Brain size, ecology and sociality: a reptilian perspective

GILLES DE MEESTER[1,*,](), KATLEEN HUYGHE[1] and RAOUL VAN DAMME[1]

[1]*Functional Morphology Group, Department of Biology, University of Antwerp, Wilrijk, Belgium*

It is often hypothesized that larger brains evolved to deal with environmental complexity, by means of enhanced cognition and behavioural flexibility. Decades of research have tried to relate relative brain size to either habitat or social complexity, but often with conflicting results. Which selective pressures favour larger brains and whether they act in the same way in different taxa is unclear, especially given that the majority of studies focused on either mammals or birds. We present the first large-scale comparative study investigating the effect of habitat and social complexity on evolution of brain size in Squamata (lizards and snakes), using a dataset of 171 species. Our analyses confirmed earlier findings that both the degree of limb reduction and the biogeographical origin of a species affect relative brain size and should be controlled for. Habitat complexity had no effect on brain size, and solitary species had larger brains than social species. These results suggest that different selective forces might drive evolution of brain size in Squamata compared with other taxa. Future comparative studies should also consider using other, non-traditional, taxa. This will contribute to a more comprehensive understanding of how the vertebrate brain evolved.

ADDITIONAL KEYWORDS: brain size – comparative method – habitat complexity –social brain hypothesis – sociality – Squamata.

INTRODUCTION

Biologists have long been fascinated by the question of why some species have relatively larger brains than others (Jerison, 1973). It is often postulated that enhanced cognition, and therefore higher behavioural flexibility, is the major advantage of possessing a large brain (Iwaniuk, 2017). Indeed, relative brain size has been positively associated with several cognitive aspects in different taxa (Reader & Laland, 2002; Lefebvre *et al.*, 2004; Benson-Amram *et al.*, 2016; but see: Healy & Rowe, 2007; MacLean *et al.*, 2014). Nevertheless, given the high energetic cost of brain tissue (expensive brain hypothesis: Aiello & Wheeler, 1995; Isler & van Schaik, 2006; Heldstab *et al.*, 2018), selection should favour larger brains only if the cognitive benefits outweigh the costs (Sol, 2009; Benson-Amram *et al.*, 2016).

It is often hypothesized that larger brains will enable species to deal with more complex information and will therefore be selected for in species with cognitively demanding lifestyles or habitats (Harvey & Krebs, 1990; Safi *et al.*, 2005; Lefebvre & Sol, 2008; Sol, 2009; Sobrero *et al.*, 2016). In particular, those species living in complex three-dimensional, heterogeneous environments (e.g. saxicolous or arboreal species) would be expected to evolve larger brains, in order to process a surplus of environmental information (Bennet & Harvey, 1985; Harvey & Krebs, 1990; Safi & Dechmann, 2005) and to find and exploit more diverse and heterogeneously distributed resources (Petren & Case, 1998; Delarue *et al.*, 2015; Steck *et al.*, 2018). Such species will also benefit from improved spatial memory (Safi & Dechmann, 2005; Shumway, 2008; Powell & Leal, 2014; White & Brown, 2015; Sobrero *et al.*, 2016; Calisi *et al.*, 2017) and better motor coordination, navigation and manoeuvrability (Bennet & Harvey, 1985; Taylor *et al.*, 1995; Calisi *et al.*, 2017; Stankowich & Romero, 2017). Larger brains are indeed associated with structural habitat complexity in fish (Pollen *et al.*, 2007; Shumway, 2008), frogs (Taylor *et al.*, 1995), birds (Bennet & Harvey, 1985) and mammals (Harvey *et al.*, 1980; Eisenberg & Wilson, 1981; Meier, 1983; Bertrand *et al.*, 2017).

Environmental complexity may also include the social environment of an animal. Living in a group is cognitively demanding, owing to the necessity to maintain and memorise social relationships, and may, therefore, select for larger brains (Byrne & Whiten,

1988; Dunbar, 1998, 2009; Dunbar & Shultz, 2007, 2017; Perez-Barberia *et al.*, 2007). This social brain hypothesis (SBH) has found support in birds (Dunbar & Shultz, 2007; West, 2014), mammals (Shultz & Dunbar, 2006; Perez-Barberia et al., 2007; Fox *et al.*, 2017) and, especially, in primates (Byrne & Whiten, 1988; Dunbar, 1998; Dunbar & Shultz, 2007, 2017; Street *et al.*, 2017).

