

Morphological constraint on egg size: A challenge to optimal egg size theory?

(parental investment/reproduction/turtles)

JUSTIN D. CONGDON AND J. WHITFIELD GIBBONS

Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29801

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ABSTRACT Some freshwater turtles appear unable to produce eggs large enough to achieve the balance between size and number of eggs predicted by optimal egg size theory. We present evidence that pelvic girdle structure constrains egg size and thus offspring size in females of smaller-bodied species (*Chrysemys picta* and *Deirochelys reticularia*). The constraint is demonstrated by the correspondence of slopes of the increase of the pelvic aperture and egg width with increasing body size. This constraint appears to be relaxed in a larger-bodied species (*Pseudemys scripta*), in which the increase in pelvic aperture relative to body size is greater than the increase in egg width. This type of structural constraint on a reproductive trait should not occur unless there is strong selection on pelvic architecture for other functions, such as locomotion, support, and limb retraction, that prevent expansion of the pelvic aperture. Although other explanations may exist for other groups of organisms that appear to vary egg size, the large variation in egg size associated with body size in some species of turtles can be reconciled with optimal egg size theory only if a pelvic constraint model is accepted.

Investment in reproduction by female animals can be expressed as material and energy allocated to (i) behavior associated with mating or defense of breeding territories, (ii) eggs or developing offspring, and (iii) parental care of the young. Optimality models, which currently comprise most life history theories, are concerned with two major aspects of reproductive investment: (i) what determines the total level of reproductive effort? (1, 2) and (ii) what determines how total reproductive output is apportioned among individual offspring? (2).

Reproductive effort is that part of an organism's total resources allocated to reproduction (1). This concept was defined in terms of energy allocation by Hirshfield and Tinkle (2). All theories of reproductive allocation assume that the energy available to an organism is finite, so that allocation of more energy to reproduction results in a concomitant reduction in the energy allocated to other elements of the total energy budget (3–6).

Optimal egg size models predict that, within a population, natural selection has optimized egg or neonate size at the point where increased Darwinian fitness associated with increased egg size equals the reduction in fitness caused by a reduction in offspring number (7, 8). Evolutionary theory, in general, identifies the individual as the unit of selection, and only in cases in which reproduction consisted of producing one offspring would the fitness of the offspring and the parent be equal. In relatively stable environments, size of individual offspring should most often be under strong normalizing selection that reduces variation in egg and offspring size. Thus, among organisms that produce more

than one offspring per reproductive bout, the majority of variation in total reproductive output accompanying changes in available resources, age, or body size should result from changes in numbers of eggs rather than from changes in egg size.

Optimal egg sizes should be most evident in species with large clutch sizes and no postovulatory parental care (9), because their investment in an offspring is closely represented by the material or energy content in each egg. These features make some reptiles excellent organisms for testing hypotheses about optimal egg size. Variation in egg size within many lizard populations is negligible (10–17), suggesting that egg size is optimal, so that most of the variation in clutch mass associated with changes in resources or body size is caused by changes in the number of eggs.

Some lizards do appear to exhibit differences in egg size between early and late clutches within a year (18). Within the assumptions of optimal egg size theory, this suggests that different optima exist within a population at different times. However, the degree of difference between clutches in lizards is substantially smaller than the range in variation in egg size found in turtle populations of some species (19, 20). The option for adjustments in clutch size of course does not apply to lizards with fixed clutch size such as geckos, some skinks, most microteids, and iguanid lizards of the genus *Anolis*. If the optimal egg size model is to have generality among reptiles, the assumptions of the model must be applicable to groups other than lizards. Data from turtles were used to test the hypothesis that egg size within a species is optimized.

MATERIALS AND METHODS

Three species of freshwater emydid turtles (*Chrysemys picta*, *Deirochelys reticularia*, and *Pseudemys scripta*) were examined to determine relationships among clutch size, egg size, and female body size. Female turtles (*C. picta* from Livingston County, Michigan; *P. scripta* and *D. reticularia* from Aiken and Barnwell Counties, South Carolina) were captured in baited aquatic traps, at terrestrial drift fences, or by hand. All gravid females were measured, weighed, and x-rayed (21) to determine clutch size, egg width, and width of the pelvic aperture. Measurements were taken only from x-ray photographs that showed a symmetrical view of the pelvic aperture; aperture width was considered to be the shortest distance between the ilia. Some x-rayed females were given injections of oxytocin (22) to induce them to lay eggs. Egg width can be determined directly from x-ray photographs and is strongly correlated with egg wet mass, dry mass, lipids or total energy content, and size of hatchlings (19). Egg length to egg width ratios of freshly laid eggs were similar for all three species: *C. picta* = 1.75; *D. reticularia* = 1.67; and *P. scripta* = 1.64. Significant variation in slopes of clutch size, egg width, and pelvic aperture width on plastron length of females occurred among species as determined by Type III sums-of-squares in covariance analyses using the

SAS GLM procedure (23). Confidence intervals on regression slopes were computed by using studentized range statistics based on a pooled estimate of residual variance.

