

Does nocturnal activity prolong gecko longevity?

Gavin Stark^{a,*}, Rachel Schwarz^a and Shai Meiri^{a,b}

^aSchool of Zoology, Faculty of Life sciences, Tel Aviv University, Tel Aviv, Israel

^bThe Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

Abstract The majority of lizard clades are ancestrally and predominantly diurnal. The only major taxon in which most species are nocturnal is the Gekkota (geckos and pygopodids). As ectothermic thermoregulators, lizard metabolic rates are highly temperature dependent, and diurnal lizards therefore demonstrate higher metabolic rates than nocturnal ones. Furthermore, exposure to solar radiation is thought to reduce ectothermic longevity by increasing both metabolic costs and the rate of accumulating harmful mutations through UV radiation (UVC specifically). In being nocturnal, ectothermic species may reduce their intrinsic mortality rates and thus live longer. To test this hypothesis, we collected literature data on the maximum longevity of 740 lizard species, of which 185 are geckos. We examined whether geckos live longer than other lizards, and whether activity time affects gecko longevity. While geckos live relatively long for lizards of their size, their activity time was found to be unrelated to longevity, contradicting our predictions. We suggest that diurnal species may have evolved higher resistance to UV radiation via thicker, more keratinized skin. Elevated metabolic rates do not automatically equate with faster aging. Mortality through extrinsic causes (e.g., predation) may impose much stronger selective pressures than intrinsic causes.

Keywords activity time; body size; Gekkota; intrinsic mortality; lizards; metabolic rate; solar radiation

Introduction

Longevity is a major characteristic of all animals, and one that has fascinated scientists around the world for over two millennia. Aristotle (c. 350 BCE; in his famous treatise “On longevity and shortness of life”) reflected on the diversity and variation of lifespans among plant and animal species, observing, for example, that large species generally live longer than smaller ones (see: http://classics.mit.edu/Aristotle/longev_short.html). Evolutionary theories of ageing (Medawar, 1952; Hamilton, 1966; Kirkwood, 1977; Kirkwood and Austad, 2000) have posited that longevity evolves in response to extrinsic mortality causes (e.g., from predators, competitors, epidemics and famine) or intrinsic mortality causes (e.g., spontaneous chemical reactions, errors in the DNA replication process and oxidative damage by metabolic waste products). These theories suggest that species exposed to low mortality pressures, will evolve long lives in order to maximize lifetime reproductive success (Healy et al., 2014; Valcu et al., 2014). Taxa suffering high extrinsic mortality rates in contrast, will not evolve long lives because most individuals will already have died from such extrinsic causes before natural selection can act on reducing the intrinsic causes of mortality (Williams, 1957; Hamilton, 1966; Williams and Day, 2003; Williams et al., 2006; Caswell, 2007).

UV radiation (specifically UVC) in high exposure can cause an increase in intrinsic mortality via accelerated accumulation of somatic mutations (Hart et al., 1977; Francis et al., 1981; Ley, 1985; Sinha and Häder, 2002; Paul and Gwynn-Jones, 2003; Snell et al., 2009; Rastogi et al., 2010;

Norris and Kunz, 2012; Southworth et al., 2013). Moreover, in daytime, when UV exposure is high, diurnal species are exposed to elevated ambient temperature, which causes an increase in metabolic rates (for ectothermic tetrapods in particular) and a consequently high accumulation of metabolic waste and oxidative damage (Sohal, 1986).

Ultraviolet radiation (UVA and UVB specifically) is an important factor in reptilian physiology because it affects their development and growth (Ferguson et al., 2010). UVA can regulate behaviours such as foraging for food, social communication, movement during the day and reproduction, while UVB enables the synthesis of vitamin D₃, which helps reptiles to absorb calcium (Adkins et al., 2003). However, the exposure to high levels of UV radiation (specifically UVC) can be harmful to the fundamental biological traits (such as development or growth) of animals (Faruki et al., 2005; Ghanem and Shamma, 2007; Lah et al., 2012; Heidari et al., 2016). The evolution of nocturnality can reduce exposure to the harmful effects of UV radiation (Zhang et al., 2011; Hori et al., 2014; Emerling et al., 2015; Stark and Meiri, 2018; Stark et al., 2018). Nocturnal ectotherms may therefore have lower mortality rates, leading them to live longer than diurnal ones. Moreover, nocturnal ectotherms display lower body temperatures (Meiri et al., 2013), and thus also lower resting and field metabolic rates, than diurnal ones (Huey et al., 1989; Autumn et al., 1994). Higher metabolic rates can increase intrinsic mortality rates via the accumulation of metabolic by-products and select for shorter lifespans (Sohal et al., 1989; Ku et al., 1993; Wright et al., 2004; Atanasov, 2005; Kapahi et al., 2010).

*Corresponding author. E-mail: gavinstark89@gmail.com

Healy et al. (2014) found a positive association between activity time and longevity among flying endothermic species, with crepuscular species having shorter lifespans than their nocturnal and diurnal counterparts. They associated this reduction in lifespan to the higher predation pressure (high extrinsic mortality pressure) from both diurnal and nocturnal predators on crepuscular species. Stark and Meiri (2018) found that nocturnal amphibians lived longer than diurnal ones, and they linked this to a potential reduction in exposure to predators (extrinsic mortality) and to UV radiation (intrinsic mortality rates) for nocturnal species. However, in reptiles, Stark et al. (2018) did not find differences in longevity between diurnal and nocturnal species. Despite employing a phylogenetic comparison, those authors' comparisons of animals with very different morphologies, physiologies, distributions and lifestyles, and which have evolved independently for hundreds of millions of years, such as turtles, snakes, lizards and crocodiles, may have lacked the ability to observe differences that may only exist in certain clades, or across animals sharing a similar *bauplan*. Therefore, we sought here to determine whether the evolution of nocturnality has produced (probably as a side effect) differences in maximum longevity within animals sharing a similar body plan and overall similar ecology.