Nevertheless, a large number of studies have also failed to find a positive association between brain size and either habitat (Clutton-Brock & Harvey, 1980; Schuck-Paim *et al.*, 2008; Powell & Leal, 2014; Liao *et al.*, 2015; Powell *et al.*, 2017; Heldstab *et al.*, 2018) or social complexity (Finarelli & Flynn, 2009; MacLean *et al.*, 2014; Benson-Amram *et al.*, 2016; DeCasien *et al.*, 2017; Fedorova *et al.*, 2017; Powell *et al.*, 2017; Kverková *et al.*, 2018). Which selective forces shape variation in brain size is, therefore, still under discussion (Healy & Rowe, 2007; West, 2014). Given these diverse results, the context in which large brains evolve might differ among vertebrate taxa (Healy & Rowe, 2007). In particular, whether the SBH can be considered as a general rule for brain evolution, rather than being specific for primates, has been brought into question (Holekamp, 2007; Finarelli & Flynn, 2009; van der Bijl & Kolm, 2016; Kverková *et al.*, 2018). Unfortunately, most studies on brain size evolution appear to focus on either mammals or birds (Iwaniuk, 2017), which is a major weakness within the field of comparative cognition (Shettleworth, 2009).

The Squamata (lizards and snakes) provide an interesting opportunity to test the effect of environmental complexity on relative brain size. Squamata show immense ecological diversity and have adapted to a variety of lifestyles in a broad range of terrestrial ecosystems (Pianka & Vitt, 2003; Whiting *et al.*, 2018). Although often overlooked, Squamata also show varying levels of sociality, ranging from solitary species, through species that form transitory aggregations, to those living in stable associations with consistent membership across seasons or years (Mouton, 2011; Gardner *et al.*, 2016; Halliwell *et al.*, 2017; Whiting & While, 2017).

To date, brain evolution in Squamata has been studied in the context of sexual selection (Hoops *et al.*, 2017a), communication (Robinson *et al.*, 2015) and ecology (Powell & Leal, 2012, 2014; Allemand *et al.*, 2017; Hoops *et al.*, 2017b). Ecological studies, however, have mostly focused on brain morphology in specific taxa and rarely tested the differences in whole brain size. We hereby present the first large-scale comparative study investigating the effect of habitat complexity and sociality on brain size evolution within Squamata, using a dataset of 171 species. We hypothesize that arboreal and saxicolous species have relatively larger brains compared with fossorial and ground-dwelling species, and that social species have relatively larger brains than solitary squamates. In addition, given that it is hypothesized that larger brains facilitate behavioural flexibility, large-brained species should be found in a broader range of habitats.

MATERIAL AND METHODS

DATA COLLECTION

Data on body and brain masses from 171 Squamata (155 lizards and 16 snakes) were obtained from the literature by searching for 'Squamata', 'lizard', 'snake', 'amphisbaenia' or 'reptile' in combination with 'brains', 'brain mass', 'brain size', 'brain volume', 'brain weight', 'encephalization' or 'brain-to-body ratio' in ISI Web of Science and Google Scholar (see Supporting Information, File S1). Brain and body mass data from the tuatara (*Sphenodon punctatus*) were also included. Both published and unpublished data (e.g. unpublished theses found in online university libraries) were used. Weighted averages were calculated if a species' brain mass was available from multiple sources. When data were sourced via experimental studies (e.g. bioaccumulation of pesticides), only data from the control group were used for further analyses. We only retained data from studies in which brains were dissected and either weighed directly, sectioned and measured or scanned using magnetic resonance imaging. Brain volumes were converted to brain masses, following the general assumption that 1 cm³ brain tissue weighs 1.036 g (Northcutt, 2013). Given that the brain mass/body mass ratio is known to vary with age (Patnaik & Jena, 1972), no data on juvenile specimens were used.

A common critique of comparative encephalization studies is the potential bias introduced by collecting brain data from multiple sources (Healy & Rowe, 2007). However, we found no evidence for such bias in our dataset. Brain size was significantly repeatable across different sources [mixed-effect model: $R = 0.9704$, 95% confidence interval (0.9703; 0.9735); log-likelihood ratio test: $\chi^2 = 19.93$; d.f. = 3; $P < 0.001$], and there was no significant influence of brain-measuring technique (wet weights vs. magnetic resonance imaging scans; mixed-effect model: $F_{1,7} = 0.187$; $P = 0.68$) within species for which brain data were available from multiple sources ($N = 8$).

