

The importance of energetic versus pelvic constraints on reproductive allocation by the eastern fence lizard (*Sceloporus undulatus*)

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In ectothermic species, females often produce larger eggs in colder environments. Models based on energetic constraints suggest that this pattern is an adaptation to compensate for the slower growth of offspring in the cold. Yet, females in cold environments also tend to be larger than females in warm environments. Consequently, thermal clines in egg size could be caused by pelvic constraints, which stem from the inability of large eggs to pass through a small pelvic aperture. Models based on energetic constraints and models based on pelvic constraints predict similar relationships between maternal size and egg size. However, pelvic constraints should produce these relationships both within and among populations, whereas energetic constraints would not necessarily do so. If pelvic constraints are important, we might also expect small females to compensate by producing eggs that are relatively rich in lipids (i.e. high energy density). The present study aimed to assess whether energetic or pelvic constraints generate geographical variation in egg size of the lizard *Sceloporus undulatus*. Pelvic width is very highly correlated with body length in *S. undulatus*, making maternal size a suitable measure of pelvic constraint. Although maternal size and egg mass (dry and wet) covaried among populations, these variables were generally not related within populations. Energetic density of eggs tended to increase with decreasing egg mass (dry and wet), but this relationship was strongest in populations where no relationship between maternal size and egg mass was observed. Our results do not support the pelvic constraint model and thus indicate energetic constraints play a greater role in generating geographical variation in egg size. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 91, 513–521.

ADDITIONAL KEYWORDS: ectotherms – egg size – life history – lizards – maternal size – temperature.

INTRODUCTION

All organisms make the critical decisions of how much energy to invest in reproduction and how to partition this investment among offspring. Reproductive decisions are influenced by environmental conditions, which cause the natural selection of eggs of a particular size. In a given environment, natural selection favours the egg size resulting in the highest fitness for the parent: the optimal egg size (Smith & Fretwell, 1974). Recently, biologists have gathered direct evidence that natural selection affects egg size. For exam-

ple, experimental reduction of yolk in reptilian eggs yielded smaller offspring that suffered poorer locomotor performance and lower survivorship than offspring from unmanipulated eggs (Sinervo, 1999; Warner & Andrews, 2003). Therefore, we expect egg size to vary in accordance with the net benefits of enhancing the performance of offspring.

As with any phenotype, the optimal egg size is partly determined by constraints (Maynard Smith, 1978; Arnold, 1992). A fundamental constraint is the finite supply of energy, which can be deposited in few large or many small eggs. Early models of optimal reproduction focused primarily on energetic constraints (Smith & Fretwell, 1974; Parker & Begon, 1986; McGinley, Temme & Geber, 1987). Such models predict that females will produce larger eggs in poorer

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environments if this allocation enhances the performance of offspring. Moreover, a negative relationship between egg size and clutch size should be observed when energy availability varies little among females (Van Noordwijk & DeJong, 1986). These energetic constraints are relaxed when mothers can obtain additional energy. For example, larger females often have more energy for reproduction than smaller females because of greater rates of acquisition and greater capacities for storage. In these cases, large females can use their additional energy to produce more and/or larger eggs than small females. Under certain conditions of density dependence, larger females should use their additional energy to produce larger eggs (Parker & Begon, 1986).

Subsequent to early models of reproductive allocation, an additional constraint has come into focus. Congdon & Gibbons (1987) proposed that the size of a female constrains the size of her egg. Because eggs must pass through the pelvic aperture, large eggs produced by small females can jam or rupture during oviposition (Sinervo & Licht, 1991; Sinervo, 1999). After factoring in such risks, the optimal egg size for a small female might be smaller than that of a large female. This idea, usually referred to as the pelvic constraint hypothesis, predicts that egg size will be positively correlated with pelvic size, or some proxy such as body size (Congdon, Gibbons & Greene, 1983; Congdon & Gibbons, 1987; Michaud & Echternacht, 1995). Undoubtedly, both energetic and pelvic constraints cause variation in egg size within and among species of vertebrates.

The present study aimed to assess the relative importance of energetic and pelvic constraints in generating geographical variation in egg size. The eastern fence lizard (*Sceloporus undulatus*) exhibits phenotypic covariation that supports models based on either energetic or pelvic constraints. Females in colder environments lay larger eggs (Angilletta, Oufiero & Sears,

2004), possibly because cold environments retard the growth of offspring (Perrin, 1988; Yampolsky & Scheiner, 1996). On the other hand, females in colder environments tend to be larger (Angilletta *et al.*, 2004), which could enable them to store more energy, pass larger eggs, or both. How can we distinguish which constraints are the primary cause of this geographical variation?

