Biological Journal of the Linnean Society, 2006, **88**, 527–532. With 2 figures

Body-size effect on egg size in eublepharid geckos (Squamata: Eublepharidae), lizards with invariant clutch size: negative allometry for egg size in ectotherms is not universal

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Received 1 February 2005; accepted for publication 5 December 2005

Within a single clutch, smaller species of ectotherms generally lay a smaller number of relatively larger eggs than do larger species. Many hypotheses explaining both the interspecific negative allometry in egg size and egg size–number trade-off postulate the existence of an upper limit to the egg size of larger species. Specifically, in lizards, large eggs of large species could have too long a duration of incubation, or they could be too large to pass through the pelvic opening, which is presumably constrained mechanically in larger species. Alternatively, negative allometry could be a result of limits affecting eggs of smaller species. Under the latter concept, hatchling size in smaller species may be close to the lower limit imposed by ecological interactions or physiological processes, and therefore smaller species have to invest in relatively larger offspring. Contrary to these lower limit hypotheses, explanations based on the existence of an upper limit always predict negative egg-size allometry even in animals with invariant clutch size, in which naturally there is no egg size–number trade-off. We studied egg-size allometry in lizards of the family Eublepharidae, a monophyletic group of primitive geckos with large variance in body size and an invariant number of two eggs per clutch. We found an isometric relationship between egg and female size that does not support the upper limit hypotheses. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, **88**, 527–532.

ADDITIONAL KEYWORDS: constraint – egg mass – *Eublepharis* – life history – reproductive effort – reptile.

INTRODUCTION

Strong interspecific negative allometry for egg size has been documented in taxonomically widespread groups of ectotherms (e.g. spiders: Marshall & Gittleman, 1994; insects: Berrigan, 1991; García-Barros, 2000; fish: Blueweiss *et al.*, 1978; turtles: Elgar & Heaphy, 1989; snakes: Shine *et al.*, 1998; lacertid lizards: Bauwens & Díaz-Uriarte, 1997; Molina-Borja & Rodríguez-Domínguez, 2004; monitor lizards: Thompson & Pianka, 2001). Interspecific negative egg-size allometry means that among species, individual egg size increases much more slowly than does animal size, i.e. large animals have proportionally smaller eggs. It has been suggested that negative egg-size allometry is a general, although as yet unexplained, feature of ectotherm biology (Bauwens & Díaz-Uriarte, 1997). For example, in lizards, three testable hypotheses have been proposed to explain negative allometry (reviewed by Bauwens & Díaz-Uriarte, 1997). First, the duration of egg incubation could serve as a constraining factor, as the duration of egg incubation at a given temperature is assumed to increase with egg size. Larger species would thus be forced to lay relatively smaller eggs to prevent the cost of late hatching. The second hypothesis is based on the assumption of negative scaling of the diameter of the pelvic opening, which would serve as a mechanical constraint to maximum egg size. In the third hypothesis, hatchling size in smaller species may be close to the lower limit imposed by ecological interactions or

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*Corresponding author. E-mail: lukkrat@email.cz physiological processes, and therefore smaller species would have to invest in relatively larger offspring.

Previous authors have noted that negative egg-size allometry is associated with an increment in clutch size and the macroevolutionary trade-off between the size and the number of offspring. As a consequence of all three negative allometry hypotheses, smaller species invest resources during the reproductive bout in few, relatively large, offspring, while larger species invest in more, relatively small, offspring. However, under the first two hypotheses, the egg size–number trade-off arises from an upper limit on the egg size affecting larger species; the third hypothesis emphasizes the necessity of relatively large egg size in small species, which occurs at the cost of reduced egg number. Larger clutches of larger species are then the outcome of the fitness effect of investment in additional young, rather than investment in increased size of each offspring.