HABITAT COMPLEXITY

Using scientific literature, species were classified into four ecological guilds, based on whether they are primarily active underground and actively burrowing

(fossorial, $N = 7$), on terrestrial surfaces (ground-dwelling, $N = 96$), on rock surfaces (saxicolous, $N = 20$) or in trees and shrubs (arboreal, $N = 48$). No brain data were found on completely aquatic species, and semi-aquatic species were classified according to their habitat use on land. Although these guilds are not always mutually exclusive, each species was classified according to how it was most commonly referred to in the literature.

SOCIALITY

Information on sociality was taken from the datasets of Gardner *et al.* (2016) and Halliwell *et al.* (2017). Social species are species for which at least temporal aggregations have been reported in the literature ($N = 24$). Species were classified as solitary ($N = 44$) only if no aggregations have been reported for a particular species and if this species is well studied (for criteria, see Halliwell *et al.*, 2017). Data on sociality were available for only a subset of our data ($N = 68$).

HABITAT GENERALISM

Using field guides and literature data, we noted the presence or absence of each species in 13 habitat categories (see Supporting Information File S2, Supplementary Methods). The total number of categories in which a species occurred was used as an indicator of its ecological generalism (Stuart-Fox & Owens, 2003; Sol *et al.*, 2005; Ducatez *et al.*, 2015).

CONFOUNDING VARIABLES

As already suggested by Platel (1979) and recently confirmed by Heesy *et al.* (2017), limb reduction in Squamata is associated with a decrease in relative brain size. Therefore, for each species we noted the status of the limbs (absent, reduced or present; for details, see Supporting Information File S2, Supplementary Methods).

A second possible confounding variable is the geographical origin of the specimen. Previous research suggested that selection for larger or smaller brains might differ among biogeographical regions in reptiles (Amiel *et al.*, 2011). Biogeographical region of origin was, therefore, also included as an additional covariate (for details, see Supporting Information File S2, Supplementary Methods).

STATISTICS

The software program R v.3.5.1 (Ihaka, R. & Gentleman, R., University of Auckland, New Zealand) was used for all statistical analyses.

The time-calibrated phylogenetic tree constructed by Tonini *et al.* (2016), which combines molecular tools and taxonomic assignment, represents the most complete and most recent phylogeny of the Squamata and was, therefore, used as a basis for all further phylogenetic analyses. Before analyses, this tree was pruned to include only 172 species (including the tuatara outgroup) in our dataset, and polytomies were randomly resolved using the function *multi2di* in the R package *ape* (Paradis *et al.*, 2004).

Both body and brain mass were $\log_{10}$-transformed before all analyses, and the association between both variables was tested using a phylogenetic generalized least squares (PGLS) regression with the *gls* function in the *nlme* package (Pinheiro *et al.*, 2014) with Pagel correlation structure. The value for Pagel's λ was determined through maximum likelihood. Pagel's λ is a scaling parameter indicating how much similarity between species in a trait can be attributed to their relatedness (Pagel, 1999), and it ranges from zero (no phylogenetic signal) to one (strong phylogenetic signal). Given that brain and body mass were positively correlated (see Results), body mass was controlled for by including it as a covariate in all further statistical models. Residuals of the brain to body mass regression were used for visualization of the results.

The phylogenetic signals of absolute brain mass, absolute body mass and relative brain size (residuals from the brain to body mass regression) were calculated as Pagel's λ using the function *phylosignal* in the R package *phytools* (Revell, 2012). The phylogenetic signal for habitat generalism was calculated in the same way, but for ecological guild and sociality (categorical variables) the function *fitDiscrete* in the R package *geiger* (Harmon *et al.*, 2008) was used. The evolution of relative brain size was visualized by estimating the maximum likelihood ancestral states using the function *contMap* in the package *phytools* (Revell, 2012).

To test which ecological (habitat generalism + complexity) and social variables influenced brain size, we ran PGLS models to take phylogenetic relatedness of species into account, with brain mass as the response variable and body mass as the covariate (both $\log_{10}$-transformed). Separate models were run for the ecological and social variables because of differences in sample size. Owing to convergence problems with the social model when including limb status as a covariate, we tested the effect of sociality only in fully limbed species (51 of the 68 species for which social data was available). Limb status was, therefore, included as a fixed factor only in the ecological model, where biogeographical realm was a covariable in both models. *Sphenodon punctatus* was excluded from these analyses.

