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## Egg shape and size allometry in geckos (Squamata: Gekkota), lizards with contrasting eggshell structure: why lay spherical eggs?

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### Abstract

Hard, highly calcified eggshells evolved several independent times during the history of amniotes. Because of phylogenetic conservatism of this trait, lineages in which closely related taxa differ in eggshell structure are rare. Four gekkotan families (Carphodactylidae, Diplodactylidae, Eublepharidae and Pygopodidae) have eggs with soft shells, while their close relatives (Gekkonidae) lay eggs with hard shells. Geckos thus offer a rare opportunity to compare the impact of the emergence of a hard eggshell on the economy of egg architecture. Because a sphere has the smallest surface area of all three-dimensional solids of a given volume, spherical eggs in geckos with hard eggshells reduce calcium investment and should therefore be advantageous. Here, we document that hard-shelled gekkonid eggs are indeed more spherical than those of the other gecko lineages. However, within gekkonids, small species lay more elongated eggs than larger species. We speculate that miniature gekkonid females, which lay larger eggs relative to body size compared with large gekkonids, produce elongate eggs in order to pass the egg through a limited pelvic opening.

**Key words:** constraint – cost of reproduction – egg size allometry – life history – lizard – reproductive effort

### Introduction

A hard, calcareous eggshell evolved independently in different lineages of amniote vertebrates (turtles, geckos, crocodiles and birds; Pough et al. 1998). The occurrence of a hard eggshell during the history of these lineages was a key evolutionary novelty with a large impact on the reproductive physiology and life history of the animals involved. The emergence of hard shells occurred early in amniote history. As a result, we cannot make direct observations when investigating the consequences of the presence of hard eggshells. We are therefore restricted to comparative studies between the hard-shelled lineages and their relatives with soft shells. Unfortunately, in most cases we do not know the closest living relatives with a contrasting state of eggshell softness or these relatives differ radically in body shape and way of life.

In squamate reptiles, the generally flexible and poorly mineralized parchment-like eggshell is clearly ancestral, with hard shells occurring only in the gecko family Gekkonidae (Andrews 2004). Close relatives of Gekkonidae, geckos of the families Carphodactylidae, Diplodactylidae, Pygopodidae and Eublepharidae, have ancestral soft eggshells (with the sole exception of the diplodactylid genus *Eurydactylodes* Wermuth, 1965; Russell and Bauer 2002). Geckos thus offer a rare opportunity to compare the impact of the emergence of a hard eggshell on the economy of egg architecture among closely related organisms. Throughout this paper, we follow the high-order classification of the living Gekkota recently suggested by Han et al. (2004). However, we should note that this classification is not definitive. Most authors agree that Eublepharidae are the sister group of all remaining gekkotans and that Gekkonidae are a well-supported monophyletic group. However, while the mutual position and exclusive monophyly of Carphodactylidae, Diplodactylidae and Pygopodidae are still questionable, it is clear that these groups form monophyly with respect to Gekkonidae and Eublepharidae (cf. Kluge 1987; Donnellan et al. 1999; Han et al. 2004).

Another advantage of geckos for comparative analysis of egg shape is that female geckos of all species lay invariant

clutches of one or two eggs (Shine and Greer 1991). Consequently, gecko females have no more than one developing egg in a single ovary at a time. The potential influence of the clutch size on egg shape (Elgar and Heaphy 1989) is therefore considerably minimized.

A hard eggshell undoubtedly offers a better protection against invertebrate predators and desiccating environmental conditions than a soft shell (Gardner 1985). For instance, the eggs of many gekkonids can be successfully incubated in an almost dry environment (Rösler 2005; Kratochvíl, personal observation). On the contrary, the highly mineralized hard eggshell is much more costly to produce, as calcium is a limited element for most terrestrial organisms. In fact, a decrease in bone compactness in reproductive females due to deposition of skeletal calcium into eggs or offspring has been reported in birds, turtles and crocodiles (groups with heavily calcified eggshells), but also in a viviparous snake and a lizard species with poorly mineralized eggshell (de Buffrénil and Francillon-Vieillot 2001, and references therein).