Lizards are predominantly a diurnal group and are well known for their usually heliothermic behaviour (Autumn and De Nardo, 1995; Garrick, 2008). One major clade of lizards, however, the Gekkota (geckos and pygopodids), which diverged early from other squamates (Tonini et al., 2016), is mostly nocturnal (Gamble et al., 2015). Nocturnality arose early on in gecko evolution (Pinto et al., 2019; Schott et al., 2019). Additionally, members of several gecko lineages have shifted their activity time repeatedly in the course of their evolution. While nocturnality itself probably evolved for reasons unrelated to the evolution of longevity per se, this frequent shift in activity pattern enables us to study its effects on maximal longevity. This will allow us to determine whether factors such as reduced temperature and radiation operate within a clade demonstrating a relatively conservative form and function. The Gekkota is the only predominantly nocturnal lizard clade (72–80% of the species are active at night; Gamble et al., 2015; Meiri, 2018), in contrast to most other lizard clades, which are predominately diurnal (67% of non-gekkotan lizard species are strictly diurnal; Meiri, 2018; Meiri 2020; this volume.). Geckos have evolved many adaptations to nocturnal living (Bauer, 2007), such as changes to the visual system (e.g., enlargement of the eyes to enhance photon capture, and changes in the photoreceptor cells; Röhl, 2001), the absence of a parietal foramen, highly acute and specialized vocalization, olfactory communication, enhanced capability for activity at low temperatures (Autumn et al., 1994, 1999; Hare and Cree, 2016) and distribution patterns that allow them to avoid excessively cold night-time temperatures (Vidan et al., 2017). However, not all gekkotan species are nocturnal; many species are either diurnal (20% of the species) or cathemeral (= active at any time of night or day, according to prevailing circumstances; about 8% of gecko species are cathemeral according to this definition; Tattersall, 1987; Gamble et al., 2015; Meiri, 2020, this

volume). Diurnal and cathemeral geckos have evolved adaptations that enable them to live and forage in habitats (e.g., desert environments) in which the solar exposure is intense and temperatures are extremely hot. Examples of such adaptations are as diverse as those of smaller eyes (in relation to nocturnal species), rounder pupils, production of proteins that filter ultraviolet rays and a shift to active foraging strategies (Pianka and Huey, 1978; Autumn, 1999; Röhl, 2001; Werner and Seifan, 2006).

The effect of nocturnality on gecko longevity has never been formally tested. Here, we sought to determine for the first time whether longevity in this large, ecologically diverse and phylogenetically unique group is affected by similar activity patterns (i.e. nocturnal activity) to those found to be important in amphibians (Stark and Meiri, 2018). We predicted that:

1. Geckos, being mostly nocturnal, would live longer than other lizards (which are mostly diurnal) of similar body sizes.
2. Diurnal geckos would have shorter lifespans than nocturnal ones of similar body sizes (with cathemeral species intermediate). We predicted that this would also be the case across lizards and within both the Gekkota and its largest family, the Gekkonidae, for the following reasons:

1) Nocturnal lizards are expected to have lower metabolic rates than diurnal ones, because night temperatures are lower than those during the day (Hare et al., 2010). Lower metabolic rates, in turn, may reduce intrinsic mortality due to the lower production of metabolic by-products (Sohal, 1986), and thereby increase lifespan. 2) We hypothesized that nocturnality enables gekkotan species to reduce their intrinsic mortality pressure by reducing their solar exposure in general, with a subsequently lower exposure to the extremely harmful UVC radiation (Faruki et al., 2005; Ghanem and Shamma, 2007; Lah et al., 2012; Heidari et al., 2016). Such lower exposure will select in favour of nocturnal lizard species, which will live longer than diurnal and cathemeral species.

Methods

Data collection

We collected literature data (see Scharf et al., 2015; Meiri, 2018; Stark et al., 2018) on the maximum longevity of 740 lizard species belonging to 36 out of the 42 families currently recognized world-wide (Uetz, 2019). Of these 740 species, 185 were geckos, divided among all seven gekkotan families (Carphodactylidae [6 species]; Diplodactylidae [40]; Eublepharidae [8]; Gekkonidae [87]; Phyllodactylidae [22]; Pygopodidae [4] and Sphaerodactylidae [18]). The other species (n = 437) belonged to 29 lizard families. Almost all the lizard taxa for which we have longevity data except the geckos, are nearly 100% diurnal (see Supplementary Appendix S1 for the list of sources). We therefore compared the longevity of gekkotan species (n = 185) to those of all other lizard clades (n = 555). We further compared

nocturnal geckos to diurnal geckos. The only other family in our database containing both nocturnal and diurnal species in high enough numbers for comparison was the Scincidae (skinks). We thus introduce a sensitivity analysis in which we compared longevity of diurnal and nocturnal skinks.

The longevity records refer to maximum lifespan in years, reported for each species. The use of maximum values as estimates of longevity has both advantages and disadvantages. Maxima may be unrepresentative of the species (Carey, 2003), and estimates based on higher numbers of individuals will be higher, whereas means are probably unbiased (Meiri, 2007). Therefore, we recorded the sample sizes for which longevity was estimated for each species. We introduced a sensitivity analysis using only species for which longevity estimates were based on large sample sizes ($n \geq 30$; based on the central limit theorem), and tested the difference between the longevity of nocturnal and diurnal species in all lizards, then only in gekkotans, and finally only in members of the largest gekkotan family, the Gekkonidae (we performed these separate analysis in order to determine whether progressively finer phylogenetic subsets and hence animals more similar to each other, vary along the diurnal to nocturnal axis). Longevity of captive individuals is often higher than that of wild ones (e.g., Tidière et al., 2016; Stark and Meiri, 2018). However, preliminary analyses revealed no effect of origin (captive or wild) on maximum longevity. We therefore did not correct for origin data in our analyses.

