

# Why reduce clutch size to one or two eggs? Reproductive allometries reveal different evolutionary causes of invariant clutch size in lizards

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## Summary

1. Large clutch size is unambiguously an ancestral state in reptiles. However, females of several lizard lineages lay just one or two eggs per clutch, called invariant clutch size. Selective forces leading to a dramatic drop in fecundity during a single reproductive bout are poorly understood.
2. We compared interspecific egg and clutch mass allometries in four lizard lineages with contrasting ways of reproduction. Lacertids and sceloporines have ancestral variable clutch size, while anoles and eublepharid geckos independently evolved invariant clutch size. To reconstruct the anoles' ancestral situation more precisely, we included data from a member of the closely related genus *Polychrus*, which is also arboreal but possesses variable clutch size.
3. We found the relative mass of the eublepharid double-egg clutch is comparable with the relative mass of the whole clutch in lizards with variable clutch size. Clutch mass in eublepharids and lizards with variable clutch size increases proportionally to female size. However, single-egg anole clutches show similar negative allometry as the sole egg of lizards with variable clutch size.
4. It appears that invariant clutch size evolved under (and is maintained by) selection on offspring enlargement in geckos, but selection on reducing female reproductive burden in anoles, i.e. the phenomenon of invariant clutch size apparently evolved in these individual groups for different reasons.
5. Besides understanding lizard life history, our study illustrates how singular events in life-history evolution can be reconstructed by comparing the ancestral and evolved reproductive allometries.

*Key-words:* allometry, *Anolis*, egg size, gecko, life history

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## Introduction

Animal's clutch sizes can be divided into two basic groups: variable clutch size (VCS) or invariant clutch size (ICS). In VCS, females lay large clutches, the egg number varying according to female's size and/or physical condition; however, in ICS females produce small clutches of constantly one or two eggs per a clutch. In reptiles, VCS is unequivocally the ancestral state occurring in crocodiles, tuataras, most turtles, and squamate reptiles. ICS evolved in lizards independently through more than 20 independent events and is present in all anoles, gekkotan lizards, Dibamidae, and even in certain species from groups where VCS dominates, i.e. some skinks, agamids and gymnophthalmids

(Shine & Greer 1991). Although some ecological correlates of the evolution of ICS, such as arboreality (Andrews & Rand 1974; Shine *et al.* 1998) or conversely fossoriality (Ashton 2005) are well known, the selective forces leading to a dramatic drop in fecundity during a single reproductive bout are poorly understood.

Evidence suggests natural selection favours a limited number of large clutches in a seasonal climate; particularly if the suitable reproductive periods are relatively short (Tinkle, Wilbur & Tilley 1970; Andrews & Rand 1974; James & Shine 1988). The current model is that organisms exposed to seasons will utilize VCS while organisms inhabiting an aseasonal location will employ ICS. However, the relationship between clutch size and climate does not completely explain the whole pattern. Many tropical lizards have VCS and certain lizards inhabiting in a strongly seasonal climate lay clutches of invariant size (Inger & Greenberg 1966; Anderson 1999).

In some cases, ICS evolution is clearly linked to body size miniaturization (Shine & Greer 1991). ICS often occurs in miniature species of the lineages that normally utilize VCS. This phenomenon probably occurs as a consequence of the widespread negative egg size allometry (negative allometry indicates larger species have relatively smaller traits, i.e. egg size). Larger species employing VCS invest resources during the reproductive bout into a larger number of relatively small eggs, while smaller species invest resources into a few relatively large eggs (discussed, e.g. by Kratochvíl & Frynta 2006a). Owing to the trade-off between offspring size and number, small species are forced to produce relatively large eggs in small clutches and, in extreme cases, produce only one or two eggs.