Nonetheless, not all species of ectotherms exhibit offspring size–number trade-off. In several lizard lineages, clutch size is fixed and the female is not able to divide the energy invested during the single reproductive bout into more offspring (Andrews & Rand, 1974; Shine & Greer, 1991). In lizards possessing invariant clutch size, we can test the fundamental predictions of hypotheses explaining negative egg-size allometry. If valid and general, the first (incubation time limitation) and the second (pelvic girdle limitation) hypotheses always predict negative allometry, even in lizards with invariant clutch size. The egg size in these species should thus follow the allometry of the individual egg in species with variable clutch size. On the other hand, the third (lower limit) hypothesis predicts that, without the possibility to divide resources into more eggs in larger species, the egg mass in the species with fixed clutch size should follow the allometry of the whole clutch mass in species with variable clutch size. In other words, under the third hypothesis, the predicted allometric pattern for groups with invariant clutch size is either isometry, as the total clutch mass increases in direct proportion to female size [e.g. in lacertid lizards (Bauwens & Díaz-Uriarte, 1997)], or negative allometry, which is the total clutch mass allometry in other groups [e.g. monitor lizards (Thompson & Pianka, 2001)].

To test these three hypotheses, we determined egg-size allometry in the members of the gecko family Eublepharidae, i.e. in a phylogenetically and ecologically homogenous group of lizards with invariant clutch size.

MATERIAL AND METHODS

SPECIES AND DATA

The family Eublepharidae is a small, monophyletic assemblage, the sister group of all other gekkotan lizards (Kluge, 1987). The phylogenetic relationships among the eublepharid species are relatively well corroborated (phylogeny based on morphology: e.g. Grismer, 1988; molecular approach: Ota *et al*., 1999; total evidence tree: Kratochvíl & Frynta, 2002). These lizards exhibit considerable diversity in body size (Kratochvíl & Frynta, 2003; Starostová, Kratochvíl & Frynta, 2005). All eublepharids except *Aeluroscalabotes felinus* (Günther, 1864), the only semiarboreal form, share similar ecology, being terrestrial and nocturnal (Grismer, 1988).

We studied captive individuals of nine species of eublepharids, including both the smallest and the largest species in the family. Specifically, from our laboratory breeding stocks between the years 1996 and 2004 we studied: two North American species, *Coleonyx brevis* Stejneger, 1893 and *C. variegatus* (Baird, 1858); two Middle American species, *C. elegans* Gray, 1845 and *C. mitratus* (Peters, 1845); two species from the Middle East, *Eublepharis angramainyu* Anderson & Leviton, 1966 and *E. macularius*; two species from the Far East, *Goniurosaurus luii* Grismer, Viets et Boyle, 1999 and *G. lichtenfelderi* (Mocquard, 1897); one West African species, *Hemitheconyx caudicinctus* (Duméril, 1851). All our data came from captive-bred eublepharids. Data from field observations remain scarce or nonexistent for many species, as all species share a secret, nocturnal way of life and often fieldwork is complicated further by the political situation in the areas that they inhabit.

Experimental animals were kept in glass cages with a shelter, water dish and substrate (wet peat moss or sand according to preferred humidity). They were placed in a centrally heated room with a temperature of between 25 and 27 °C (near the preferred body temperature in eublepharids; Dial & Grismer, 1992) and a light–dark cycle of 12 : 12. Water and food (vitaminized crickets, cockroaches and mealworms, and occasionally neonatal mice for large species) were provided three times a week. All females of each species were examined at feeding time and the stage of egg development was determined. When a female was considered to be gravid (oviductal eggs are recognizable easily through the abdomen wall), we gave her a small box with a wet substrate for egg laying. Gravid females were checked daily.