More information on methods and statistics can be found in the Supporting Information (File S2, Supplementary methods; also in File S3, R script with statistical models) .

RESULTS

Brain and body size data were obtained for 171 species of Squamata. Brain mass ranged from 0.0045 (*Lerista muelleri*) to 2.44 g (*Varanus niloticus*). Relative brain size also exhibited considerable variability, with *Anolis stratulus* and *Lerista bipes* having, respectively, the largest and smallest brains relative to their body size. There was a significant positive correlation between body mass and brain mass (slope = 0.578 ± 0.016; $F_{1,170}$ = 1309; $P < 0.001$, λ = 0.87; Fig. 1).

All morphological traits carried a strong phylogenetic signal (brain mass, λ = 0.94; body mass, λ = 0.91; residual brain size, λ = 0.87; all $P < 0.001$). Both ecological guild and sociality showed a high phylogenetic signal (λ of 0.95 and 1.00, respectively), whereas habitat generalism had a much lower (0.31) but still significant λ signal ($P < 0.001$). Given these strong phylogenetic signals in our dataset, the use of PGLS models seems appropriate. The ancestral state reconstruction for relative brain size is shown in Figure 2. A more detailed phylogenetic tree with ancestral state reconstruction and residual brain size
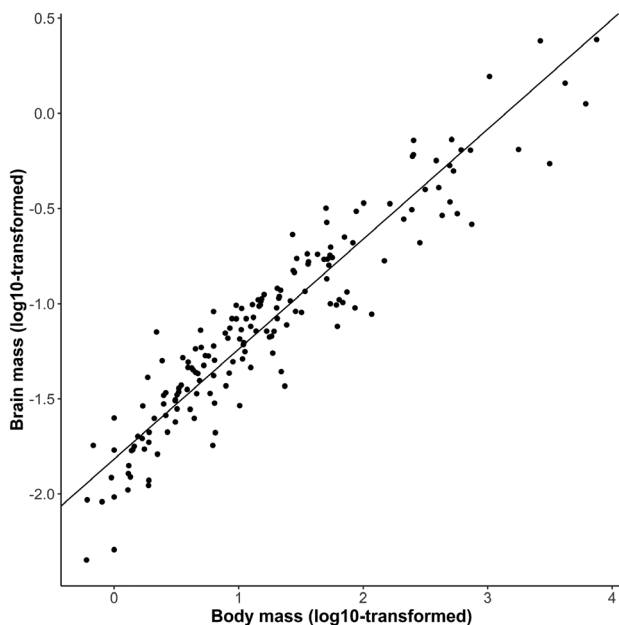
per species is presented in the Supporting Information (File S2, Fig. S1).