However, ICS does not occur solely in miniaturized lizards and not all hypotheses regarding its origin suggest negative egg size allometry. Ecological hypotheses addressing emergence of ICS are divided into two groups and differ in their fundamental predictions. The first group considers ICS a selection result to reduce female reproductive burden thereby maintaining female agility during pregnancy. These hypotheses predict a smaller relative clutch mass in lizards with ICS vs. their ancestors with VCS. Under the arboreal hypothesis, ICS evolved in arboreal species to relieve a gravid female in the locomotory-complicated environment (Andrews & Rand 1974; Shine *et al.* 1998). Similarly, according to the predation hypothesis, ICS results from the pressure to decrease total clutch mass, which should facilitate increased spryness during predator encounters (Andrews & Rand 1974). However, a group of alternative hypotheses postulate selection for larger offspring. The selective agents could be size-specific predation on juveniles, giving an advantage to larger hatchlings (Ashton 2005), a resource acquisition advantage of larger offspring (James & Shine 1988; Ashton 2005), or the 'safe harbour'. The later hypothesis expects increased investment per individual offspring in a protected environment, i.e. in the presence of parental care or hard shells (Smith & Fretwell 1974; Christian & Bedford 1993). Although these hypotheses expect larger individual egg sizes, they do not necessarily predict an increase in total clutch mass, especially considering the total clutch mass cannot exceed certain limits. Total clutch mass is constrained by an isometrically increasing maternal body cavity space (Shine 1992). This factor probably determines proportional increase of clutch mass with female mass among species of lizards with VCS. Therefore, according to the hypotheses of the second group, a relative clutch mass in lizards with ICS should be comparable with relative clutch mass of lizards with VCS.

ICS is fixed in two large, unrelated lizard groups: anoles and geckos. Both groups experienced extensive radiations (geckos – more than 1000 species, anoles *c.* 350 species; Uetz 2006), with considerable body size diversification. The occurrence of ICS likely impacted the other life-history and ecological features of these

animals. We can speculate that just ICS became the key evolutionary novelty contributing to their evolutionary success. In any event, ICS emerged early in the history of these groups. Even though we cannot make direct observations, we can use phylogenetic comparative studies to investigate the evolutionary causes for ICS emergence in geckos or anoles. We reconstructed the evolutionary mechanisms leading to ICS in these two important reptile lineages using comparison of ancestral and derived reproductive allometries to test if they fit the above-mentioned predictions.

## Materials and methods

We compared the interspecific egg and clutch mass allometries in lizard lineages with contrasting ways of reproduction. Inclusion criteria for a lineage were: (1) sufficient variability in body size to allow allometric coefficient determination with adequate power; (2) comparable body sizes (as different influences can operate in animals with unmatched sizes and so, for this reason, we omitted monitor lizards; Thompson & Pianka 2001); and (3) reliable data availability on egg number, clutch mass and body size in the appropriate number of species or populations. We compiled the already published and our own data in four lineages. We focused on anoles and eublepharid geckos, which possess independently evolved ICS; and on lacertids and sceloporines, which have ancestral VCS. Anoles lay a single egg per clutch, while geckos usually lay two eggs per clutch (although secondarily miniaturized geckos can also lay one egg per clutch, but this state is derived within geckos (Doughty 1996). To reconstruct the ancestral situation in anoles more precisely, we included data on a single species of the genus *Polychrus* Cuvier 1817, a close anole relative (Cooper & Vitt 2002) which is arboreal as well, but possess VCS (Vitt & Lacher 1981). In geckos, we used data on the family Eublepharidae, because we intended to reconstruct the cause of evolutionary origin of ICS and eublepharids are the basal gekkotan group (Kluge 1987). Eublepharids share egg-shape and egg-size allometry with carphodactylid and diplodactylid geckos (Kratochvíl & Frynta 2006b). These allometries are ancestral for the whole clade Gekkota, where different, unequivocally derived allometries occur only in pygopodids and gekkonids (Kratochvíl & Frynta 2006b), the groups forming the terminal gekkotan cladogram branches (Han, Zhou & Bauer 2004).