After egg laying, we recorded the snout–vent length (SVL) and postpartum body mass of the female, and the width, length, and mass of each individual egg. Longitudinal measurements were taken to the nearest 0.05 mm using calipers; egg masses were determined with an OHAUS balance to the nearest 0.1 g. Egg volumes were calculated from the formula for a prolate spheroid: $(1/6) \times \pi \times (\text{egg length}) \times (\text{egg width})^2$. As eublepharid eggs increase their volume during development, all eggs included in this analysis were measured less than 24 h after being laid. We measured 689 eggs from 358 clutches of 229 eublepharid females (264 eggs from 137 clutches of 62 *C. elegans* females; 172 eggs from 87 clutches of 60 *C. mitratus* females; 116 eggs from 61 clutches of 50 *E. macularius* females; 19 eggs from 12 clutches of seven *E. angramainyu* females; six eggs from three clutches of three *C. brevis* females; 42 eggs from 21 clutches of 16 *C. variegatus* females; 26 eggs from 14 clutches of 14 *H. caudicinctus* females; 36 eggs from 19 clutches of 15 *G. luii* females; eight eggs from four clutches of two *G. lichtenfelderi* females). We added previously published data for three other species (*A. felinus*, *Eublepharis turcmenicus* Darevsky, 1978 and *Coleonyx reticulatus*, Davis & Dixon, 1958). The data in other studies were obtained also from laboratory populations, and are thus comparable to ours.

STATISTICAL PROCEDURES

Average measurements of eggs in a given clutch were taken as an estimation of egg characteristics in a particular clutch. Next, for each variable, we calculated a single value for an individual female as a mean of the data from her subsequent clutches. We used these values for derivation of species means. Log_{10}-transformed species means were used in the estimation of interspecific allometries. All 'non-phylogenetic' allometries were analysed using an ordinary least squares linear regression model instead of the reduced major axis regression, as differences between these models are minimal when the correlation coefficient is higher than 0.9, as in all cases here (Harvey & Pagel, 1991). Deviations of isometric slopes were considered significant if the expected isometric slope fell outside the 95% CI of the estimated slope. To investigate whether relative egg size changes with body size, we also used an alternative method. We computed relative clutch mass (RCM) as the ratio of the clutch mass to the total maternal (clutch plus body) mass (Shine, 1992), and searched for correlations between body size (SVL) and RCM. In species with invariant clutch size, RCM is a direct estimate of egg size. All phylogenetically uncorrected calculations were performed using STATISTICA, version 6.0 (StatSoft Inc., 2001).

As species data are not independent because of shared phylogeny among more closely related taxa, we carried out phylogenetically controlled analysis using an independent contrast method (Felsenstein, 1985). We generated the independent contrasts of transformed female SVL, female mass, egg mass, egg length, egg width and egg volume using the software COMPARE vers. 4.5 (Martins, 2003), which employs a phylogenetic hypothesis based on both morphological and molecular characters (i.e. total evidence tree computed by Kratochvíl & Frynta, 2002). All branch lengths were set to 1. The diagnostic proposed by Garland, Harvey & Ives (1992) revealed that the contrasts were appropriately standardized. All correlations and regressions using contrasts were computed through the origin. We were unable to incorporate data on all species of eublepharid; however, simulations show that independent contrasts can be robust to incomplete taxon sampling (Ackerly, 2000).

RESULTS

The mass of measured eublepharid eggs ranged from approximately 0.3 g in *C. brevis* to at most 13.5 g in *E. angramainyu,* encompassing a 45-fold range (Fig. 1). Summary data are provided in Table 1. Two eggs were laid in 332 (nearly 93%) of all registered clutches, while the remaining 26 clutches encompassed only a single egg. Therefore, eublepharids can be considered as a group with almost invariant clutch size.