RESULTS AND DISCUSSION

Differences in the relationships of clutch size, egg width, and pelvic opening width on body size (plastron length) of females exist among the three species (Fig. 1). The results seriously

challenge present versions of optimal egg size models by demonstrating that egg size in two of the species (*C. picta* and *D. reticularia*) changes substantially as a function of female body size.

One possible explanation for why some turtle species depart from the general pattern observed in reptiles is that maximum (and optimal?) egg width might be constrained by the size of the pelvic aperture (19, 20, 24). Although the pelvic aperture must be large enough to accommodate the passage

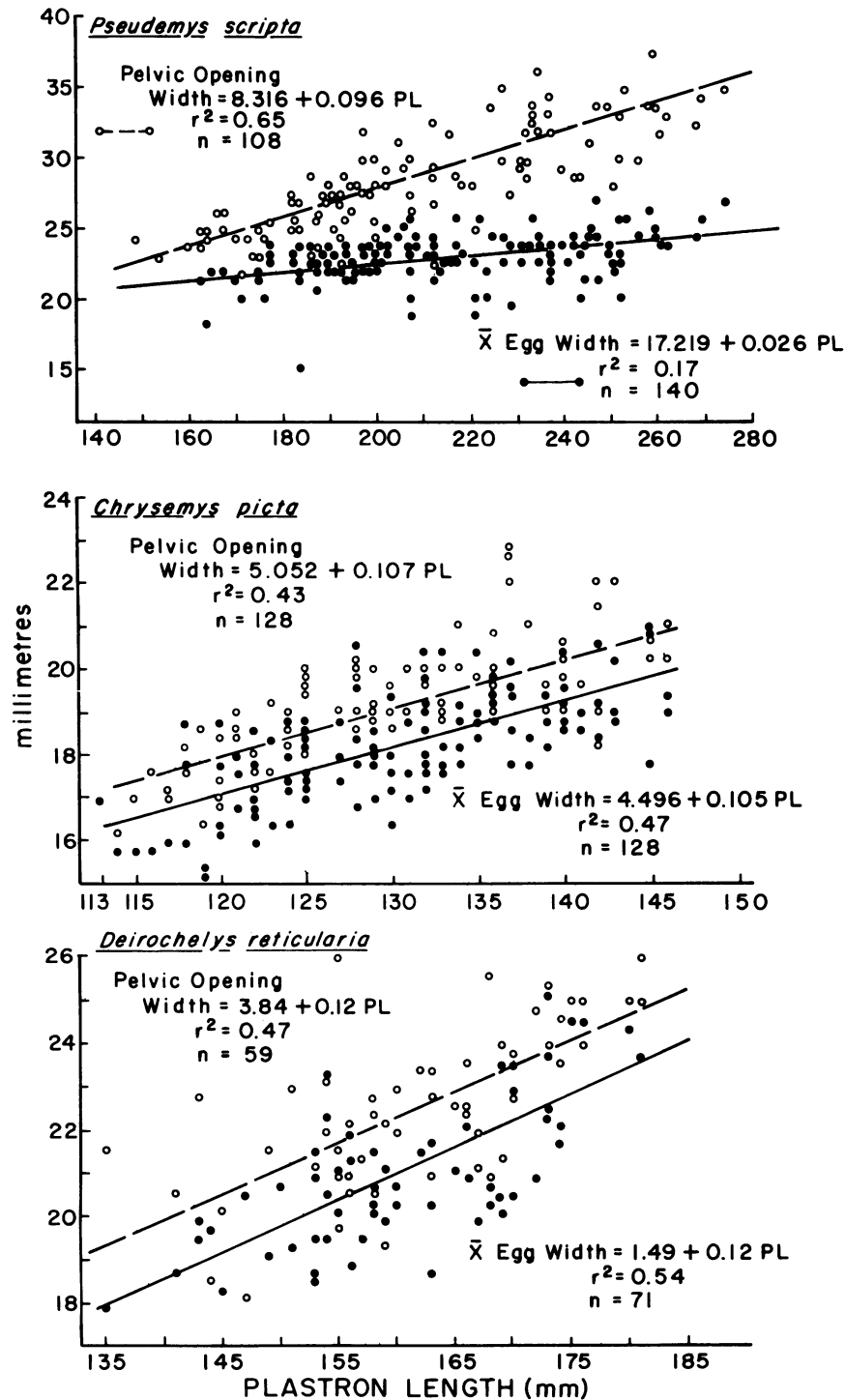


FIG. 1. Clutch size, egg size, and pelvic aperture width all increase as body size (plastron length, PL) of adult female turtles increases. However, the relationships of these three traits to body size are substantially different. The variation in clutch size (not shown) attributed to body size of *P. scripta* ($r^2 = 0.58$) was almost 3 times that of *C. picta* and *D. reticularia* ($r^2 < 0.20$). The variation in egg width attributed to body size of *C. picta* or *D. reticularia* ($r^2 > 0.45$) was approximately 3 times that of *P. scripta* ($r^2 = 0.07$). Slopes of pelvic aperture width among all three species were not significantly different (common slope 0.11) ($r^2 = 0.92$).