We gathered original data on total clutch mass, egg mass, and body size from the papers by Tinkle *et al.* (1970), Tinkle & Ballinger (1972), Andrews & Rand (1974), Vitt & Lacher (1981), Dunham & Miles (1985), Schleich, Kästle & Kabisch (1996), Bauwens & Díaz-Uriarte (1997) and Kratochvíl & Frynta (2006a,b). We included data from several different populations where available. Most authors presented data on mean total clutch mass and mean clutch size. In such cases (usually in sceloporines), we estimated mean egg masses as

the total clutch mass divided by mean egg number per clutch. It should be also noted that three included species of sceloporines are viviparous. In them, 'mean egg mass' estimated from clutch mass and size is the proxy of juvenile size, not egg size. Because of data limitations, we used maximal female snout-vent length (SVL) for a species or population as a female body size proxy, although using SVL as a measure of body size in scaling analyses can be problematic (for the various objectives see Thompson & Pianka 2001 and Kratochvíl *et al.* 2003). However, searching for the main scaling pattern, we were aware of potential influences in allometric coefficients, e.g. the multiple data origins or body shape differences within and predominantly among lineages. Shine (1992) demonstrated anoles and geckos do not substantially differ from lizards with VCS in body shape, at least in respect to body volume amount available for eggs within female abdomens.

To determine scaling of egg or clutch mass ( $M$ ) on female SVL ( $L$ ) among species within individual lizard lineages, we applied the power function  $M = aL^b$  (Huxley 1932), in its  $\log_{10}$ -transformed form ( $\log_{10} M = \log_{10} a + b \log_{10} L$ ). When considering isometric relationship, the expected slope ( $b$ ) is 3.0, as mass increases with the third power of linear dimension ( $L$ ). All allometries were analysed using an ordinary least squares linear regression model. Deviations from isometry were considered significant if the expected isometric slope fell outside the 95% confidence interval. Furthermore, we employed ANCOVA (general linear model, homogeneity of slopes procedure in STATISTICA) with  $\log_{10}$  (SVL) as a continuous predictor, family as a categorical predictor, and  $\log_{10}$  (clutch mass), respectively,  $\log_{10}$  (egg mass) as a dependent variable to test the differences among lizard clades. All calculations were performed using STATISTICA, version 6.0 (StatSoft Inc. 2001).

A comparative analysis should not assume species data points are statistically independent (Harvey & Pagel 1991). Usually, phylogenetic comparative methods are used to control for species nonindependence; this study calculated standardized independent contrasts (Felsenstein 1985). We generated the independent contrasts of  $\log_{10}$ -transformed SVL, egg, and clutch mass using COMPARE ver. 4.5 (Martins 2003), separately for each examined lizard clade. Phylogenetic relationships for anoles were taken from Poe (2004).

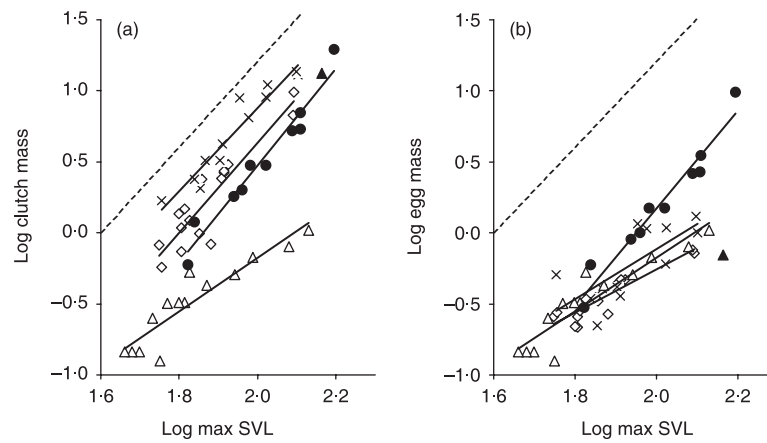
The mutual relationship between *Anolis trachyderma* Cope 1876, *A. polylepsis* Peters 1874, and *A. biporcatus* (Wiegmann 1834)–*A. lemurinus* Cope 1861 clade were treated as unresolved. Relationships within the genus *Sceloporus* Wiegmann 1828 followed the tree based on a combination of molecular and morphological data constructed by Wiens & Reeder (1997) and supplemented with the phylogenetic position of particular populations of *Sceloporus undulatus* (Bosc 1801) in a taxonomic congruence tree published by Miles *et al.* (2002). For lacertids and eublepharids, we employed phylogenies used by Bauwens & Díaz-Urriarte (1997) and Kratochvíl & Frynta (2006a) in their independent contrasts analyses of reproductive allometries. Computing independent contrasts, we set all branch lengths to 1. The diagnostic proposed by Garland, Harvey & Ives (1992) demonstrated the contrasts were appropriately standardized. All correlations and regressions using contrasts were computed through the origin.