Comparative studies of intraspecific variation in egg size will help to answer this question (Congdon & Gibbons, 1987; Michaud & Echternacht, 1995). Pelvic constraints should produce similar relationships between maternal size and egg size within and among populations, as long as the allometry of the pelvis remains relatively constant. Hence, qualitative differences in the relationship between maternal size and egg size among populations should cast doubt on the importance of pelvic constraints (Fig. 1). Nevertheless, the same differences would not refute hypotheses based on energetic constraints because optimal egg size would not scale with maternal size in all environments (Parker & Begon, 1986). Thus, a comparison of maternal size–egg size relationships within species can help to assess the relative importance of pelvic and energetic constraints. Here, we use such a comparison to show that pelvic constraints are probably not a major cause of geographical variation in the egg size of *S. undulatus*.

MATERIAL AND METHODS

SAMPLING AND CARE OF FEMALES

Gravid females were collected from populations belonging to two clades, which are distributed along latitudinal gradients (Leaché & Reeder, 2002). From a midwestern clade, we sampled a northern population in Indiana (Monroe County) and a southern population in Florida (Santa Rosa County). From an eastern clade, we sampled a northern population in New Jer-

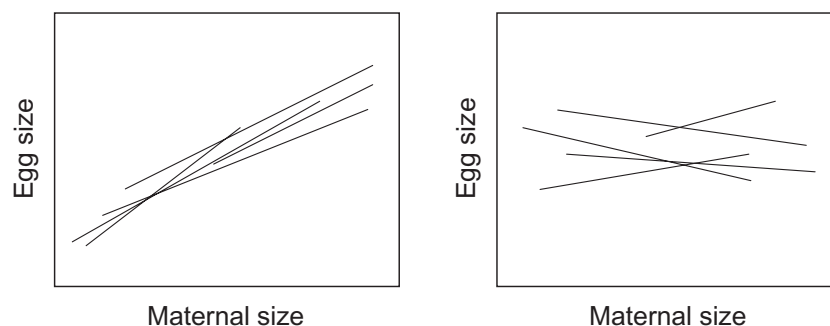


Figure 1. Hypothetical relationships between maternal size and egg size for multiple populations of a species. When relationships for different populations resemble one another (left), either energetic or pelvic constraints could explain the pattern. When relationships differ qualitatively (right), pelvic constraints are less likely to explain the pattern than are energetic constraints.

sey (Burlington County) and a southern population in South Carolina (Aiken County). We also sampled a population in Virginia (Montgomery and Craig Counties) from the eastern clade because this population occurs at high altitude (660 m). Mean air temperatures in New Jersey, Virginia, and Indiana (12.4°, 11.0°, and 11.9 °C, respectively) are much lower than those in South Carolina and Florida (18.0° and 19.2 °C, respectively). Females from cold environments tend to be larger than females from warm environments (Angilletta *et al.*, 2004).

Gravid females were housed in 38-L terraria, which were kept in an environmental chamber under a 12 : 12 h light/dark cycle and an ambient temperature of 23 °C. An incandescent bulb was placed above one end of each terrarium to enable behavioural thermoregulation. Crickets (*Acheta domestica* Linnaeus) were offered three times per week, and water was provided *ad libitum*.

COLLECTION AND ANALYSIS OF EGGS

Eggs were collected by hormonally inducing females to oviposit (Andrews *et al.*, 1999). Each female was injected intraperitoneally with 0.3–0.5 mL of oxytocin. Just prior to injection, the snout–vent length (SVL) was measured to the nearest mm (hereafter referred to as maternal size); SVL is an excellent proxy for pelvic width when access to radiographic equipment is not available (Fig. 2; Congdon & Gibbons, 1987; Michaud & Echternacht, 1995). Following injection, females were placed in ventilated plastic containers, which were kept in an illuminated incubator that maintained a temperature of 30 °C (Model 818, Preci-

sion Inc.). Females were observed periodically until oviposition was completed. As each egg was laid, it was weighed to the nearest 0.1 mg. Two to four eggs per clutch were stored in glass vials filled with nitrogen and were frozen at –80 °C for analysis of energy content and energy density.