of eggs, the pelvic girdle has other functions. In many species of freshwater turtles the pelvic girdle is subjected to the stresses of limb retraction, suspension of a large body mass on widely spaced supports during terrestrial locomotion when males search for mates and females make nesting migrations, and also nest construction by females, all critical aspects of their life histories. Thus, the selective forces operating on the architecture of the pelvic girdle may be complex and in opposition to one another, and, in turn, result in constraint of egg size by the pelvic aperture width, which would explain why egg size is positively related to body size in some species.

Slopes of both clutch size ($F_{2, 434} = 0.81$; $P = 0.44$) and pelvic opening width ($F_{2, 222} = 1.33$; $P = 0.27$) on body size among the three species were not significantly different. Similar slopes for pelvic aperture width on plastron length for the three species suggest that constraints on the architecture of the pelvic girdle might exist in emydid turtles. Slopes of the relationships of egg width to body size were significantly different among species ($F_{2, 239} = 37.12$; $P = 0.0001$). However, the slope of the relationship of egg width to body size was approximately one-fifth of that for *P. scripta* (slope = 0.020; 95% confidence limits = 0.011), the species that increased egg size least, than it was for *C. picta* or *D. reticularia* (Table 1). The potential for the pelvic opening width to constrain egg size in *C. picta* and *D. reticularia* is clearly demonstrated by the comparison of slopes of egg width on body size and pelvic opening width on body size (Table 1). These slopes are similar and indicate that each millimeter increase in pelvic opening is accompanied by an equivalent increase in egg width. The correspondence of slopes indicates that the response to selection pressure for increased egg size is limited by the rate of expansion of the pelvic aperture in *C. picta* and *D. reticularia* but not in *P. scripta*.

We have presented strong evidence that the width of the pelvic girdle constrains egg size, and thus offspring size (19), in some species of turtles. The constraint is present in both of the smaller-bodied species (*C. picta* and *D. reticularia*) and does not diminish over the range of adult body sizes examined in these two species, but it is not apparent at any body size in *P. scripta*, the species with the largest body size. This suggests that where the constraint occurs, the architecture of the pelvic girdle is under strong counter-selection pressure associated with the requirements of locomotion, limb retraction, and body support that prevents expansion of the aperture to accommodate greater parental investment in individual offspring. A structural constraint of this type would be categorized as an "adaptive compromise" (25) and is therefore not analogous to the concept of spandrels or an architectural constraint as a nonadaptive by-product that results from selection acting on other aspects of the phenotype (26).

Table 1. Comparison of slopes of linear regressions of egg width and pelvic aperture width on plastron length of female turtles from which paired measurements were obtained

Species	Regression slope	
	Egg width	Pelvic aperture width
<i>C. picta</i>	0.09 ± 0.02 (n = 104)	0.12 ± 0.02 (n = 104)
<i>D. reticularia</i>	0.11 ± 0.03 (n = 58)	0.12 ± 0.03 (n = 58)
<i>P. scripta</i>	0.02 ± 0.01 (n = 63)	0.10 ± 0.02 (n = 63)

Slopes are presented ± 95% confidence limits. The numbers of individuals studied are given in parentheses.

Optimal egg size, as defined in terms of a female's fitness, in relation to the size and number of her offspring does not appear to be obtainable by *C. picta* or *D. reticularia* of any body size within the populations examined. Attainment of sexual maturity by females at a relatively small body size may result in offspring of suboptimal size and lower individual fitness. However, the probability of a fitness gain by the female producing such offspring must be weighed against the probability of her mortality associated with further delay in reproduction.

We predict that at larger body sizes both *C. picta* and *D. reticularia* will show the same lack of correspondence of the relationship between pelvic opening and egg width to body size that is demonstrated in *P. scripta*. An opportunity to test this prediction exists in the populations of larger-bodied individuals of both species: *D. reticularia* in Florida and *C. picta belli* in the north central United States and Canada. In addition, constraint of the pelvic aperture on egg size may occur in lizards with fixed clutch size, in which egg size has been shown to increase with body size of females.

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