A more spherical hard-shelled egg would minimize the consumption of calcium, because a sphere has the least surface area of all solids of a given volume. In the present study, we use interspecific comparative methods to test the hypothesis that geckos producing hard-shelled eggs have more spherical eggs than geckos with soft eggs. Indeed, anecdotal evidence suggests that the gekkotan families differ in egg shape: carphodactylids, diplodactylids and eublepharids produce elongated eggs, whereas gekkonids have much more spherical eggs (Doughty 1997). Here, we perform the first direct comparison of egg shape in geckos at the family level and quantify the egg shape allometry of different gecko groups. The perfectly spherical egg would be the most economical from the perspective of calcium consumption; however, we found that most (but not all) hard-shelled gecko eggs are somewhat elongated. Are these deviations from ideal shape random, or does the shape variation relate to variations in size?

## Materials and Methods

### Data on egg size and shape

Data were collected from taxonomic works and field guides (Loveridge 1947; Szczerbak and Golubev 1986; Manthey and Grossmann 1997; Branch 1998; Greer 2003) and from herpetological and herpetocultural books and journals (Easterla and Reynolds 1975; Gallo and Reese 1978; Mudrack 1985a,b; Vitt 1986; Ulber and Ulber 1987; Grossmann and Stein 1988; Henkel 1988; Stein 1988; Grossmann and Ulber 1990; Leptien and Zilger 1991; Schäfer 1991, 1993; Seuffer 1991; Kovář 1992; Havelka 1993a,b, 1994; Leptien et al. 1994; Rickert 1994; Hulbert 1995; Rickert 1995; Doughty 1996, 1997; Röhl 1996, 1998, 1999, 2000a,b, 2003; Laube 1997, 2001, 2002; Leptien and Lui 1997; Vitt and Zani 1997; Laube and Seipp 1998, 1999; Trautmann 1998; Leptien 1999; Pietschmann and Klusmeyer 1999; König 2000; Schröder and Röhl 2000, 2002, 2003; Seipp and Henkel 2000; Barts et al. 2001; Vergen 2001; Anders 2002; Barts 2002a,b; Pouliček 2002; Funk 2003; Funk and Vrabec 2004; Vences et al. 2004; Rösler 2005), as well as from our own observations (especially our analysis of 358 clutches of eublepharid geckos; Kratochvíl and Frynta 2006). The complete dataset is available upon request to the corresponding author. As eggs with leathery eggshells increase their volume during incubation, only data of freshly laid eggs were included for groups with soft eggs. The EMBL database (Uetz 2005) was used to identify synonymous names among those used in the literature. For every taxon, we took a mean of values when more than one source was available for a given taxon. Otherwise, we took a midpoint of published ranges. Altogether we compiled data for 308 taxa of geckos (13 species of eublepharids, 34 species of diplodactylids, 14 species of carphodactylids, 13 species of pygopodids and 234 species and/or subspecies of gekkonids).

### Scaling relations

To test the hypothesis on the scaling of egg length ( $l$ ) on egg width ( $w$ ) we applied the power function  $l = aw^b$  (Huxley 1932) in its  $\log_{10}$ -transformed form:

$$\log_{10} l = \log_{10} a + b \log_{10} w.$$

When considering isometric relationship, the expected slope ( $b$ ) is 1.0 as both  $l$  and  $w$  are of linear dimension. For the regression slope estimations, we employed the reduced major axis regression (RMA) model because it accounts for an error in the 'independent' variable (McArdle 1988). RMA regression coefficients were computed using RMA version 1.14b programme (Bohonak 2002). To explore whether egg shape changes with size, we also used an alternative method. We computed the egg shape parameter as the ratio of egg length to egg width and searched for an interspecific correlation between the computed variable and egg width.