Body size is a fundamental life-history trait that tends to co-vary with multiple life-history traits, including longevity (de Magalhães et al., 2007) and can thus be a confounding factor in comparative studies of aging (Speakman, 2005; de Magalhães et al., 2007). It is therefore critical to correct for body size, when carrying out statistical analyses of life-history traits (Møller, 2008). We used body mass as an index of size. While snout-vent length is the common index of size in geckos, and lizards in general, this measure is highly sensitive to differences in shape. Shape differs greatly among animals as different from each other as the legless pygopodids are from 'typical' geckos (Meiri, 2010). Variation in key biological traits that are likely to be relevant for longevity (e.g., metabolic rates), is more tightly related to mass than it is to length (Speakman, 2005). Thus, we converted length of species within each gecko clade (and within other lizard clade) to mass, using clade-specific length-to-mass conversion equations (from Feldman et al., 2016). When multiple means were available in the literature (e.g., for different populations, samples or sexes), we averaged the highest and lowest published means.

We classified species into three activity categories: diurnal (540 species, of which 42 are geckos), nocturnal (145 species, of which 122 are geckos) and cathemeral (57 species, of which 21 are geckos). Data on body size, sample sizes and activity times were gathered from the same sources used to estimate longevity. When unavailable in the works publishing longevity data, we obtained data on body lengths (which we then converted to masses) and activity times from the herpetological literature (see Supplementary Appendix S1 for the list of sources).

Phylogenetic statistical analyses

We set the $\alpha = 0.005$ of the models according to suggestions by Benjamin et al. (2018), which reduces the potential for false positives. No predictors had a Variance Inflation Factor higher than 1.5 and we thus maintain that our analyses are not biased by multi-collinearity (O'Brien, 2007).

We used an up-to-date, complete phylogenetic tree for squamates (Tonini et al., 2016) for the analysis of all lizards together and for all the Gekkota. For analyses of the Gekkonidae family we used the tree of Zheng and Wiens (2016), because it provides species-level resolution. The PASTIS tree of Tonini et al. (2016) infers the placement of species with unavailable data according to taxonomy, often resulting in genus-level polytomies. A sensitivity analysis for these two families with the Tonini et al. tree gave qualitatively identical results (i.e., same significant factors in the same direction; results not shown). We accounted for shared ancestry using phylogenetic generalized least square (PGLS) tests for all our models, implemented in the 'caper' package in R (Orme, 2013). We used the maximum likelihood value of Pagel's λ (Pagel, 1999) in all PGLS analyses (Freckleton et al., 2002).

We ran PGLS models to test the effects of nocturnality within lizards as a whole, within the Gekkota and within the largest gecko sub-clade, the Gekkonidae. In all these analyses we examined the effect of activity time on longevity, correcting for body size, sample size and phylogenetic non-independence. All means are presented ± 1 standard error. We validated that our models did not violate the assumption of normality of the residuals by running a Shapiro Wilks test for deviation from normality on the model residuals. We used a Breusch-Pagan test to examine whether the error variance is dependent on the values of the predictor variables (in which case $p < 0.05$; Breusch and Pagan, 1979). The residuals were not normally distributed (Shapiro-Wilk normality test; p -value < 0.0001), and there was heteroscedasticity present (Breusch-Pagan test; p -value = 0.02). We thus \log_{10} transformed values of maximum longevity, body mass and sample size. In the resulting PGLS model the residuals were not statistically different from normal (p -value = 0.15) and showed no significant heteroscedasticity (p -value = 0.08). We thus proceeded with \log_{10} transformed variables. All statistical analyses were performed in R 3.6.0 (R Core Team, Vienna, Austria) using RStudio (1.1.463, RStudio Inc., Boston, MA, USA).

Results

Longevity in geckos and other clades

The mean longevity of all the gekkotan species we analysed was 10.1 ± 0.6 years, ranging from 13 months in *Pachydactylus bicolor* (Slavens and Slavens, 1994) to 53 years in *Woodworthia brunnea* (Hare and Cree, 2016). This mean is very similar to the mean longevity of all the non-gekkotan species, 10.3 ± 0.4 years (range: from nine months in *Psammomodromus hispanicus*; Bauwens and Diaz-Uriarte, 1997, to 69 years in *Cyclura lewisi*; Henderson and Powell, 2009). Geckos thus have similar mean, range and median ($\bar{x} = 8.0$ years, for both groups) longevity to those of other lizards.

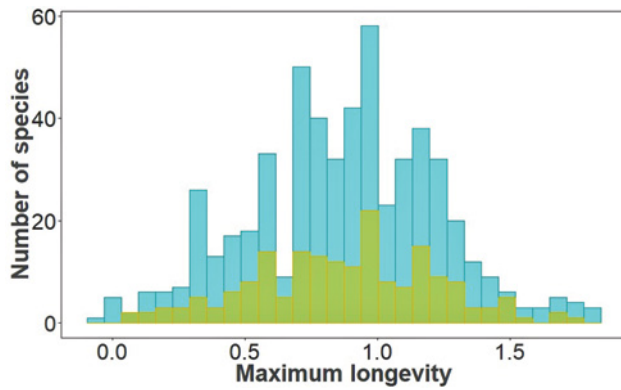


Figure 1. Distribution of the (\log_{10}) maximum longevity (in years) of the 740 lizard species. Gekkota species ($n = 185$) are represented by the green columns, and the non-gekkotan species ($n = 555$) are represented by the blue columns.

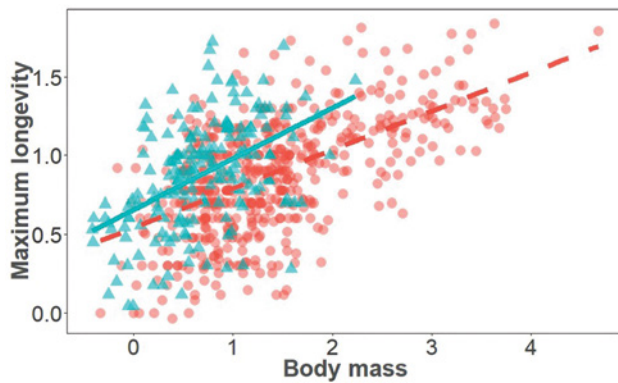


Figure 2. The relationship between maximum longevity (in years, \log_{10} transformed), and body mass (in grams, \log_{10} transformed) between gekkotan species and all the rest of the lizard clades. Gekkotan species ($n = 185$) are depicted in blue triangles (continuous blue line), and non-gekkotan lizards ($n = 555$) are depicted in red circles (red dashed line).