Inducing oviposition enabled us to weigh eggs as they were laid, avoiding changes in mass caused by water loss or gain. This method is not without its drawbacks; the duration of egg retention could have affected wet mass at oviposition (Warner & Andrews, 2003). Nonetheless, two facts lead us to conclude that variation in wet mass was not adversely affected by our method. First, a previous study of *S. undulatus* showed the use of oxytocin had a minor effect on the embryonic stage at oviposition (Parker, Andrews & Mathies, 2004). More importantly, analyses of wet masses and dry masses of eggs produce were concordant (see Results).

The energy content and energy density of each egg were measured by bomb calorimetry. Eggs were lyophilized for approximately 24 h, weighed to the nearest 0.1 mg, and homogenized using a mortar and pestle. Homogenized samples were compressed into pellets (approximately 50 mg each) and combusted in a semimicro bomb calorimeter (Model 1425, Parr Instrument Co.). The calorimeter was calibrated daily using benzoic acid as a standard. Calorimetry yielded the energy density (kJ g⁻¹) of each egg, which was multiplied by its dry mass to yield the total energy content. Because lipid and protein have different energy densities (Schmidt-Nielsen, 1997), the energy density of an egg reflects the relative proportion of these macromolecules (hereafter referred to as egg composition).

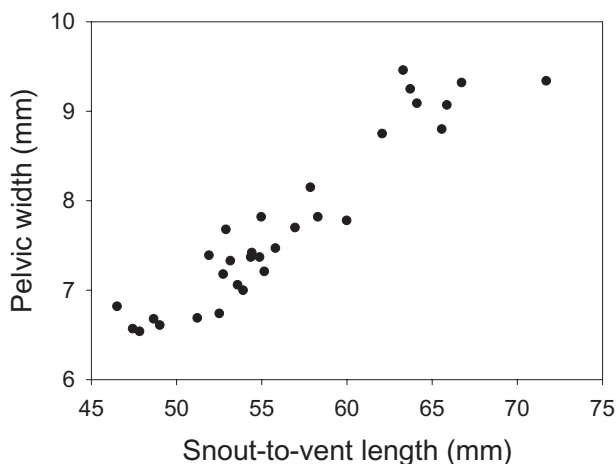


Figure 2. The snout–vent length of a female of *Sceloporus undulatus* accurately predicts its pelvic width. ($r^2 = 0.89$; $t = 15.4$, $P < 0.00001$, $N = 31$). These data were recorded from X-radiographs of gravid females from South Carolina (Angilletta, 1999).

STATISTICAL ANALYSES

We sought to describe both inter- and intraspecific covariation between maternal size and reproductive traits. First, we used a principal component analysis (PCA) to examine the covariation among maternal size, egg mass, and energy density; we also included clutch size in this analysis because models of energetic constraints predict that clutch size will be negatively related to egg size (Smith & Fretwell, 1974) or positively related to maternal size (Parker & Begon, 1986). The PCA enabled us to not only characterize the relationship between maternal size and reproductive traits, but also to determine whether this relationship was driven partly by variation among populations. We accomplished this latter goal by using analysis of variance to compare scores of the first principal component among populations. Before conducting the PCA, we used the diagnostic tests suggested by McGarigal, Cushman & Stafford (2000) to establish that our data met the assumptions. To detect a potential violation of

Table 1. Reproductive traits vary among females from different populations of *Sceloporus undulatus*

Population	N	Maternal SVL (mm)	Clutch size	Dry egg mass (mg)	kJ g ⁻¹	kJ egg ⁻¹
Indiana	17	77.4 ± 2.1	10.6 ± 1.1	184.0 ± 12.4	21.35 ± 0.63	3.921 ± 0.264
Florida	12	60.8 ± 3.4	5.0 ± 0.7	146.0 ± 14.9	23.03 ± 0.63	3.355 ± 0.317
New Jersey	15	71.9 ± 2.0	8.0 ± 1.2	188.7 ± 12.4	22.24 ± 0.87	4.172 ± 0.184
Virginia	17	71.7 ± 2.4	9.1 ± 1.4	198.3 ± 11.0	21.33 ± 0.69	4.219 ± 0.233
South Carolina	10	69.3 ± 3.8	8.3 ± 1.7	169.7 ± 12.4	22.72 ± 1.17	3.837 ± 0.19
All populations	71	70.6 ± 1.7	8.4 ± 0.6	178.0 ± 7.0	22.05 ± 0.35	3.899 ± 0.131

Data are means ± 95% confidence intervals.
SVL, snout–vent length.

the assumption of multivariate normality, we assessed the skewness, kurtosis, and normality of the scores for principal components, and examined normal probability plots for the variables and scores. To ensure that the variables met the assumption of linearity, we inspected a scatter plot of scores for the first two principal components (PC1 vs. PC2). The broken stick criterion was used to decide whether the second principal component was worthy of interpretation (Jackson, 1993).