On average, arboreal species had the largest and fossorial species the smallest brains relative to their body sizes (Fig. 3). However, differences among ecological guilds were not statistically significant ($F_{3,157}$ = 1.98; $P = 0.12$; Table 1). Neither was there an association between relative brain size and habitat generalism (slope = −0.007 + 0.005; $F_{1,157}$ = 2.84; $P = 0.08$; Table 1). There was a significant effect of limb reduction on relative brain size ($F_{2,157}$ = 62.78; $P < 0.001$), because species with reduced or absent limbs had smaller brains relative to their body size (Fig. 4A). Relative brain size also differed significantly among biogeographical realms ($F_{6,157}$ = 4.40; $P < 0.001$; see Fig. 4B).
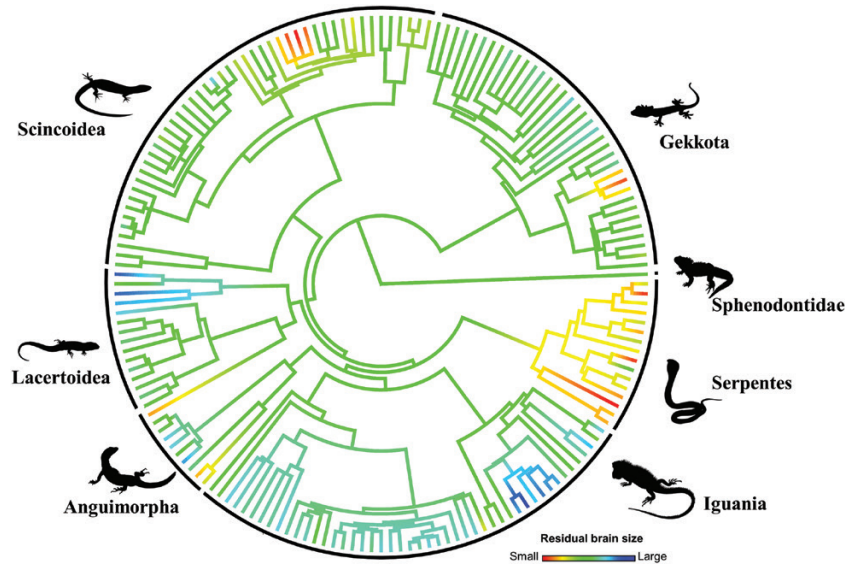
There was a significant effect of sociality on relative brain size in limbed Squamata ($F_{1,43}$ = 20; $P < 0.001$; Table 1). Surprisingly, species with a 'solitary' lifestyle had significantly larger brains relative to body size compared with 'social' species (Fig. 5). Biogeographical realm also had a significant effect on relative brain size in this subset of the data (Table 1). Given the surprising result of a negative value for Pagel's λ in this model, we re-analysed the data using both the *gls* function in the *nlme* package with restricted maximum likelihood optimization for λ and the *pgls* function in the *caper* package (Orme *et al.*, 2018). Both analyses suggested negative values for λ and gave similar results (Supporting Information File S2, Supplementary Results).

DISCUSSION

Decades of work have been dedicated to unravelling which ecological and social factors have driven the evolution of the brain, but the bulk of this work has focused on either mammals or birds. This taxonomic bias makes it difficult to understand whether the same selective forces have shaped brain size in different taxa and impedes a more complete picture of the evolution of the vertebrate brain.

Contrary to one of our main expectations, species living in more complex habitats did not have significantly larger brains than species living in simple habitats. Older studies often reported a positive effect of arboreality on relative brain size (Harvey *et al.*, 1980; Eisenberg & Wilson, 1981; Bennet & Harvey, 1985; Taylor *et al.*, 1995), but more recent phylogenetically informed analyses have not (Liao *et al.*, 2015; Powell *et al.*, 2017; Heldstab *et al.*, 2018; but see Stankowich & Romero, 2017). Such incongruity may arise if the variables considered exhibit a strong phylogenetic signal, as was the case for our variables. Other aspects of habitat complexity, such as environmental

Figure 1. Correlation between body mass (log$_{10}$-transformed) and brain mass (log$_{10}$-transformed) in Squamata, using a phylogenetic generalized least squares regression. N = 172 (including the tuatara outgroup).

Figure 2. Ancestral state reconstruction of relative brain size (residuals of the brain to body mass regression) along the nodes and branches of the phylogenetic tree of 171 species of Squamata. *Sphenodon punctatus* is included as an outgroup. Species with positive residuals (blue) have large brains relative to their body size, whereas species with negative residuals (yellow–red) have small brains relative to their body size. Results were visualized using the *contMap* function in R (package *phytools*; Revell, 2012).
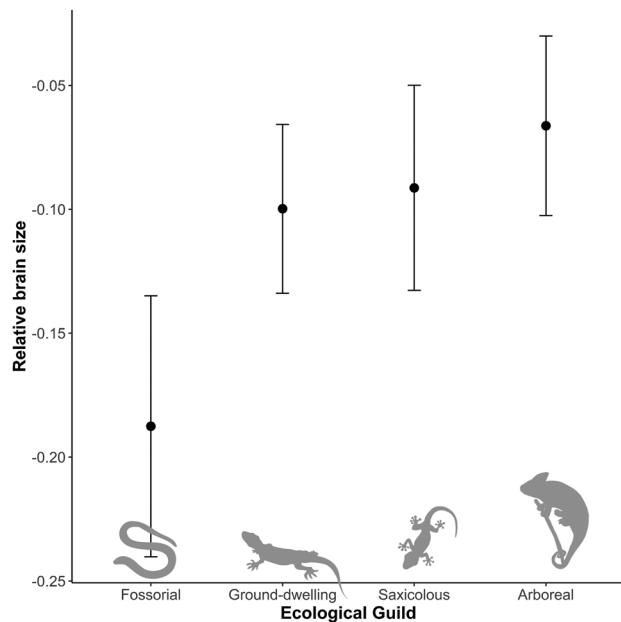
Figure 3. Relative brain size per ecological guild. Residuals of the brain to body mass regression were used for visualization of results. The model also included limb status and biogeographical realm as confounding variables. There were no statistical differences among ecological guilds. Error bars indicate standard errors.

variability, may be more important selective pressures for larger brains (Schuck-Paim *et al.*, 2008; Sayol *et al.*, 2018).