They are much smaller, however, than most other lizards (average: 4.76 ± 0.03 g in our data vs. 18.6 ± 0.03 g for other lizards), and the frequency distribution of their longevity is more uniform (Fig. 1).

Accounting for body size and phylogeny, we found that gekkotan species live longer than other lizards (intercept 0.740 ± 0.073 vs. 0.504 ± 0.093 ; $t = 31.43$, $df = 738$, $P < 0.0001$). Moreover, the allometric slope for gekkotan

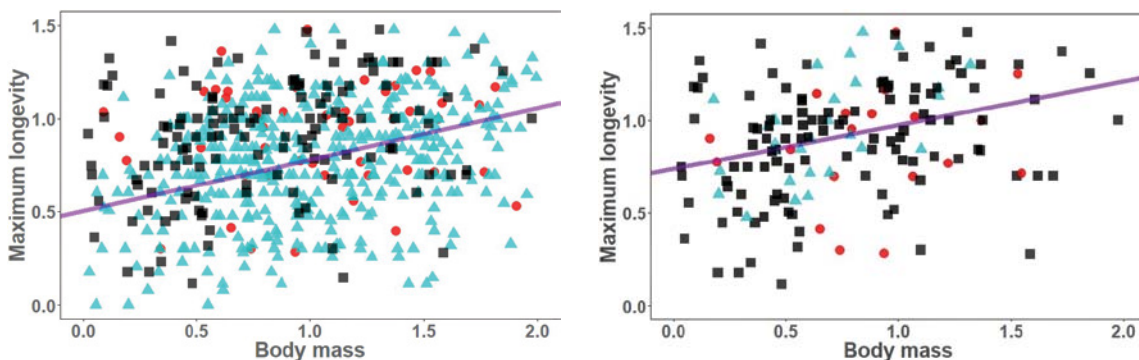


Figure 3. The relationship between maximum longevity (in years, \log_{10} transformed), and body mass (in grams, \log_{10} transformed), across activity levels (diurnal: cyan triangles; nocturnal: black squares; cathebral: red circles). Regression lines (purple) are for all species. (A) All lizards, (B) Gekkotan species only.

species (0.276 ± 0.021) is steeper than that for non-gekkotans (0.236 ± 0.049 ; difference = 0.040 ± 0.003 , $t = 15.45$, $P < 0.0001$). Such, differences thus increase with animal size (i.e. small geckos outlive small lizards by only a little, while large geckos outlive by a greater factor; Fig. 2). When analysing only species for which longevity data are based on large samples (>30 specimens per species, 221 species), we obtained a qualitatively similar result for the intercept, and the allometric slope for the Gekkota was even steeper than that for other lizard clades (see Table A1 and Supplementary Fig. S1 in Supplementary Appendix S2.1).

Nocturnality and longevity

The mean longevity of diurnal lizards were similar to those of nocturnal and cathebral lizards (Table 1, Fig. 3).

Table 1. Longevitys in relation to activity times (Nocturnal, diurnal and cathebral) for all lizard species and for Gekkota.

Clade	Activity time	Mean longevity ± 1 SE	n
All lizards	Nocturnal	10.8 ± 0.7	143
	Diurnal	10.0 ± 0.4	540
	Cathebral	11.1 ± 1.1	57
Gekkota	Nocturnal	10.5 ± 0.8	122
	Diurnal	9.7 ± 1.3	42
	Cathebral	8.7 ± 1.4	21

Table 2. The phylogenetic model for longevity of all lizards (including the Gekkota), testing the effect of all levels of activity times on longevity, while correcting for body mass and sample size (all \log_{10} transformed).

Factor	Estimate	SE	t	P
Body mass (grams)	0.248	0.022	11.0	<0.0001
Activity time (nocturnal)	0.504	0.103	0.3	
Activity time (diurnal)	0.488	0.097	0.3	0.734
Activity time (cathebral)	0.559	0.104	1.5	0.121
Sample size	0.077	0.010	7.2	<0.0001

Estimates for body mass and sample size, are slopes. Estimates for the activity times are intercepts.

P values are for differences from zero for mass and sample size, and for differences of diurnal and cathebral species, in turn, from nocturnal species.

Model $R^2 = 0.26$, $n = 740$, $\lambda = 0.676$ (95% CI: 0.538, -0.781), $p < 0.0001$.

Table 3. The model for the Gekkota infraorder, testing the effect of all levels of activity times on longevity, while correcting for body mass and sample size (all log10 transformed).

Factor	Estimate	SE	t	P
Body mass (grams)	0.250	0.055	4.5	<0.0001
Activity time (nocturnal)	0.626	0.078	0.1	
Activity time (diurnal)	0.629	0.088	0.1	0.965
Activity time (cathe- meral)	0.646	0.100	0.1	0.844
Sample size	0.116	0.023	5.0	<0.0001

Estimates for body mass and sample size, are slopes. Estimates for the activity times are intercepts.

P values are for differences from zero for mass and sample size, and for differences of diurnal and cathe-
meral species, in turn, from nocturnal species.

Model $R^2 = 0.30$, $n = 185$, $\lambda = 0.518$ (95% CI: 0.223, -0.754), $p < 0.0001$.

Table 4. The model for the family Gekkonidae, testing the effect of all levels of activity times on longevity, while correcting for body mass and sample size (all log10 transformed)..

Factor	Estimate	SE	t	P
Body mass (grams)	0.242	0.076	3.1	0.002
Activity time (nocturnal)	0.628	0.080	1.5	
Activity time (diurnal)	0.465	0.104	-1.5	0.136
Activity time (cathe- meral)	0.527	0.122	0.4	0.635
Sample size	0.142	0.035	4.0	0.0001

Estimates for body mass and sample size, are slopes. Estimates for the activity times are intercepts.

P values are for differences from zero for mass and sample size, and for differences of diurnal and cathe-
meral species, in turn, from nocturnal species.