When species values were used without regard to phylogenetic relationships, the logarithmic regression of egg volume on SVL had an allometric constant of 3.05 ± 0.27 (SE), which was not significantly different from 3, i.e. the expected slope of volume vs. SVL in isometry. The amount of variance in egg volume explained by this regression was 92.9%, and this remained comparably high (92.8%) when we forced the regression to have a slope of 3. The same was true for all other variables. Forcing the regression to isometry (i.e. slope of 3 in mass and volume, slope of 1 in longitudinal measurements), the amount of explained

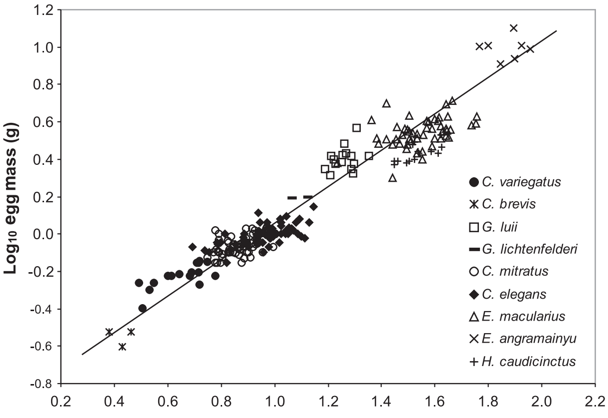

Figure 1. Mean egg mass plotted against mean female postoviposition body mass in nine species of eublepharid geckos from our laboratory. Each point represents a single female. Depicted line ($y = -0.918 + 0.977x$) denotes interspecific allometry as estimated using ordinary least squares regression from species means.

Table 1. Species means ± SE of female and egg characteristics for 12 species of eublepharid lizards

Species	Female SVL (mm)	Female mass (g)	Egg mass (g)	Egg length (mm)	Egg width (mm)	RCM
*A. felinus**	105.00	–	1.50	20.00	12.00	–
C. brevis	53.21 ± 3.42	2.67 ± 2.75	0.28 ± 0.24	12.73 ± 0.89	7.33 ± 0.39	0.18
C. elegans	84.45 ± 0.75	9.40 ± 0.61	1.00 ± 0.05	18.57 ± 0.20	9.84 ± 0.09	0.18
C. mitratus	76.30 ± 0.77	7.42 ± 0.62	0.87 ± 0.05	18.13 ± 0.20	9.39 ± 0.09	0.19
C. reticulatus†	84.00	–	–	22.00	11.00	–
C. variegatus	66.96 ± 1.48	4.56 ± 1.19	0.60 ± 0.10	16.31 ± 0.39	8.61 ± 0.17	0.21
E. angramainyu	158.10 ± 2.24	74.68 ± 1.80	9.95 ± 0.15	38.74 ± 0.58	21.76 ± 0.26	0.21
E. macularius	118.92 ± 0.84	35.53 ± 0.67	3.46 ± 0.06	27.36 ± 0.22	14.65 ± 0.10	0.17
E. turcmenicus‡	120.60	–	–	31.00	19.20	–
G. lichtenfelderi	93.83 ± 4.19	12.44 ± 3.37	1.57 ± 0.29	19.98 ± 1.09	12.00 ± 0.48	0.20
G. luii	105.54 ± 1.53	18.32 ± 1.23	2.55 ± 0.11	26.42 ± 0.40	13.47 ± 0.17	0.22
H. caudicinctus	114.15 ± 1.58	34.34 ± 1.27	2.71 ± 0.11	27.73 ± 0.41	13.18 ± 0.18	0.14

Relative clutch mass (RCM) estimates include clutch mass in both the numerator and the denominator. See text for sample sizes.

*Data from Manthey & Grossmann (1997). †Data from Easterla & Reynolds (1975); Gallo & Reese (1978). ‡Data from Sczerbak & Golubev (1986).