The lack of differences among ecological guilds can, however, be explained by two alternative hypotheses. Firstly, as predicted by the mosaic brain hypothesis, selection may act independently on different parts of the brain (Barton & Harvey, 2000; Salas *et al.*, 2003; Healy & Rowe, 2007; Powell & Leal, 2014). Indeed, studies on fish and anurans have shown a positive effect of habitat complexity on the size of the cerebellum (motor coordination) and telencephalon (spatial memory) independent of the size of the whole brain (Pollen *et al.*, 2007; Gonzalez-Voyer & Kolm, 2010; Liao *et al.*, 2015). Unfortunately, for most species in our dataset only the size of the complete brain was available.

Secondly, it is also possible that membership of a particular guild may not adequately reflect the degree of habitat complexity with which each individual species is confronted. For example, arboreal species, such as *Anolis* lizards, are often specialized in specific microhabitats, which can differ considerably in structural complexity (e.g. trunk vs. canopy of trees; Powell & Leal, 2014). Nevertheless, such differences in microhabitats do not necessarily lead to interspecific differences in brain anatomy (Powell & Leal, 2012, 2014). It is also possible that the structural complexity of the environment is determined primarily at a broader ecological scale. For instance, whether a species is arboreal or ground-dwelling, a tropical forest remains a more complex environment compared with a desert (Delarue *et al.*, 2015). Specific habitat data, at both micro- and macro-scales, were not available

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Table 1. Outcome of the phylogenetic generalized least squares regression for the model containing ecological variables ($N = 171$) and the model containing social variables ($N = 51$)

Model	Predictor	Effect	F-statistics	Significance	λ
Brain size*ecology	Body size	$b = 0.564 \pm 0.012$	$F_{1,157} = 2476$	$P < 0.001$	0.37
	Ecological guild	Ar > Sa and GD > Fo	$F_{3,157} = 1.98$	$P = 0.12$	
	Habitat generalism	$b = -0.007 \pm 0.005$	$F_{1,157} = 2.84$	$P = 0.09$	
	Limb status	A < R < P	$F_{2,157} = 62.8$	$P < 0.001$	
	Biogeographical realm	NT > AU, NA	$F_{6,157} = 4.40$	$P < 0.001$	
Brain size*sociality	Body size	$b = 0.568 \pm 0.013$	$F_{1,43} = 18*10^4$	$P < 0.001$	−0.88
	Sociality	Solitary > social	$F_{1,43} = 20.00$	$P < 0.001$	
	Biogeographical realm	NT > AU, PA	$F_{5,43} = 7.00$	$P < 0.001$	