The investigation based on comparative analysis of interspecific data requires a phylogenetic framework. The approach employed in this study is the calculation of standardized independent contrasts (Felsenstein 1985). As a control for the phylogenetic relationship and the calculation of independent contrasts in eublepharids and pygopodids, we used fully resolved phylogenetic hypotheses proposed by Kratochvíl and Frynta (2002) and Jennings et al. (2003) respectively. Currently, there is no available, fully resolved phylogeny for all carphodactylids, diplodactylids and gekkonids. Therefore, we used a method for phylogenetic analysis of comparative data when the phylogeny is only partly known (Housworth and Martins 2001). Using MESQUITE version 1.02 software (Maddison and Maddison 2004), we generated mostly unresolved phylogenies separately for carphodactylids + diplodactylids and gekkonids, with the constraint that the species grouped in one genus and subspecies of one species should always go together in a clade. Moreover, as an additional constraint for carphodactylids + diplodactylids we used Greer's (1989) cladogram of carphodactylid and diplodactylid genera supplemented with recently proposed phylogenies for the genera *Diplodactylus* Gray, 1832 (Melville et al. 2004), *Phyllurus* Schinz, 1817 and *Saltuarius* Couper, Covacevich et Moritz, 1993 (Hoskin

et al. 2003) and *Rhacodactylus* Fitzinger, 1843 (Good et al. 1997). For gekkonids, we grouped together several genera generally recognized as related (*Phyllodactylus* Gray, 1828 – *Paroedura* Günther, 1879 – *Asaccus* Dixon et Anderson, 1973 – *Christinus* Wells et Wellington, 1983 – *Dixonius* Boulenger, 1898 – *Afrogecko* Daudin, 1802 – *Goggia* Gray, 1838 – *Euleptes* Fitzinger, 1843; *Gymnodactylus* Spix, 1825 – *Cyrtodactylus* Gray, 1827 – *Cyrtopodion* Fitzinger, 1843 – *Bunopus* Blanford, 1874; *Pachydactylus* Wiegmann, 1834 – *Tarentola* Gray, 1825 including *Geckonia* Mocquard, 1895 – *Rhopropus* Peters, 1869 – *Chondrodactylus* Peters, 1870 – *Palmatogecko* Anderson, 1908; *Gekko* Laurenti, 1768 – *Gehyra* Gray, 1834 – *Hemiphyllodactylus* Bleeker, 1860 – *Lepidodactylus* Fitzinger, 1843 – *Pseudogecko* Taylor, 1922 – *Ptychozoon* Kuhl et van Hasselt, 1822; *Hemidactylus* Gray, 1825 – *Cosymbotus* Fitzinger, 1843 – *Teratolepis* Günther, 1870; *Lygodactylus* Gray, 1864 – *Phelsuma* Gray, 1825; Russell and Bauer 2002). Within the genera *Phelsuma* and *Tarentola* (including *Geckonia*) we used phylogenetic hypotheses published by Carranza et al. (2002) and Austin et al. (2004). After the derivations of constrained trees, we tested the robustness of a scaling relationship to phylogenetic effects using an analysis by independent contrasts for each 'phylogeny.' The regression slopes were calculated using PDAP: PDTREEpackage for MESQUITE version 1.00 (Midford et al. 2002). In phylogenetic analyses we set all branches to the same lengths, because estimations of branch lengths are available neither for eublepharids nor for groups with partially unknown phylogeny. Thus in contrasts analyses we assumed a punctuational model of evolution. All regression analyses based on independent contrasts scores were constrained to pass through the origin.

### Estimation of calcium saving of spherical versus elliptical eggs

Actual calcium deposition into eggshells must be specified empirically. However, to roughly estimate the saving of calcium owing to egg rounding (neglecting the differences in eggshell thickness and mineral density), we compared the approximated surface of a gekkotan egg with the surface of a sphere of the same volume. We calculated egg volume ( $V$ ) and egg surface ( $S$ ) from the formulae for a prolate spheroid:  $V = (4\pi/3)ab^2$ ,  $S = 2\pi b(b + a \arcsin[e]/e)$ , where  $a = (\text{egg length})/2$ ,  $b = (\text{egg width})/2$ ,  $e = (a^2 - b^2)^{1/2}/a$ . Next, we calculated surface of a sphere with the same volume as an individual species' egg:  $S' = 4\pi r^2$ , where  $r = (3V/4\pi)^{1/3}$ . We took  $s = (S/S' - 1) \times 100$  as an estimation of a potential saving of calcium that could be implemented by making ideally spherical eggs, and compared  $s$  values between and within groups.