We used linear regression to estimate the effect of maternal size on reproductive traits within populations. Relationships between maternal size and egg mass (wet and dry) were examined for evidence of pelvic constraints. Additionally, the relationship between dry egg mass and energy density was quantified to see whether females altered the composition of their eggs to compensate for potential constraints on egg size. We avoided the possibility of pseudo-replication by analysing the mean egg mass and mean energy density of each clutch rather than measures of individual eggs. All analyses were conducted using Statistica, version 6.0 for Windows (StatSoft, Inc., 2003). Descriptive statistics are provided as means ± 95% confidence intervals.

RESULTS

The reproductive traits of *S. undulatus* vary greatly throughout its natural range (Niewiarowski, Angilletta & Leaché, 2004), and this variation can be seen among the five populations that we sampled (Table 1). The PCA defined a linear combination of maternal size, clutch size, egg mass, and energy density that explained 60% of the variation in these traits (Table 2). This principal component indicates that larger females produced larger clutches of heavier eggs. Interestingly, these heavier eggs were less dense energetically. Consequently, the difference between the energy contents of small and large eggs was less than expected from an isometric scaling of energy content with egg mass.

Table 2. Principal components relating female size to three measures of reproductive allocation

Variable	PC1	PC2
Maternal SVL	-0.898	-0.316
Clutch size	-0.747	-0.605
Mass of eggs	-0.762	0.462
Energy density of eggs	0.689	-0.558
Eigenvalue	2.42	0.99
% Variance	60.53	24.77
Total variance	60.53	85.30

The first principal component (PC1) shows that larger females tend to make larger clutches of larger eggs that have a lower energy densities.
SVL, snout–vent length.

Our comparison of PC scores (Fig. 3) revealed that maternal size and reproductive traits varied significantly among populations (PC1: MS = 16.77, $F_{4,67} = 18.18$, $P < 0.0001$; PC2: MS = 2.01, $F_{4,67} = 3.80$, $P < 0.01$). In the eastern clade, the mean PC score of females from Virginia was significantly lower than the mean PC score of females from South Carolina (-0.78 ± 0.44 vs. 0.53 ± 0.61 ; Tukey's test, $P < 0.01$). The mean PC score of females from New Jersey (-0.27 ± 0.62) did not differ significantly from the mean PC score of females from Virginia or South Carolina ($P > 0.05$ for both pairwise comparisons). In the midwestern clade, females from Indiana had a significantly lower mean PC score than females from Florida (-0.93 ± 0.49 vs. 1.78 ± 0.61 ; $P < 0.01$). Based on these comparisons, we conclude that females in colder environments were larger and produced more eggs of a larger size but lower energy density.

Based on our regression analyses, the relationship between maternal size and egg size differed greatly among populations (Fig. 4). In the midwestern clade (Florida and Indiana), larger females produced heavier eggs (dry egg mass: $\beta = 0.78$, adjusted