Brain size and body size were both $\log_{10}$-transformed. Abbreviations for ecological guild: Ar, arboreal; Fo, fossorial; GD, ground-dwelling; Sa, saxicolous. Abbreviations for limb status: A, absent; P, present; R, reduced. Abbreviations for biogeographical realm: AF, Afrotropics; AU, Australasian; NA, Nearctic; NT, Neotropics; PA, Palaearctic.
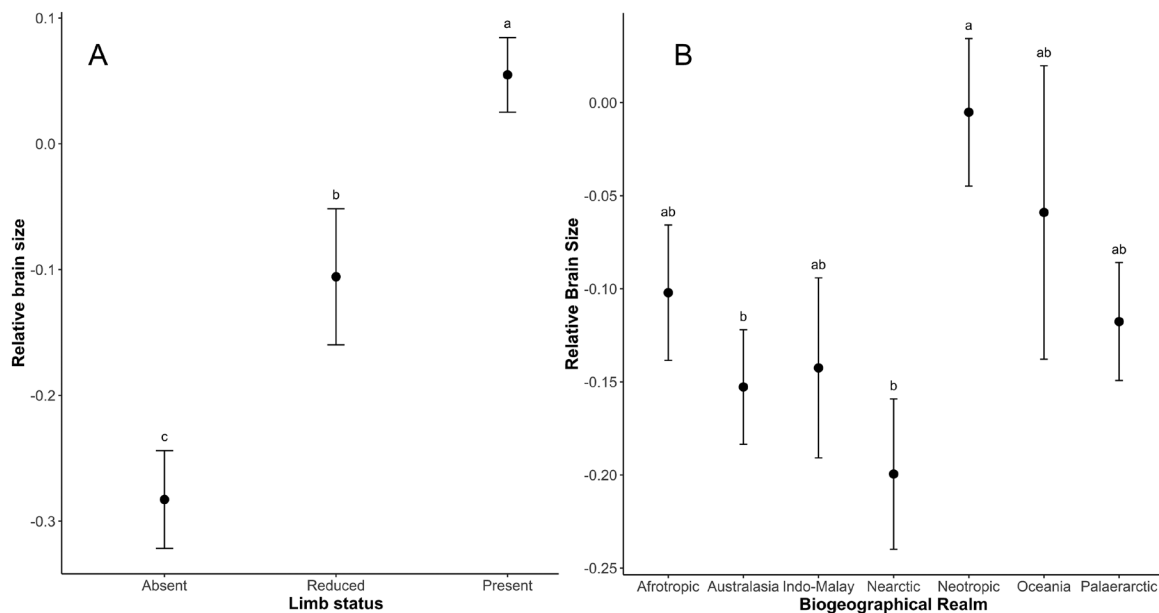

Figure 4. Effect of two 'confounding' variables on relative brain size. A, decrease in relative brain size with a higher degree of limb reduction. B, average relative brain size per biogeographical realm. Residuals of the brain to body mass regression were used for visualization of results. Groups indicated by different letters differ significantly at $P < 0.05$. Error bars represent standard errors.

for our specimens, but further research incorporating those could provide interesting insights into the ecological factors influencing reptilian brain size.

Despite the general assumption that larger brains lead to higher behavioural flexibility, no association between brain size and habitat generalism was found (Iwaniuk, 2017). The ability to survive in a broader range of habitats might depend more on specific personality traits rather than cognitive skills (Chapple *et al.*, 2012). Birds with greater colonizing success were more willing to eat novel food items, but did not have larger brains (Ducatez *et al.*, 2015). Bezzina *et al.* (2014) found no differences in learning ability between invasive and non-invasive

skinks (*Lampropholis delicata* and *Lampropholis guichenoti*), although their results suggested higher explorative behaviour in the invasive species.

Limb reduction in our dataset was associated with a decrease in relative brain size, which is in line with previous findings (Platel, 1979; Heesy *et al.*, 2017). This can be explained by a reduced need for motor coordination, because the reduction in brain size in limbless species is mainly the result of a smaller cerebellum (Black, 1983; Heesy *et al.*, 2017). Our results clearly demonstrate the necessity to correct for limb reduction in further comparative studies on brain size in Squamata.
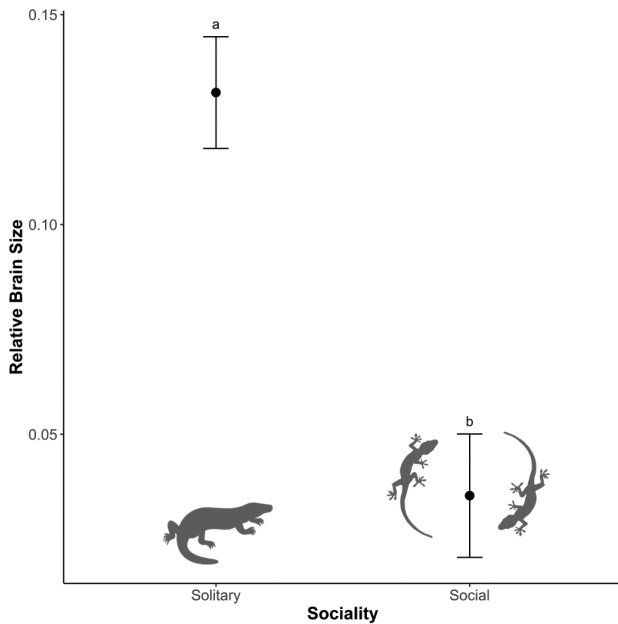
Figure 5. Relative brain size and sociality in Squamata. Residuals of the brain to body mass regression were used for visualization of results. Groups indicated by different letters differ significantly at $P < 0.05$. Error bars represent standard errors.