Model $R^2 = 0.42$, $n = 87$, $\lambda = 0.458$ (95% CI: 0.040, -1.000), $p < 0.0001$.

Across all lizards, body mass and sample size were associated with lizard maximum lifespan (Table 2), but activity times were not. When we analysed only species with >30 specimens ($n = 221$), body size (but not sample size or activity time) was the only factor correlated with longevity. Moreover, activity time did not influence longevity among the Scincidae (see Tables A2–4 in Supplementary Appendices S2.2 and 2.3).

The model for the Gekkota revealed no relationship between longevity and activity times; however, body mass and sample size were positively correlated with gecko longevity (Table 3). When analysing only species ($n = 41$) for which longevity data were based on a large sample ($n > 30$), body size (but not sample size or activity time) was the only factor correlated with longevity (see Table A5 in Supplementary Appendix S2.3).

The model only for the family Gekkonidae revealed the same qualitative results as the models for the Gekkota and for lizards as a whole, with activity time not influencing lifespan (Table 4). Examining only species ($n = 14$) for which longevity data were based on a large sample ($n > 30$), resulted in no significant association between longevity and any other tested factors (including body mass and sample size) and no phylogenetic signal – presumably

because of the small sample size (see Table A6 in Supplementary Appendix S2.3).

Discussion

We found that geckos indeed demonstrate higher maximum longevity than similar-sized lizards from other clades. However, nocturnality did not emerge as an important predictor of longevity, either in lizards as a whole, in gekkotans as a whole or in members of the Gekkonidae (or in skinks). Our initial prediction, derived from the evolutionary theories of senescence (Medawar, 1952; Hamilton, 1966; Kirkwood, 1977; Kirkwood and Austad, 2000), that nocturnality would promote longer lives, is therefore refuted. Although nocturnality may reduce exposure to intense solar radiation, thereby reducing body temperature (Kearney and Predavec, 2000) and consequently lowering metabolic rate, it did not appear to influence longevity in any of the groups we tested. The findings in Stark et al. (2018) and in the present study are thus consistent: activity pattern and maximum longevity are not associated. Our present findings confirm that, regardless of the taxonomic scope, nocturnality does not drive a longer lifespan in lizards.

Although high doses of UV radiation (at least UVC) may be harmful to animals (and reptiles specifically), some UV radiation is probably beneficial to lizards (and geckos are no exception). First, it enables them to grow and develop more efficiently and regulates the way in which they forage for food, reproduce or communicate with other individuals of the same species (Ferguson et al., 2010). Moreover, it benefits reptiles specifically by means of synthesizing vitamin D3, which helps them to absorb calcium and build a stronger skeleton (Adkins et al., 2003).

This may also be that the reason why we could not find any differences between the lifespans of nocturnal, diurnal, and cathe-
meral species: i.e., diurnal lizards (including geckos) have evolved morphological and physiological traits that promote higher resistance to UV radiation. While nocturnal geckos often possess relatively transparent skin, with reduced peritoneal pigmentation (e.g., Boulenger, 1885, p. 5; Doughty, 1997; Aaron Bauer, pers. comm.), the skin of diurnal lizards is usually much more strongly keratinized, with stronger peritoneal pigmentation (Bauer and Meiri, unpublished). Thicker skin and scales, more highly-keratinized skin and darker pigmentation may counter the effects of UV radiation (e.g., Häder, 2001; Singaravelan et al., 2008; Jablonski and Chaplin, 2010; Wasmann et al., 2010). Furthermore, many diurnal species are thigothermic, avoiding direct solar radiation (Garrick, 2008). It would be interesting to examine whether the former live longer than heliothermic species.

Despite the fact that nights are typically cooler than days at a given location, nocturnal lizard species are generally absent from cold regions, that are nonetheless inhabited by diurnal species (Vidan et al., 2017). Nocturnal species may employ diurnal, ‘cryptic’ basking (elevating body temperature via seeking cover near the surface, or seeking cover in warm places while keeping out of direct sunlight), in order to increase their metabolic rate. We suggest that cellular repair mechanisms may be less efficient at

the lower temperatures (Roos and Vincent, 1998) in which nocturnal geckos are active. This may negate the advantages that nocturnal species might have enjoyed due to their lower metabolic rates (Addo-Bediako et al., 2002). Another possibility to explain our null results is that intrinsic mortality may exert a relatively weaker selection pressure on the evolution of maximum longevity than extrinsic mortality. Mortality agents such as predation, intense intraspecific competition and extreme famine may play a major part in shaping the variation in longevity among small animals such as lizards (Stark et al., 2018), with intrinsic factors (e.g., those associated with nocturnality) playing a minor role. For example, predatory species may have become nocturnal in order to access more prey and avoid competition with diurnal animals (Healy et al., 2014), resulting in high predation pressure during the night and leading in turn to a shorter lifespan in nocturnal animals. It may also be that many diurnal species are preyed upon, while sleeping, by nocturnal predators (e.g., the vine snake, *Ahetulla nasuta* preys at night upon diurnal lizards when they sleep exposed on branches; Webb et al., 2010), and vice versa. This can cause mortality rates to be similar across the diel cycle. We have no direct data on predation rates, radiation effects or the efficacy of cellular repair mechanisms that would allow us to test any of these hypotheses.

In conclusion, our results do not support the evolutionary hypotheses of senescence that have been proposed to explain the variation in longevity among and within animal groups (Medawar, 1952; Hamilton, 1966; Kirkwood, 1977; Kirkwood and Austad, 2000). Nocturnality does not select for longer lifespan either in geckos or in other lizards. The non-significant relationship between lifespan and activity pattern in the Gekkota infraorder and the Gekkonidae family, suggests that the different activity patterns of reptilian species is indeed not a determinant of their variation in maximum longevity. Our study (and previous ones, such as Stark et al., 2018) offers a preliminary investigation into the relationship between nocturnality and longevity with the hope that future studies may gain a deeper, understanding of the possible mechanisms (such as predation or intraspecific competition rates in each habitat in which a species dwells) driving longevity in reptiles in general and in geckos in particular.