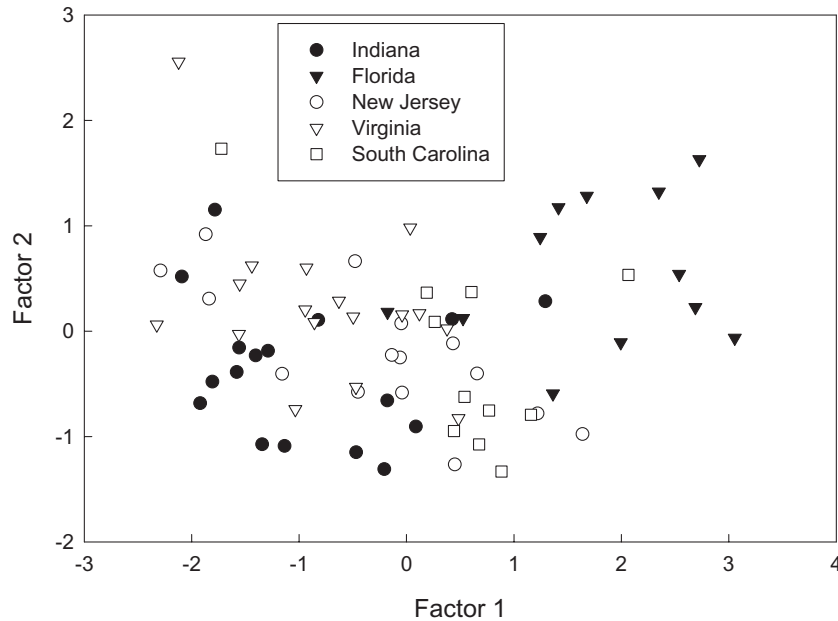


Figure 3. Principal component scores indicate lizards from cold environments (Indiana, New Jersey, and Virginia) generally laid larger clutches of larger eggs than lizards from warm environments (Florida and South Carolina). Each principal component (PC1 and PC2) describes a linear combination of maternal size, clutch size, egg mass, and energy density (Table 2). An analysis of variance revealed significant variation in both PC1 ($MS = 16.77$, $F_{4,67} = 18.18$, $P < 0.0001$) and PC2 ($MS = 2.01$, $F_{4,67} = 3.80$, $P < 0.01$) among populations.

Table 3. Regression models of the relationship between dry egg mass (g) and energy density (kJ g^{-1}) in five populations of *Sceloporus undulatus*

Population	N	β	α	F	Adjusted r^2	P
Indiana	17	-14.00	23.92	1.25	0.015	0.281
Florida	12	-15.10	25.23	1.49	0.043	0.249
New Jersey	15	-51.98	32.05	15.20	0.503	0.002
Virginia	17	-21.15	25.48	1.97	0.054	0.179
South Carolina	10	-58.15	32.79	5.49	0.310	0.044

The coefficient (β) and intercept (α) of each model are provided as estimates of the size of the effect.

$r^2 = 0.59$, $P < 0.01$; wet egg mass: $\beta = 0.65$, adjusted $r^2 = 0.40$, $P < 0.01$) with more energy ($\beta = 0.69$, adjusted $r^2 = 0.45$, $P < 0.01$), suggesting that pelvic constraints could have influenced reproductive allocation. In the eastern clade, neither egg mass (dry egg mass: $\beta = 0.09$, adjusted $r^2 = 0.09$, $P = 0.56$; wet egg mass: $\beta = -0.06$, adjusted $r^2 = -0.02$, $P = 0.68$) nor total energy ($\beta = -0.04$, adjusted $r^2 = -0.02$, $P < 0.78$) was related to maternal size. Given these markedly different patterns, we conclude that pelvic constraints are a poor explanation of variation in egg mass or energy content in *S. undulatus*.

Interestingly, we observed a negative relationship between egg mass and energy density within and among populations (Tables 2, 3, Fig. 4D). These relationships were statistically significant for lizards from

New Jersey and South Carolina, but the common trend among all five populations suggests the phenomenon could be more general. Energy densities indicate smaller eggs contained a greater proportion of lipids than larger eggs. This variation in energy density did not compensate completely for variation in egg mass, but smaller eggs contained more energy than would be expected from an isometric scaling of energy content with egg mass. For example, a two-fold difference in dry egg mass yielded only a 1.5-fold difference in energy content (Fig. 4D).

DISCUSSION

We examined variation in reproductive allocation within and among populations to assess the role of