## Results

The allometric coefficients estimated for individual groups are shown in Table 1. Lizards with VCS (lacertids and sceloporines) and eublepharid geckos share an isometric relationship between clutch mass and body size (Table 1; Fig. 1a). Neither the slopes nor the intercepts of their allometric lines differ significantly between these clades (ANCOVA:  $P > 0.30$ ) and the slopes do not substantially depart from 3 indicating isometry. Thus, clutch mass increases in direct proportion to female body size. Clutch mass in *Polychrus* seems to fit a similar rule. The single point reflecting *Polychrus acutirostris* Spix 1825 is close to the allometric line of lacertids, eublepharids and sceloporines, but distant from the anole line (Fig. 1a). Anoles have negative clutch-mass allometry (Table 1). Across species, their clutch mass increases much more slowly than female body mass. As their clutch size is reduced to a single egg, their clutch-mass allometry is simultaneously an egg-mass allometry. Egg-mass allometries of anoles and lizards with VCS are similar (Table 1; ANCOVA:  $P > 0.65$ ). Interestingly, *Polychrus acutirostris* lies near these lines (Fig. 1b). In monitor lizards (VCS), the ordinary least squares regression slope of egg mass on female SVL in a log-log transformation is

**Table 1.** Coefficients of interspecific regression of egg and clutch mass on adult female SVL based on  $\log_{10}$ -transformed data (mean  $\pm$  SE are given). All regressions are highly significant ( $P < 0.00001$  in all cases). Slopes significantly deviating from isometry, i.e. expected 3.0, are highlighted with asterisks

	Clutch mass allometry			Egg mass allometry			No. of species/ populations
	$r$	Intercept	Slope	$r$	Intercept	Slope	
Lacertids	0.92	-6.187 $\pm$ 0.683	3.428 $\pm$ 0.364	0.82	-3.302 $\pm$ 0.315	1.521 $\pm$ 0.168*	16
Sceloporines	0.96	-4.970 $\pm$ 0.513	2.927 $\pm$ 0.264	0.74	-3.665 $\pm$ 0.999	1.776 $\pm$ 0.514*	12
Eublepharids	0.97	-6.398 $\pm$ 0.564	3.435 $\pm$ 0.281	0.97	-6.699 $\pm$ 0.564	3.435 $\pm$ 0.281	10
Anoles	0.90	-3.789 $\pm$ 0.505	1.806 $\pm$ 0.270*	0.90	-3.789 $\pm$ 0.505	1.806 $\pm$ 0.270*	14



**Fig. 1.** Allometries of (a) clutch mass and (b) egg mass in four lizard lineages. Dashed line indicates isometry (slope = 3). Solid lines represent the ordinary least square regression for a given clade. Legend: empty triangles – anoles; filled triangles – *Polychrus acutirostris*; circles – eublepharid geckos; squares – lacertids; crosses – sceloporines.