Acknowledgements

We thank Simon Jamison for constructive discussion and Maria Novosolov for assistance in statistical modelling. We thank Yuval Itescu and an anonymous referee for comments on a previous draft of this manuscript. We thank Erez Maza from the Steinhardt Museum of Natural History in Tel Aviv University for the help with the museum specimens. We are grateful to Naomi Paz for English editing on an earlier draft of the manuscript.

Supplementary material

Supplementary material is available online at: <https://doi.org/10.6084/m9.figshare.11347007>

References

- Addo-Bediako, A., Chown, S. L., & Gaston, K. J. (2002). Metabolic cold adaptation in insects: a large-scale perspective. *Funct. Ecol.*, 16, pp. 332–338.
- Adkins, E., Driggers, T., Ferguson, G., Gehrmann, W., Gyimesi, Z., May, E., ... & Klaphake, E. (2003). Ultraviolet light and reptiles, amphibians. *J. Herpetol. Med. Surg.*, 13, pp. 27–37.
- Atanasov, A. T. (2005). The linear allometric relationship between total metabolic energy per life span and body mass of poikilothermic animals. *Biosystems*, 82, pp. 137–142.
- Autumn, K., & De Nardo, D. F. (1995). Behavioral thermoregulation increases growth rate in a nocturnal lizard. *J. Herpetol.*, 29, pp. 157–162.
- Autumn, K. (1999). Secondly diurnal geckos return to cost of locomotion typical of diurnal lizards. *Physiol. Biochem. Zool.*, 72, pp. 339–351.
- Autumn, K., Weinstein, R. B., & Full, R. J. (1994). Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiol. Zool.*, 67, pp. 238–262.
- Autumn, K., Jindrich, D., DeNardo, D., & Mueller, R. (1999). Locomotor performance at low temperature and the evolution of nocturnality in geckos. *Evolution*, 53, pp. 580–599.
- Bauer, A. (2007). *The foraging biology of the Gekkota: Life in the middle*. In S. Reilly, L. McBrayer, & D. Miles (Eds.), *Lizard Ecology* (pp. 371–404). Cambridge: Cambridge University Press. doi:10.1017/CBO9780511752438.014.
- Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of life-history traits in lacertid lizards: a comparative study. *Am. Nat.*, 149, pp. 91–111.
- Benjamin, D. J., Berger, J. O., Johannesson, M., Nosek, B. A., Wagenmakers, E. J., Berk, R et al. (2018). Redefine statistical significance. *Nat. Hum. Behav.*, 2, pp. 6–10.
- Boulenger, G. A. (1885). *Catalogue of the Lizards in the British Museum* (Nat. Hist.) I. Geckonidae, Eublepharidae, Uroplattidae, Pygopodidae, Agamidae. London: Trustees of the British Museum.
- Breusch, T. S., & Pagan, A. R. (1979). A simple test for heteroscedasticity and random coefficient variation. *Econometrica*, 47, pp. 1287–1294.
- Carey, J. R. (2003). *Longevity: the biology and demography of life span*. Princeton University Press. USA.
- Caswell, H. (2007). Extrinsic mortality and the evolution of senescence. *Trends Ecol. Evol.*, 22, pp. 173–174.
- Doughty, P. (1997). The effects of “fixed” clutch sizes on lizard life-histories: reproduction in the Australian velvet gecko, *Oedura lesueurii*. *J. Herpetol.*, 31, pp. 266–272.
- Emerling, C. A., Huynh, H. T., Nguyen, M. A., Meredith, R. W., & Springer, M. S. (2015). Spectral shifts of mammalian ultraviolet-sensitive pigments (short wavelength-sensitive opsin 1) are associated with eye length and photic niche evolution. *Proc. Biol. Sci.*, 282, pp. 20151817.
- Faruki, S. I., Das, D. R., & Khatun, S. (2005). Effects of UV-radiation on the larvae of the lesser mealworm, *Alphitobius diaperinus* (Panzer)(Coleoptera: Tenebrionidae) and their progeny. *Pak. J. Biol. Sci.*, 5, pp. 444–448.
- Feldman, A., Sabath, N., Pyron, R. A., Mayrose, I., & Meiri, S. (2016). Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Glob. Ecol. Biogeogr.*, 25, pp. 187–197.
- Ferguson, G. W., Brinker, A. M., Gehrmann, W. H., Bucklin, S. E., Baines, F. M., & Mackin, S. J. (2010). Voluntary exposure of some western-hemisphere snake and lizard species to Ultraviolet-B radiation in the field: how much Ultraviolet-B should a lizard or snake receive in captivity? *Zoo Biol.*, 29, pp. 317–334.
- Francis, A. A., Lee, W. H., & Regan, J. D. (1981). The relationship of DNA excision repair of ultraviolet-induced lesions to the maximum life span of mammals. *Mech. Ageing Dev.*, 16, pp. 181–189.

- Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.*, 160, pp. 712–726.
- Gamble, T., Greenbaum, E., Jackman, T. R., & Bauer, A. M. (2015). Into the light: diurnality has evolved multiple times in geckos. *Biol. J. Linn. Soc.*, 115, pp. 896–910.
- Garrick, D. (2008). Body surface temperature and length in relation to the thermal biology of lizards. *Biosci. Horizons*, 1, pp. 136–142.
- Ghanem, I., & Shamma, M. (2007). Effect of non-ionizing radiation (UVC) on the development of *Trogoderma granarium* Everts. *J. Stored Prod.*, 43, pp. 362–366.
- Häder, D. P. (2001). *Adaptation to UV stress in algae*. In *Algal adaptation to environmental stresses* (pp. 173–202). Springer, Berlin, Heidelberg.
- Hamilton, W. D. (1966). The moulding of senescence by natural selection. *J. Theor. Biol.*, 12, pp. 12–45.
- Hare, K. M., Pledger, S., Thompson, M. B., Miller, J. H., & Daugherty, C. H. (2010). Nocturnal lizards from a cool-temperate environment have high metabolic rates at low temperatures. *J. Comp. Physiol. B*, 180, pp. 1173–1181.
- Hare, K. M., & Cree, A. (2016). *Thermal and metabolic physiology of New Zealand lizards*. In *New Zealand Lizards* (pp. 239–267). Springer, Cham.
- Hart, R. W., Setlow, R. B., & Woodhead, A. D. (1977). Evidence that pyrimidine dimers in DNA can give rise to tumors. *Proc. Natl. Acad. Sci. U.S.A.*, 74, pp. 5574–5578.
- Healy, K., Guillerme, T., Finlay, S., Kane, A., Kelly, S.B.A., McClean, D. et al. (2014). Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. Lond., B, Biol. Sci.*, 281, pp. 20140298.
- Heidari, N., Sedaratian-Jahromi, A., & Ghane-Jahromi, M. (2016). Possible effects of Ultraviolet ray (UV-C) on biological traits of *Callosobruchus maculatus* (Col.: Chrysomelidae). *J. Stored Prod.*, 69, pp. 91–98.
- Henderson, R.W. & Powell, R. (2009). *Natural History of West Indian Reptiles and Amphibians*. University Press of Florida, Gainesville, Florida, U.S.A. 495 pp.
- Holmes, D. J., & Austad, S. N. (1994). Fly now, die later: life-history correlates of gliding and flying in mammals. *J. Mammal.*, 75, pp. 224–226.
- Hori, M., Shibuya, K., Sato, M., & Saito, Y. (2014). Lethal effects of short-wavelength visible light on insects. *Sci. Rep.*, 4, pp. 7383.
- Huey, R. B., Niewiarowski, P. H., Kaufmann, J., Herron, J. & C. (1989). Thermal biology of nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures? *Physiol. Zool.* 62, pp. 488–504.
- Jablonski, N. G., & Chaplin, G. (2010). Human skin pigmentation as an adaptation to UV radiation. *Proc. Natl. Acad. Sci. U.S.A.*, 107, pp. 8962–8968.
- Kapahi, P., Chen, D., Rogers, A. N., Katewa, S. D., Li, P. W. L., Thomas, E. L., & Kockel, L. (2010). With TOR, less is more: a key role for the conserved nutrient-sensing TOR pathway in aging. *Cell Metab.*, 11, pp. 453–465.
- Kearney, M., & Predavec, M. (2000). Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology*, 81, pp. 2984–2996.
- Kirkwood, T. B. (1977). Evolution of ageing. *Nature*, 270, pp. 301–304.
- Kirkwood, T. B., & Austad, S. N. (2000). Why do we age? *Nature*, 408, pp. 233–238.
- Ku, H. H., Brunk, U. T., & Sohal, R. S. (1993). Relationship between mitochondrial superoxide and hydrogen peroxide production and longevity of mammalian species. *Free Radic. Biol. Med.*, 15, pp. 621–627.
- Lah, E. F. C., Musa, R. N. A. R., & Ming, H. T. (2012). Effect of germicidal UV-C light (254 nm) on eggs and adult of house dustmites, *Dermatophagoides pteronyssinus* and *Dermatophagoides farinae* (Astigmata: Pyroglyphidae). *Asian. Pac. J. Trop. Biomed.*, 2, pp. 679–683.
- Ley, R. D. (1985). Photoreactivation of UV-induced pyrimidine dimers and erythema in the marsupial *Monodelphis domestica*. *Proc. Natl. Acad. Sci. U.S.A.*, 82, pp. 2409–2411.
- Magalhães, J. P. D., Costa, J., & Church, G. M. (2007). An analysis of the relationship between metabolism, developmental schedules, and longevity using phylogenetic independent contrasts. *J. Gerontol. A Biol. Sci. Med. Sci.*, 62, pp. 149–160.
- Medawar, P. B. (1952). *An unsolved problem of biology* (pp. 24). London: H. K. Lewis.
- Meiri, S. (2007). Size evolution in island lizards. *Glob. Ecol. Biogeogr.*, 16, pp. 702–708.
- Meiri, S. (2010). Length–weight allometries in lizards. *J. Zool.*, 281, pp. 218–226.
- Meiri, S. (2018). Traits of lizards of the world: variation around a successful evolutionary design. *Glob. Ecol. Biogeogr.*, 27, pp. 1168–1172.
- Meiri, S. (2020). What geckos are – an ecological-biogeographic perspective. *Isr. J. Ecol. Evol.*
- Møller, A. P. (2008). Relative longevity and field metabolic rate in birds. *J. Evol.*, 21, pp. 1379–1386.
- Norris, A.L., Kunz, T.H., (2012). *Effects of solar radiation on animal thermoregulation*. In: Babatunde, E.B. (Ed.), *Solar Radiation*. InTech, Croatia, pp. 195–220.
- O’Brien, R. M. (2007). A caution regarding rules of thumb for variance inflation factors. *Qual. Quant.*, 41, pp. 673–690.
- Orme, D. (2013). The caper package: comparative analysis of Phylogenetics and evolution in R. *R package version*, 5, pp. 1–36.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, pp. 877.
- Paul, N. D., & Gwynn-Jones, D. (2003). Ecological roles of solar UV radiation: towards an integrated approach. *Trends Ecol. Evol.*, 18, pp. 48–55.
- Pianka, E. R., & Huey, R. B. (1978). Comparative ecology, resource utilization and niche segregation among gekkonid lizards in the southern Kalahari. *Copeia*, 1978, pp. 691–701.
- Pinto, B. J., Nielsen, S. V. and Gamble, T. (2019). Transcriptomic data support a nocturnal bottleneck in the ancestor to gecko lizards. *Mol. Phylogenetics Evol.* 141, pp. 106639.
- Promislow, D. E., & Harvey, P. H. (1990). Living fast and dying young: A comparative analysis of life-history variation among mammals. *J. Zool.*, 220, pp. 417–437.
- Rastogi, R. P., Kumar, A., Tyagi, M. B., & Sinha, R. P. (2010). Molecular mechanisms of ultraviolet radiation-induced DNA damage and repair. *J. Nucleic Acids*, 2010, pp. 32.
- Röll, B. (2001). Multiple origin of diurnality in geckos: evidence from eye lens crystallins. *Naturwissenschaften*, 88, pp. 293–296.
- Roos, J. C., & Vincent, W. F. (1998). Temperature dependence of UV radiation effects on Antarctic cyanobacteria. *J. Phycol.*, 34, pp. 118–125.
- Scharf, I., Feldman, A., Novosolov, M., Pincheira-Donoso, D., Das, I., Böhm, M., Uetz, P., Torres-Carvajal, O., Bauer, A., Roll, U. and Meiri, S., (2015). Late bloomers and baby boomers: ecological drivers of longevity in squamates and the tuatara. *Glob. Ecol. Biogeogr.*, 24, pp. 396–405.
- Schott, R. K., Bhattacharyya, N. and Chang, B. S. W. (2019). Evolutionary signatures of photoreceptor transmutation in geckos reveal potential adaptation and convergence with snakes. *Evolution* 73, pp. 1958–1971.
- Singaravelan, N., Grishkan, I., Beharav, A., Wakamatsu, K., Ito, S., & Nevo, E. (2008). Adaptive melanin response of the soil fungus *Aspergillus niger* to UV radiation stress at “Evolution Canyon”, Mount Carmel, Israel. *PLoS one*, 3, pp. e2993.
- Sinha, R. P. & Häder, D.-P. (2002). UV-induced DNA damage and repair: a review. *Photochem. Photobiol. Sci.* 2002, pp. 225–236
- Snell, K. R., Kokubun, T., Griffiths, H., Convey, P., Hodgson, D. A., & Newsham, K. K. (2009). Quantifying the metabolic cost to an Antarctic liverwort of responding to an abrupt