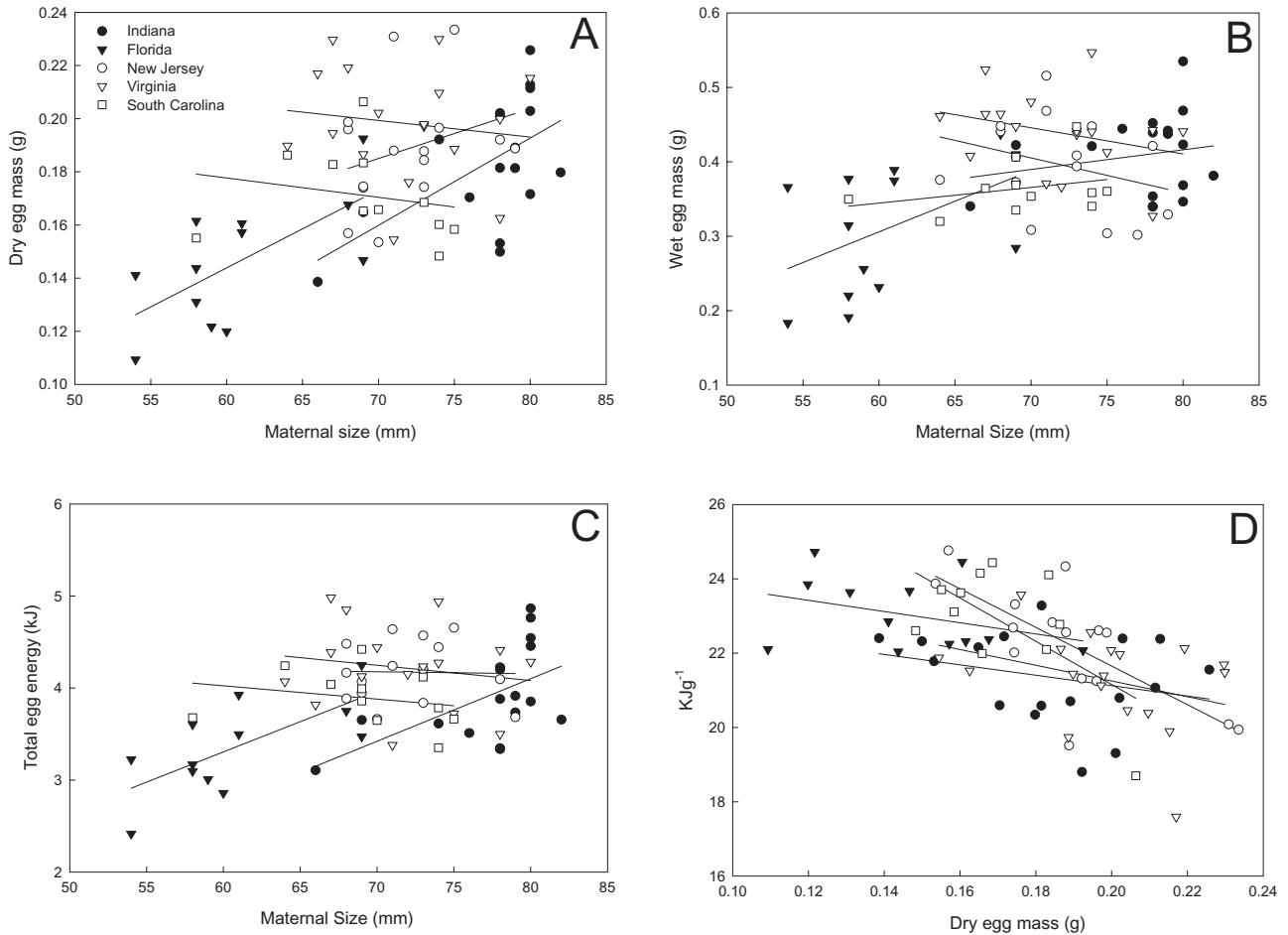


Figure 4. Relationships between maternal size and dry egg mass (A), wet egg mass (B), and total energy content (C), and between dry egg mass and energy density (D) in five populations of *Sceloporus undulatus*. In populations from the midwestern clade (filled symbols), dry egg mass, wet egg mass, and total energy were positively related to maternal size. In populations from the eastern clade (unfilled symbols), no significant relationships were observed for these three variables. In New Jersey and South Carolina, energy density decreased significantly with increasing dry egg mass (for model parameters, see Table 3).

energetic vs. pelvic constraints in generating geographical variation in egg size. Both energetic and pelvic constraints can affect the optimal egg size (Smith & Fretwell, 1974; Parker & Begon, 1986; Congdon & Gibbons, 1987). Nevertheless, their relative impact on natural variation in egg size can be difficult to assess when both kinds of constraints lead to similar predictions about optimal egg size. Models of energetic constraints predict females in colder environments should lay larger eggs (Perrin, 1988). Yet thermal clines in maternal size suggest models of pelvic constraints might better explain thermal clines in egg size. To make matters worse, models of energetic constraints also predict larger females will lay larger eggs under certain conditions (Parker & Begon, 1986). If pelvic constraints are important, variation in egg size is dictated by the physical capacity to successfully pass an egg. If pelvic constraints are not important,

variation in egg size could reflect adaptive strategies of energy allocation. The distinction between these two mechanisms is critical to evaluating the evidence favouring one model over the other. For us to consider pelvic constraints as a viable hypothesis, we must observe a positive correlation between maternal size and egg mass both within and among populations. Although variation among populations suggests either mechanism, variation within populations does not consistently support the pelvic constraint hypothesis.