**Table 2.** Slopes of interspecific regression of egg and clutch mass on adult female SVL based on independent contrasts (mean  $\pm$  SE are given). Slopes significantly deviating from isometry, i.e. expected 3.0, are highlighted with asterisks

	Clutch mass allometry		Egg mass allometry	
	<i>r</i>	Slope	<i>r</i>	Slope
Lacertids	0.88	2.753 $\pm$ 0.404	0.79	1.626 $\pm$ 0.338*
Sceloporines	0.94	2.749 $\pm$ 0.317	0.57	1.170 $\pm$ 0.539*
Eublepharids	0.98	3.208 $\pm$ 0.275	0.97	3.208 $\pm$ 0.275
Anoles	0.92	2.008 $\pm$ 0.262*	0.92	2.008 $\pm$ 0.262*

1.51 (Thompson & Pianka 2001), similar to the negative allometric slopes of anoles and VCS clades examined here. In contrast, eublepharids hold broadly isometric relationship between egg and female size (Table 1; Fig. 1b).

We assumed clutch and egg mass are fundamental life-history traits and their balance after body size shift is reached quickly and independently in every species. Therefore, the phylogenetic signal in these traits should be weak. Using 'raw' data to compute the allometries should give similar results as any phylogenetic comparative method. Previous analyses on two lizard lineages (lacertids: Bauwens & Díaz-Uriarte 1997; geckos: Kratochvíl & Frynta 2006a,b) as well as our present analysis on anoles and sceloporines support this view. The differences between 'raw' analysis and phylogenetic contrasts were minor in all cases. Independent contrasts confirmed the clutch mass isometry in lacertids, sceloporines and eublepharids, as well as the negative egg-mass allometry in lacertids, sceloporines and anoles (Table 2).

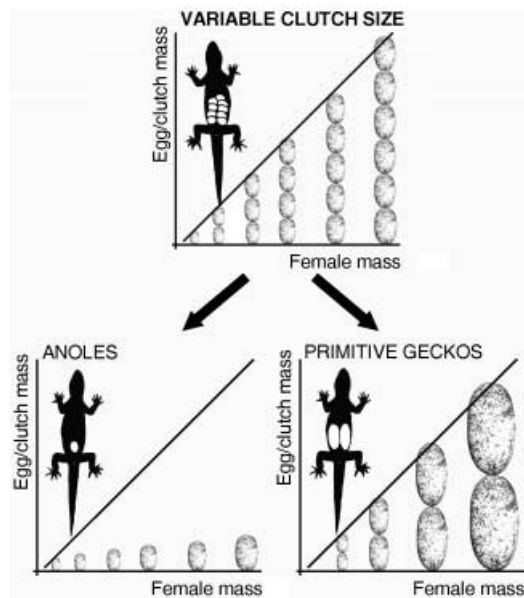
## Discussion

Although included lineages with ancestral VCS are distantly related and underwent radiation in body size

independently, we demonstrate they share both clutch-mass and egg-mass allometries. In classical phylogenetic hypotheses, investigating the relationships between squamate reptiles, lacertids belong to the clade Scleroglossa and sceloporines belong to the clade Iguania. Thus, lacertids are more related to geckos than to sceloporines, which are closely related to Polychrotidae (Estes, de Queiroz & Gauthier 1988; Cooper & Vitt 2002). Recently proposed molecular phylogenies (Vidal & Hedges 2005) placed gekkotan lizards at the base of squamate tree. However, occurrence of VCS in tuataras and other reptile outgroups of Squamata confirms the common squamate ancestor possessed VCS. Therefore, we feel quite confident the negative egg-mass allometry and clutch mass isometry are ancestral for the lizard clades.