## Results

As expected, geckos exhibit extensive interspecific variation in egg size and shape (Fig. 1). As Carphodactylidae and Diplodactylidae differ neither in slope nor in intercept of the regression line of egg length on egg width (GLM ANCOVA, both  $p > 0.28$ ), we combined data for both these groups in all subsequent analyses. Allometric slopes for eublepharid (95% CI of the slope =  $0.981 \pm 0.175$ ,  $r = 0.96$ ), carphodactylid and diplodactylid geckos (CI =  $0.986 \pm 0.086$ ,  $r = 0.96$ ) computed by RMA regression are very close to an isometric slope and they do not statistically differ from 1.0. The slope for pygopodids is somewhat lower (CI =  $0.898 \pm 0.285$ ,  $r = 0.88$ ), but still does not statistically differ from 1.0. This data suggests that egg shape does not change with egg size. In contrast, the slope for members of the family Gekkonidae is significantly  $< 1.0$  (CI =  $0.893 \pm 0.038$ ,  $r = 0.95$ ). Analysis of the egg shape parameter confirms that egg shape in eublepharids, diplodactylids, carphodactylids and pygopodids does not change with size (Pearson's  $r$  between egg shape parameter and egg width non-significant in all families,  $p > 0.10$ ), but that smaller eggs of gekkonids are more elongated than larger ones ( $r = -0.48$ ,  $p < 0.0001$ ,  $n = 234$ ).

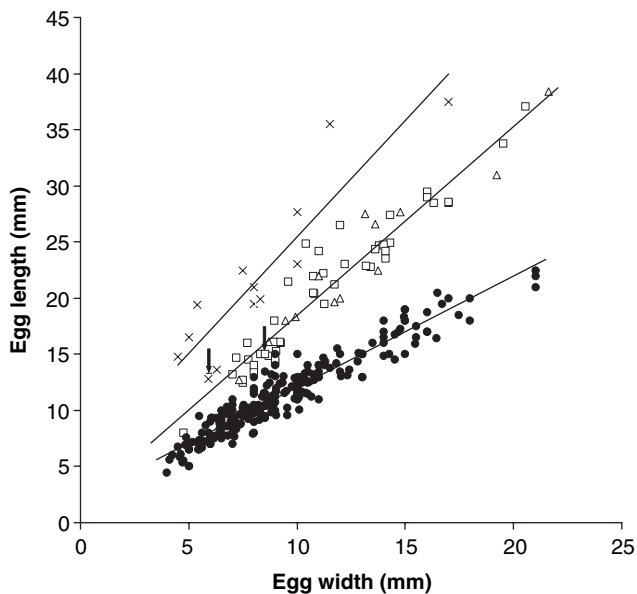


Fig. 1. Biplot of egg width and egg length for gekkotan lizards. Each mark represents one (sub)species. Gekkonidae ( $n = 234$ ), circles; Eublepharidae ( $n = 13$ ), triangles; Carphodactylidae and Diplodactylidae ( $n = 48$ ), squares; Pygopodidae ( $n = 13$ ), crosses. Lines illustrate trends calculated by least square regression. The lines of eublepharid and diplodactylid geckos are indistinguishable. Arrows indicate species of the genus *Eurydactyloides*.

Taking phylogeny into account in the derivation of allometric relationships, we obtained very similar results. The 95% CI for regression slopes including sampling variance and variance due to unknown phylogeny of egg length contrasts on egg width contrasts include 1.0 in eublepharids (CI =  $0.926 \pm 0.289$ ,  $r = 0.88$ ) as well as in carphodactylids + diplodactylids (CI =  $0.923 \pm 0.138$ ,  $r = 0.94$ ) and pygopodids (CI =  $0.954 \pm 0.426$ ,  $r = 0.80$ ). Therefore, we cannot disprove the isometric relationship of egg shape in these groups. On the contrary, the phylogenetic contrasts analysis confirmed the negative allometry of egg length on egg width in gekkonids (CI =  $0.891 \pm 0.058$ ,  $r = 0.94$ ).