We found that Neotropical species had relatively larger brains than Nearctic and Australasian species. These results corroborate findings by Amiel *et al.* (2011), who noted that small-brained reptiles and amphibians were more successful invaders of Australian ecosystems. The Neotropical region is characterized by high net primary productivity and resource availability (Foley *et al.*, 1996), and species living here might, therefore, afford to develop relatively large and energetically expensive brains (Aiello & Wheeler, 1995; Isler & van Schaik, 2006). Large parts of the Nearctic and Australasian realm have low resource availability, leading to selection against expensive brains (Foley *et al.*, 1996; Amiel *et al.*, 2011). The complexity of neotropical ecosystems might also favour the evolution of larger brains (Delarue *et al.*, 2015). However, a more detailed analysis, using productivity and resource availability at the exact location where specimens were collected, is required for more conclusive insights.

In sharp contrast to the expectations of the SBH, we found that, within limbed Squamata, solitary species had larger brains than social species. Surprisingly, all models run with the social data gave values of λ lower than or equal to zero, suggesting that related species resemble each other less than expected. Possibly, this is attributable to the limited number of Squamata for which sociality has been confirmed to be either present

or absent (< 1%; see Gardner *et al.*, 2016). The SBH was initially proposed for and well supported within primates (Byrne & Whiten, 1988; Dunbar, 1998, 2009; Dunbar & Shultz, 2007, 2017). However, our study contributes to a growing list of literature failing to support the hypothesis in other taxa, and therefore questioning the validity of the SBH for species other than primates (Holekamp, 2007; Finarelli & Flynn, 2009; Reddon *et al.*, 2016; Kverková *et al.*, 2018). But even within primates, it has been suggested that both sociality and large brains are consequences of other ecological variables, such as diet or predation pressure (van der Bijl & Kolm, 2016; DeCasien *et al.*, 2017; Powell *et al.*, 2017). Interestingly, Perez-Barberia *et al.* (2007) suggested that, in mammals, relatively simple social systems can evolve without an enlargement of the brain. Reptilian social systems are often believed to exhibit, for example, more modest levels of communication and cooperation compared with mammals or birds (Gardner *et al.*, 2016), and group living in reptiles is rarely obligatory or permanent (Whiting & While, 2017). Sociality in reptiles might be less cognitively demanding and, therefore, might not require larger brains. Interestingly, in this context, social learning has been documented in both solitary (Noble *et al.*, 2014; Damas-Moreira *et al.*, 2018) and social (Whiting *et al.*, 2018) lizards, but differences in, for example, learning speed between them have not yet been investigated. On the contrary, many solitary species are highly territorial and will thus benefit from, for example, improved spatial memory (Maille & Schradin, 2016; Araya-Salas *et al.*, 2018) through larger brains. To our knowledge, this is the first study to test the SBH in Squamata. Future research should investigate the costs and benefits of sociality in Squamata, which will contribute to a better understanding of our results.

CONCLUSION

Although it is generally hypothesized that evolution towards larger brains is driven by environmental complexity, it has recently been questioned whether the same selective forces act on the brain in different vertebrate taxa. In contrast to our expectations, our study found no effect of habitat complexity on relative brain size in Squamata, and solitary species had larger brains than social species. Nor was there a significant correlation between habitat generalism and relative brain size.

Our results might indicate that different selective forces drive the evolution of brain size in Squamata vs. mammals or birds. Further research should incorporate more detailed ecological information (e.g. complexity at the micro- and macrohabitat

level) and will benefit from a better understanding of Squamata sociality. We strongly encourage comparative studies on brain size in understudied taxa, such as reptiles and amphibians, in order to obtain a more complete picture of how the vertebrate brain evolved.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Detailed ancestral state reconstruction of relative brain size (residuals of brain mass on body mass regression) in Squamata (N = 171) including the tuatara outgroup.
File S1. Data on brain sizes, body sizes, habitat and sociality for all species in this study, including bibliographic references.
File S2. Supplementary Methods and Results.
File S3. R script with code for all statistical models used for analysis of our data.