Table 2. Summary statistics of interspecific regression ($P < 0.00001$ in all cases) of egg and female mean characteristics on mean adult female snout–vent length based on phylogenetically uncorrected $\log_{10}$-transformed data

Dependent variable	*r*	a ± SE	b ± SE	*F*	d.f.
Egg volume	0.964	–2.788 ± 0.526	3.047 ± 0.266	131.37	1, 10
Egg mass	0.985	–6.004 ± 0.376	3.143 ± 0.190	272.71	1, 8
Egg length	0.957	–0.629 ± 0.189	1.000 ± 0.095	109.93	1, 10
Egg width	0.956	–0.939 ± 0.196	1.023 ± 0.099	106.86	1, 10
Female mass	0.992	–5.184 ± 0.308	3.217 ± 0.156	422.61	1, 7

No variable deviated significantly from isometry.

a, intercept; b, slope.

variance dropped from 97.2%, 98.4%, 91.7% and 91.4% to 96.9%, 97.9%, 91.7% and 91.4% in the case of egg mass, female mass, egg length and egg width, respectively (for values of estimated coefficients see Table 2). Analysis of RCM supported that egg size in eublepharids increases nearly proportionally to body size. We found no interspecific correlation between RCM and SVL ($r = 0.04$, $P = 0.92$, $N = 9$).

The results of analysis of phylogenetically corrected data were similar to those of the raw data. All slopes computed by COMPARE were not significantly different from isometry, i.e. their 95% CI overlapped with 1 in longitudinal measurements, and with 3 in volume and mass (egg length: $r = 0.90$, slope = 1.04 ± 0.16; egg width: $r = 0.86$, slope = 0.93 ± 0.18; egg volume: $r = 0.89$, slope = 2.90 ± 0.47; egg mass: $r = 0.98$, slope = 2.83 ± 0.21; female mass: $r = 0.98$, slope = 2.94 ± 0.25; all regressed against SVL; slopes are given as means ± SE).

Thus, the results of the analysis of both raw data and phylogenetic contrasts showed that egg size in eublepharids scale nearly perfectly isometrically with female size (Fig. 2).

DISCUSSION

We have shown the existence of a strong interspecific correlation between egg size and female body size in eublepharid geckos. Contrary to the general trend in ectotherms, this relationship was isometric instead of negatively allometric. The differences in allometric slopes of eublepharid geckos and those of other ectotherms including other lizard groups were pronounced. For example, the expected value of the regression slope of egg mass on female SVL under a model of geometric similarity is 3. Ordinary least squares regression slopes of this relationship are 1.51

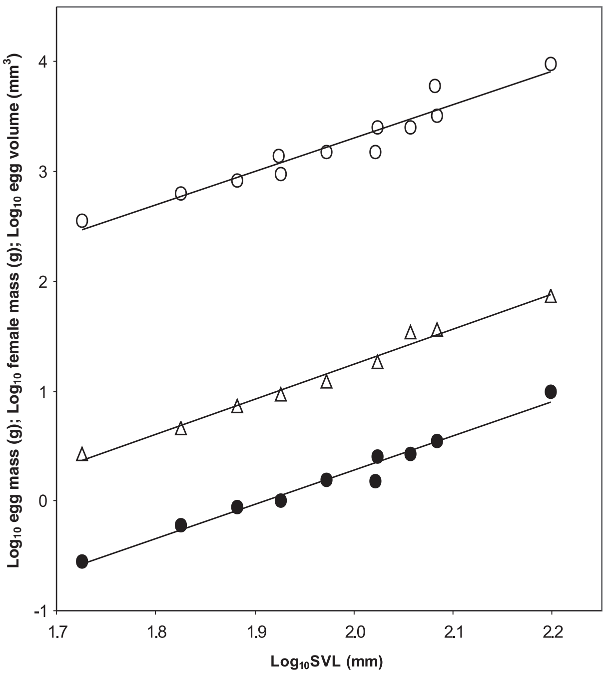

Figure 2. Interspecific relation of egg mass (●), postpartum female mass (△), and egg volume (○) with mean female snout–vent length (SVL) for eublepharid geckos. Ordinary least squares regression lines are depicted.

in monitor lizards and 1.68 in lacertids (Bauwens & Díaz-Uriarte, 1997; Thompson & Pianka, 2001), but they were 3.14 (not statistically distinguishable from 3) in eublepharids. In fish, amphibians and generally in reptiles, the regression slope of the individual egg mass on female mass is below 0.5 (0.42–0.43; Blueweiss *et al*., 1978), but it was nearly 1 (0.98) in eublepharids (1 is expected for isometry). Eublepharids thus present a rare exception to the negative egg-size allometry rule for ectotherms. As such, they offer an opportunity to test the hypotheses explaining interspecific egg-size allometry. The isometric relationship of eublepharid eggs is contrary to the predictions of the upper limit hypotheses (incubation limitation or pelvic girdle limitation hypotheses) for a group of lizards with invariant clutch size. The failure of the upper limit hypotheses to predict egg-size allometry in eublepharids questions their generality.