Based on our rough estimation, if eublepharids and carphodactylids + diplodactylids made spherical eggs preserving the same volume, they would save on average  $5.81 \pm 0.43$  (SE) and  $6.09 \pm 0.22\%$  of egg surface respectively. Assuming the same thickness and mineral density, the corresponding deposition of calcium into each individual eggshell would also be saved. In the same way, pygopodids would save even  $15.18 \pm 0.42\%$  of egg surface by producing spherical eggs. As gekkonids make more spherical eggs than the other geckos, their potential saving is much smaller ( $s = 1.06 \pm 0.10\%$ , range 0–4.88). Across gekkonid species, potential savings because of further egg rounding decreases with egg width (Pearson's  $r = -0.44$ ,  $p < 0.00001$ ), which confirms that the larger gekkonid species save calcium more effectively than smaller gekkonids thanks to the shape of their eggs.

## Discussion

Geckos are medium to small lizards; their clade includes the smallest known amniote vertebrate (Hedges and Thomas 2001). It is evident that there has been extensive size evolution during the history of all gekkotan groups. Even though

eublepharid, carphodactylid and diplodactylid geckos evolved, in parallel, body size in both directions (Grismer 1988; Greer 2003; Kratochvil and Frynta 2003; Starostová et al. 2005), they share the same, ancestral egg shape allometry (Fig. 1). In all these groups, eggs are elongated and their shape does not change considerably with egg size. During the evolutionary history of gekkotan lizards, egg shape allometry changed considerably twice: in pygopodids and in gekkonids. The more prolate egg shape in Pygopodidae probably reflects their snake-like body form. On the contrary, gekkonids lay much more spherical eggs than all other gekkotan groups. The occurrence of the more spherical egg shape in the evolution of geckos together with the appearance of hard calcified eggshells suggests that these two traits are functionally correlated. However, the elongated egg shape of the hard-shelled eggs of the members of diplodactylid genus *Eurydactyloides* somewhat questions the validity of this statement.

Interestingly, although hard eggshells are not present in other squamate reptiles (Andrews 2004), they have appeared twice during the phylogeny of geckos. A calcified egg surface typifies family Gekkonidae, but it is also present in the diplodactylid genus *Eurydactyloides*. In both groups, strongly calcified eggs evolved along with enlarged endolymphatic sacs, most probably the calcium-storing organ (Russell and Bauer 2002). Thus, according to our calcium limitation hypothesis, hard-shelled eggs of *Eurydactyloides* should have acquired a more spherical form than the soft eggs of their relatives. However, eggs of *Eurydactyloides* are elongated, and their shape does not depart from the egg shape allometry of other diplodactylids (Fig. 1). We ascribe this phenomenon to phylogenetic inertia and stress that the situation in this obscure genus deserves further and more thorough investigation (note: for practical reasons we further use the term 'hard-shelled geckos' just for gekkonids).

Although gekkonids lay much more spherical eggs than species of the other gekkotan families, many of them still produce rather elongated eggs (up to over 1.7 egg length to egg width ratio). The existence of the prolate eggs in gekkonids is surprising, as elongated eggs have larger surface and are thus disadvantageous both from the large use of calcium deposition into highly mineralized shells and from the higher risk of drying. We further demonstrated that the tendency to produce spherical eggs in hard-shelled geckos decreases with gecko size. What mechanism could prevent small gekkonid species from making an ideal, spherical egg shape?

The 'pelvic limitation hypothesis' could explain the observed pattern. This idea is based on the notion that the pelvic opening could serve as the mechanical constraint to maximal egg width during egg expulsion (e.g. Elgar and Heaphy 1989; Sinervo and Licht 1991). The pelvic limitation hypothesis predicts that lizards producing relatively larger eggs are forced to increase egg length rather than egg width. In geckos, this restriction would mean that lineages with soft- versus hard-eggshells should differ in egg length, but not in egg width relative to body size. To test this prediction, we compiled data on body size in examined species of geckos. Using available data on snout-to-vent length (SVL), we tested the differences in relative egg width and egg length among gecko families 144 taxa (25 diplodactylids + carphodactylids; 12 eublepharids; 107 gekkonids; data available from corresponding author upon request). We employed full factorial general linear model in STATISTICA version 6.0 (StatSoft, Inc. 2001) with  $\log_{10}(\text{SVL})$  as a continuous predictor, family as a categorical predictor,