- increase in UVB radiation exposure. *Glob. Change Biol.*, 15, pp. 2563–2573.
- Sohal, R. S. (1986). *The rate of living theory: a contemporary interpretation*. In *Insect aging* (pp. 23–44). Springer, Berlin, Heidelberg.
- Sohal, R. S., Svensson, I., Sohal, B. H., & Brunk, U. T. (1989). Superoxide anion radical production in different animal species. *Mech. Ageing Dev.*, 49, pp. 129–135.
- Southworth, L. O., Holick, M. F., Chen, T. C., & Kunz, T. H. (2013). Effects of sunlight on behavior and 25-hydroxyvitamin D levels in two species of Old-World fruit bats. *Dermatoendocrinology*, 5, pp. 192–198.
- Speakman, J. R. (2005). Body size, energy metabolism and lifespan. *J. Exp. Biol.*, 208, pp. 1717–1730.
- Stapp, P. (1994). Can predation explain life-history strategies in mammalian gliders?. *J. Mammal.*, 75, pp. 227–228.
- Stark, G., & Meiri, S. (2018). Cold and dark captivity: Drivers of amphibian longevity. *Glob. Ecol. Biogeogr.*, 27, pp. 1384–1397.
- Stark, G., Karin, T., Itescu, Y., Feldman, A., Meiri, S. (2018). Cold and isolated ectotherms: drivers of reptilian longevity. *Biol. J. Linn. Soc.*, 125, pp. 730–740.
- Tattersall, I. (1987). Cathemeral activity in primates: a definition. *Folia Primatol.*, 49, pp. 200–202.
- Tidière, M., Gaillard, J. M., Berger, V., Müller, D. W., Lackey, L. B., Gimenez, O., ... & Lemaître, J. F. (2016). Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. *Sci. Rep.*, 6, pp. 36361.
- Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W., & Pyron, R. A. (2016). Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biol. Conserv.*, 204, pp. 23–31.
- Uetz, P., Freed, P. & Hošek, J. (eds.) (2019). *The Reptile Database*, <http://www.reptile-database.org>, accessed [16/07/2019].
- Valcu, M., Dale, J., Griesser, M., Nakagawa, S., & Kempenaers, B. (2014). Global gradients of avian longevity support the classic evolutionary theory of ageing. *Ecography*, 37, pp. 930–938.
- Vidan, E., Roll, U., Bauer, A., Grismer, L., Guo, P., Maza, E., Novosolov, M., Sindaco, R., Wagner, P., Belmaker, J. & Meiri, S., (2017). The Eurasian hot nightlife: Environmental forces associated with nocturnality in lizards. *Glob. Ecol. Biogeogr.*, 26, pp. 1316–1325.
- Wassmann, M., Moeller, R., Reitz, G., & Rettberg, P. (2010). Adaptation of *Bacillus subtilis* cells to Archean-like UV climate: relevant hints of microbial evolution to remarkably increased radiation resistance. *Astrobiology*, 10, pp. 605–615.
- Webb, J. K., Pike, D. A., & Shine, R. (2009). Olfactory recognition of predators by nocturnal lizards: safety outweighs thermal benefits. *Behav. Ecol.*, 21, pp. 72–77.
- Werner, Y. L., & Seifan, T. (2006). Eye size in geckos: asymmetry, allometry, sexual dimorphism, and behavioural correlates. *J. Morphol.*, 267, pp. 1486–1500.
- Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. *Evolution*, 11, pp. 398–411.
- Williams, P. D., & Day, T. (2003). Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. *Evolution*, 57, pp. 1478–1488.
- Williams, P. D., Day, T., Fletcher, Q., & Rowe, L. (2006). The shaping of senescence in the wild. *Trends Ecol. Evol.*, 21, pp. 458–463.
- Wright, A. F., Jacobson, S. G., Cideciyan, A. V., Roman, A. J., Shu, X., Vlachantoni, D., ... & Riemersma, R. A. (2004). Lifespan and mitochondrial control of neurodegeneration. *Nat. Genet.*, 36, pp. 1153–1158.
- Zhang, C. Y., Meng, J. Y., Wang, X. P., Zhu, F. & Lei, C. L. (2011). Effects of UV-A exposures on longevity and reproduction in *Helicoverpa armigera* and on the development of its F1 generation. *Insect Sci.* 18, pp. 697–702.
- Zheng, Y., & Wiens, J. J. (2016). Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Mol. Phylogenet. Evol.*, 94, pp. 537–547.