Relative clutch mass in eublepharid geckos is similar to lizards with VCS (Kratochvíl & Frynta 2006a; cf. Fig. 1a). In eublepharids, individual egg mass increases in direct proportion to female size; while it increases more slowly than female size in lizards with VCS. Therefore, we conclude primitive geckos possess principally the same clutch-mass allometry as their ancestors but their egg-mass allometry evolved. This pattern is consistent with the hypothesis that ICS in geckos appeared as a result of the selection on egg enlargement. Previous reports utilizing the Gekkonidae family suggest geckos have a smaller relative clutch mass when compared with lizards with VCS (Shine 1992). However, gekkonid egg and clutch mass allometries were derived much later within gekkotan radiation, probably as a consequence of hard shell emergence in the family's ancestor (Kratochvíl & Frynta 2006b). Therefore, using gekkonids is misleading to investigate evolutionary origin of ICS in gekkotans.

Conversely to eublepharid geckos, anoles possess ancestral egg-mass allometry, but their clutch-mass allometry is altered. Compared with lizards with VCS, anoles have a lower relative clutch mass. Although the small relative clutch mass in anoles is well known



**Fig. 2.** Simplified schema of the probable evolution of invariant clutch size and interspecific reproductive allometries in anoles and geckos. Two eggs in a clutch of eublepharids increase up nearly to the size of the whole clutch in lizards with variable clutch size. By contrast, anoles reduced their clutch to a single egg of the size of a sole egg of lizards with variable clutch size. For simplicity, cross-point of axes is not (0,0).

(Andrews & Rand 1974; Shine 1992; Sinervo & Licht 1991), it was not directly compared with egg-mass allometries of lizards with VCS. Position of *Polychrus acutirostris* in Fig. 1 indicates, that it still has clutch-mass allometry typical for lizards with VCS. Inclusion of *Polychrus* suggests primitive Polychrotidae turned to the arboreal lifestyle but maintained ancestral reproductive features. Polychrotidae likely evolved clutch-mass allometry only later in their history, probably as a result of selection for reduced female reproductive burden.

In summary, anoles reduced their clutches to a single egg from the clutch of lizards with VCS. In contrast, eublepharid geckos expanded their eggs (each in a single ovary) nearly up to the ancestral clutch with numerous eggs (Fig. 2). Our aim was to investigate past selective regimes leading to ICS evolution in anoles and geckos. We also illustrated how to reconstruct singular events in life-history evolution comparing ancestral and derived reproductive allometries. We conclude that the phenomenon of ICS evolved in these individual groups for different reasons such as reducing female reproductive burden or offspring enlargement.

However, our conclusions have one important caveat. We cannot unequivocally prove the processes forming allometries observable in the present clade members were also responsible for origin of ICS. ICS could occur for reasons different from those assumed from the current allometries. For example, we can imagine ICS evolved in a miniaturized ancestor and

remained even after body size increases throughout subsequent evolution ('bottlenecking' hypothesis; Andrews & Rand 1974; Shine & Greer 1991). Nevertheless, we have some evidence (based on phylogenetic comparisons) that the ancestor of eublepharids was a mid-sized lizard (Kratovichil & Frynta 2002; Starostová, Kratochvil & Frynta 2005). Moreover, in contrast to the hypotheses of egg expansion in geckos and clutch-mass reduction in anoles, the miniaturized ancestor hypothesis cannot explain the allometries observed in the recent group representatives. A more parsimonious explanation is to suppose a single mechanism was involved in both ICS origin and the present allometries formation.

The interspecific reproductive allometries in primitive geckos and anoles are probably maintained by the selection on large egg mass, respectively, on small clutch mass. Clutch size, egg mass and clutch mass are important life-history traits, usually assumed to experience strong natural selection that should optimize their values in every particular species (e.g. Sinervo 2000). Although species changed their body size and reached their balance in the mentioned traits independently, they still fit the interspecific allometry of a given group (Fig. 1). Moreover, the clutch-mass allometries of primitive geckos and lizards with VCS and egg-mass allometries of anoles and lizards with VCS are remarkably concordant. There is not an easily explanation why the optimal relative egg mass should be similar for lizards living in such diverse environments and having such different lifestyles as sceloporines, lacertids and anoles. To us, the concordant interspecific allometries among lizard clades indicate the important role of allometric constraints in life-history evolution.