and  $\log_{10}(\text{egg width})$ , respectively,  $\log_{10}(\text{egg length})$  as a dependent variable. In the model, where  $\log_{10}(\text{egg width})$  was the dependent variable, just the continuous predictor was significant ( $p < 0.0001$ ). Using  $\log_{10}(\text{egg length})$  as a dependent variable, there were significant both  $\log_{10}(\text{SVL})$  ( $p < 0.0001$ ) and family –  $\log_{10}(\text{SVL})$  interactions ( $p = 0.012$ ). The slope of  $\log_{10}(\text{egg length})$  on  $\log_{10}(\text{SVL})$  is significantly lower in the family Gekkonidae than the common slope of other families. Carphodactylidae + Diplodactylidae and Eublepharidae differ neither in the slope nor in the intercept. We are aware that our data on SVL are not precise (with the exception of most species of eublepharids), and that using SVL as a measure of body size in scaling analyses is fairly problematic (Kratochvíl et al. 2003). Nevertheless, this rough preliminary analysis shows that egg widths relate to SVL more or less equally in all gecko families with similar body shape (we lack precise data on body size in pygopods). Furthermore, the truly large distinction in scaling of egg size to SVL between gekkonids and eublepharids + diplodactylids + carphodactylids is limited to egg length. These results thus strongly support the pelvic limitation hypothesis on gekkonid egg shape.

The relation of egg width and egg length to SVL is isometric, i.e. eggs grow proportionally to SVL, in eublepharids (Kratochvíl and Frynta 2006) and also in diplodactylids and carphodactylids sharing the same allometry. Therefore, we can conclude that egg length and consequently whole egg size in gekkonids, reflects negative allometry; i.e. to say, the miniature gekkonids enlarge eggs by means of relative egg length increments.

The oviductal eggs inside eublepharid, carphodactylid and diplodactylid females are positioned nearly side by side. In contrast, gekkonid lizards with two eggs per clutch place their eggs one in front of the other (Doughty 1997 and references therein). The differences in relative egg size and egg position together with the observation that eublepharid females are anorexic several days before parturition, while those of at least one gekkonid species (*Paroedura picta* Peters, 1854) were observed feeding just several hours before laying (L. Kratochvíl, personal observation), suggests that the body cavities of eublepharids, diplodactylids and carphodactylids before laying are more 'full.' The abdominal volume, which increases in proportion to body size, then constrains relative clutch mass in diplodactylids, carphodactylids and eublepharids, and the resultant egg size allometry in these groups is then isometric, a trait unique among ectotherms. On the contrary, empty space in the body cavity allows small female gekkonid lizards to enlarge eggs, but the pelvic limitation ensures that this only occurs by means of egg elongation.

Interspecific negative allometry of propagule size probably results from ecological, physiological or developmental processes constraining the minimal propagule size (Minelli 2003; Kratochvíl and Frynta 2006). This phenomenon has been documented many times in ectotherms, where the clutch size is variable and the whole clutch is laid at once (e.g. in spiders: Marshall and Gittleman 1994; many insects: Berrigan 1991; García-Barros 2000; fish: Blueweiss et al. 1978; turtles: Elgar and Heaphy 1989; snakes: Shine et al. 1998; lacertid lizards: Bauwens and Díaz-Uriarte 1997; Molina-Borja and Rodríguez-Domínguez 2004; and monitor lizards: Thompson and Pianka 2001). In such lineages, the relatively larger eggs in smaller species arise at a cost of progeny number within a

given clutch, and we then observe interspecific egg size–number trade-off. The situation in gekkos, where the progeny number in a reproductive bout is invariant, sheds new light on the origin of negative egg size allometry. We speculate that negative egg size allometry occurs in groups where the relative enlargement of egg size in smaller species is possible due to exploitable abdominal space within the female body cavity. In gekkonids, such an exploitable space is available, and the negative egg size allometry occurs at the cost of departure from ideally economical egg shape. In animals with variable clutch size, where the total clutch mass increases in direct proportion to female size (Bauwens and Díaz-Uriarte 1997) and thus equally with maximal potentially accessible abdominal volume, the exploitable space can occur solely at the expense of progeny number. Our hypothesis requires further testing in comparative studies of independently evolved lineages with fixed clutch size (e.g. anoline lizards or tse-tse flies) or variable clutch size and females differing in abdomen 'fullness'. In addition, manipulative and/or selection experiments will help to clarify our conclusions.

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