The lower limit hypothesis predicts in groups with fixed clutch size either negative egg-size allometry or isometry. We found a group with invariant clutch size possessing isometric relationship between egg and female size. Only such groups can be used to discriminate between the predictions of upper vs. lower limit hypotheses, and are therefore informative for testing alternative explanations on the negative egg-size allometry. The RCM in eublepharid geckos (range, 0.14–0.22; Table 1) was similar to that of lizards with variable clutch mass (e.g. cnemidophorines: range, 0.14–0.17; sceloporines: range, 0.19–0.32; see Shine, 1992). Our estimate of the RCM in *C. variegatus* (0.21) compares favourably with that reported for the same species by Shine in 1992 (0.22). In at least three eublepharid species, the egg mass correlates positively with female mass also intraspecifically (Kratochvíl & Frynta, 2002). Intraspecific correlations between female and egg size indicate that egg size is not optimized (otherwise both large and small females should make eggs of the same size), but is constrained by female size. Moreover, eublepharid females are anorexic several days before oviposition (L. Kratochvíl, pers. observ.). These findings support the hypothesis that eublepharid females (at least well-fed laboratory-raised animals) make eggs of maximal size until the whole space available within their body cavity is full. The egg size is then limited by a constraint imposed by the isometrically increasing amount of space available for eggs in the maternal body cavity. The support for the isometric relationship between female body size and the space available for eggs is both theoretical – based on elementary geometric rules – and empirical (Shine, 1992). We re-analysed Shine's data and found nearly perfect isometry between his measure of available abdominal volume and female body mass across 24 species of lizard (log–log regression: slope = 1.010 ± 0.048 (SE), $r = 0.976$). It can be assumed that a constraint on RCM set by physical limitations on abdominal space available to hold the clutch is more important at the interspecific than it is at the intraspecific level. Intraspecifically, reproductive output is often determined by limits imposed by energy accessibility below the maximum available abdominal space (Olsson & Shine, 1997). Under a lower limit hypothesis, in groups with fixed clutch size, when there is no selection to use the whole available body space for egg production, or when there are constraints preventing it in larger species, we can expect negative egg-size allometry.

In summary, evaluating the hypotheses explaining egg-size allometry in ectotherms in a clade with invariant clutch size, our study questions the generality of the hypotheses that assume the existence of an upper limit forcing negative egg-size allometry. This could be considered as support for the lower limit hypothesis. We stress that lineages with invariant clutch size provide a unique opportunity to test the predictions of the general life-history theory, which are usually tested in much more fecund species with variable clutch size (e.g. Elnum & Fleming, 2000 and references therein). The advantage of studying lineages with invariant clutch size is that they present a simplified model situation in which the progeny size–number trade-off is controlled, thus allowing study of life-history traits in an unusual framework.

ACKNOWLEDGEMENTS

We thank J. Moravec, J. Losos, A.F.G. Dixon and two anonymous reviewers for stimulating discussion and comments; R. Sherman, L. Kubička, J. Červenka, E. Landová and K. Zelená helped us to take care of study animals. The research was supported by the Grant Agency of the Czech Academy of Sciences (No. KJB6111302). Institutional support to L.K. was given by the Ministry of Education, Youth and Sports of the Czech Republic (project no. 0021620828). All work was performed in accordance with the regulations of the Institutional Animal Care and Use Committee of the Charles University.

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