservative. If true, this may explain why diurnal geckos maintain lower activity temperatures than other lizards. Similarly, if activity times shift faster than thermal preferences, it may explain why

when non-gekkotans evolve nocturnality, they still maintain higher body temperatures than nocturnal geckos.

One caveat needs to be made regarding lizard activity times: while geckos are the only large and diverse lizard clade to have evolved nocturnality, they are by no means the only major squamate clade to do so. Lizards are a paraphyletic group, which gave rise to the hugely diverse and successful lineage of snakes. A comprehensive review of nocturnality in snakes, and ancestral state reconstruction of their diel rhythms, are presently unavailable. Anat Feldman (pers. comm.), estimates that ~60–70% of extant snake species are nocturnal. Because nocturnality and diurnality are both widespread in many snake clades diel activity shifts are likely to have occurred multiple times during snake evolution. A comparison of the evolutionary transitions across the diel rhythms of snakes and geckos, and their associated effects on thermal physiology, may hold important insights for the evolution of activity times in general.

The fast description rates of geckos (see above, Meiri, 2016; and Uetz et al., 2020, this issue) suggest that the data presented above could well be biased. We undoubtedly underestimate the diversity of all squamates, and overestimate their range sizes, and body sizes. Because geckos are being described at much higher rates than other lizards (see above), these issues are particularly acute for them. I hypothesize, for example, that we know high latitude, and diurnal taxa better than we do desert and tropical taxa, and nocturnal species. Because of the association between these and other traits, we may be overestimating the prevalence of diurnality, omnivory, and viviparity – as well as a suite of other traits. Most worryingly, this Linnean shortfall means we probably greatly underestimate the conservation needs of geckos, because we base our conservation planning based on what we know. If what we know is biased, our planning is less effective than it should be (Meiri and Chapple, 2016). Even this is an optimistic scenario because reptiles in general are far less well protected than other vertebrate taxa (Roll et al., 2017).

More worrying still, while current knowledge – in terms of our assessed estimate of threat, suggest that geckos are doing as well (or as badly) as other lizards, there are reasons to think this is misleading. The B criteria assign risk based on small extent of occurrence (B1), or area of occupancy (B2, IUCN 2012), which are either severely fragmented or just few in number (B1a or B2a), “observed, estimated, inferred or projected” to shrink further (B1b or B2b), or fluctuate extremely (B1c, B2c). I think that these criteria, and the similar C criteria (few mature individuals which either decline in numbers, fluctuate “extremely” – or coupled with few immature animals), may actually fail the most threatened of taxa – such as many geckos. If a population started tiny, and geckos are especially predominant across lizards with extremely small ranges (Meiri et al., 2018), we are unlikely to see either declines or fluctuations, in either range size or number of individuals, before such declines and fluctuations will drive such species to extinction. Gecko taxa have especially high numbers – and proportions, of species known only from their type localities. Meiri et al. (2018) estimated that 335 gecko species have a maximum linear extent of occurrence of

10 km between the localities at the edges of their ranges. Of these 31 species were not observed for 50 years or more, and 45 species were only known from their holotype. Of the 46 gecko species described so far in 2019 (January 1st to August 11, 2019), a whopping 30 are known only from their type localities, and seven of them are known from a single individual (the holotype) only. Obviously one cannot quantify either decline, or fluctuations, or numbers of mature and immature individuals for any of these species. Gecko species are not the charismatic, large, and dangerous animals that attract most human attention – and conservation actions (Donaldson et al., 2016; Roll et al., 2016). That geckos receive so little protection in nature reserves, lower than even the dismal state of reptiles as a whole (Roll et al., 2017), imply that we are failing to protect them – or even identify them as needing protection. I think a strong effort to identify and classify geckos (and other taxa) according to both their conservation needs and in view of the protection measures already in place is direly needed if we are to retain these wonderful animals for the foreseeable future.

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