It seems that females of species with ancestral VCS and eublepharid geckos are selected to reach the maximal total clutch mass up to the limit constituted by the isometrically increasing accessible body volume. At least in three eublepharid species, the clutch, i.e. also egg, mass correlates with female mass (Kratovichil & Frynta 2002). Intraspecific correlations between female and egg size indicate egg size is not optimized but constrained by female size; otherwise both large and small females within a species should make eggs of the same optimal size. The same is true for the total clutch mass of lizards with VCS: within species, it increases with female body size as well (e.g. Olsson & Shine 1997).

The concordance between egg-mass allometries of lizards with VCS and anoles is reasonable when the minimal viable egg size is considered. The fecundity selection probably presses lizards with VCS to divide the total clutch mass into as many viable eggs as possible. If female anoles are selected to decrease their reproductive burden and to make a clutch as often as possible, they are apparently forced to make the smallest viable egg as well. Interspecific negative allometry of propagule size is documented in many oviparous

animal clades (e.g. in spiders: Marshall & Gittleman 1994; many insects: Berrigan 1991; García-Barros 2000; fish: Blueweiss *et al.* 1978; turtles: Elgar & Heaphy 1989; snakes: Shine *et al.* 1998; monitor lizards: Thompson & Pianka 2001; birds: Rahn, Paganelli & Ar 1975). The negative allometry in egg size is probably the result of ecological, physiological or developmental processes constraining the minimal propagule size (Minelli 2003; Kratochvíl & Frynta 2006a). We can only speculate why the minimal viable egg size increases with female body size. We stress the word minimal: the case of primitive geckos demonstrates the negative allometry between maternal and egg size is not always inevitable and is probably not forced by upper limits constraining egg size (such as limitation by pelvic opening or long developmental time; Kratochvíl & Frynta 2006a). Exploring minimal egg size constraints in different clades to determine whether there is any unifying principle in their formation would provide an interesting perspective to this issue.

Further research should also focus on the potentially simple proximate mechanisms enabling major evolutionary changes in reproductive allometries facilitating such a dramatic restructuring of life histories. Shifts in hormonal levels or in the roles of hormones are among the likely candidates. Gonadotrophins levels direct the number of maturing and ovulated follicles in lizards (Jones, Tokarz & LaGreek 1975; Sinervo 1999). Therefore, we predict both anoles and geckos exhibit functional alterations related to gonadotrophins – they ovulate maximally just a single egg per ovary during a reproductive bout. On the other hand, the amount of yolk given to an egg in reptiles is influenced by steroids (Jones *et al.* 1976; Bowden *et al.* 2004) and maybe dramatically different between these two groups with ICS. We can expect the mechanism controlling egg size should change especially in the gecko ancestor that started to produce larger eggs. What would be ideal for future physiological comparative studies are closely related animals differing in the mode of reproduction, e.g. *Polychrus* vs. anoles, or geckos vs. their relatives with VCS.

In summary, comparing basic reproductive allometries in four lizard lineages with contrasting reproductive methods, we show ICS in two important lizard groups (anoles and geckos) likely emerged for different reasons. In geckos, ICS evolved and is maintained by selecting larger offspring but in anoles, selection favoured reducing the female reproductive burden. Among lizards, anoles and primitive geckos seem to occupy opposite extremes in egg and/or clutch mass allometries, set by the upper limit to total clutch mass and lower limit to minimal egg size. Besides the extension of our knowledge on the evolution of ICS and general lizard life history, our study illustrates that a comparative study of ancestral and derived reproductive allometries among clades can be rather informative. In some cases, such comparisons allow us to deduce the causes of singular events in life-history

evolution and reveal constraints delimitating space of different solutions to life-history issues.

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