Inconsistent support for the pelvic constraint hypothesis leads us to focus on other mechanisms that could cause the patterns within and among populations of *S. undulatus*. Two mechanisms involving energetic constraints are plausible. First, optimality theory predicts females should produce relatively large offspring when environmental conditions retard the growth of offspring (Sibly & Calow, 1983; Taylor &

Williams, 1984; McGinley *et al.*, 1987). In ectotherms like *S. undulatus*, cold environments retard growth by reducing rates of feeding and digestion (Angilletta, 2001). Based on this thermal effect, certain theorists reasoned that females should lay smaller eggs in warmer environments (Perrin, 1988; Yampolsky & Scheiner, 1996). They based this prediction on the implicit assumptions that: (1) the thermal sensitivity of growth rate does not acclimate and (2) temperature does not affect the relationships among size, survival, and fecundity. Consistent with their prediction, lizards from cold environments (Indiana, New Jersey, and Virginia) produced larger eggs than lizards from warm environments (Florida and South Carolina).

Additionally, females from northern populations might lay larger eggs because they have more energy stores at the time of reproduction. Larger eggs are thought to enhance the competitive ability of offspring, and females with greater energy stores can afford to provision their offspring for a competitive environment without having to produce fewer offspring (Parker & Begon, 1986). A broad comparative study suggests this mechanism could be more important than thermal constraints on the growth of offspring (Angilletta, Oufiero & Leaché, 2006). Yet, nothing prevents both mechanisms from favouring large eggs in cold environments. Therefore, theorists should work to integrate these mechanisms to form a more general model of reproductive allocation.

Ultimately, experiments are needed to confirm adaptation of reproductive traits. Because experimental studies generally consume more time, energy, and money than comparative studies, analyses such as ours enable researchers to identify the most plausible hypotheses on which to focus their experimental efforts. By eliminating pelvic constraints as a plausible hypothesis, we can now focus on models based on energetic constraints. First, we could use methods of phenotypic engineering to miniaturize and gigantize eggs, providing a broad distribution of offspring sizes for field studies of selection (Sinervo, 1990; Sinervo & Licht, 1991). If cold environments favour larger offspring than warm environments do, we should be able to detect this by comparing fitness landscapes measured in warm and cold environments. Second, we could determine whether larger mothers should produce larger eggs in these environments. This prediction depends on the assumptions that larger females store more energy and that the survival of offspring depends on their density. The former assumption seems warranted, but the latter assumption needs to be validated. We could alter the densities of juveniles in natural environments and see whether the performance of individuals is affected (Ferguson & Talent, 1993; Tinkle, Dunham & Congdon, 1993). Given our findings, any of these experiments should be priori-

tized over experiments designed to evaluate models based on pelvic constraints.

If pelvic constraints are unimportant, why does egg size vary so much within populations? For example, females from Virginia produced eggs that ranged from 0.15 to 0.23 g in dry mass and 3.5–5 kJ in energy content. Furthermore, maternal size fails to explain any of this variation (Fig. 4). A similar result was obtained by Angilletta, Sears & Winters (2001) during a previous study of *S. undulatus*. Great variation in egg size does not accord with optimality models (Smith & Fretwell, 1974; McGinley *et al.*, 1987), which predict that females should produce eggs of the same size given a seemingly reasonable set of assumptions. Roosenburg & Dunham (1997) proposed that physiological constraints prevent females from varying clutch size and egg size independently. Clutch size is essentially fixed in mid-vitellogenesis, after which no additional recruitment occurs and atresia occurs only rarely (Sinervo & Licht, 1991; Shanbhag & Prasad, 1993). Thus, a female encountering additional resources between mid-vitellogenesis and the point at which eggs are shelled would not be able to increase her clutch size but could allocate additional energy to her developing follicles. Through this mechanism, differences in the acquisition of resources among females can produce variation in egg size. Even if a single optimal egg size does exist, physiological constraints on follicular development can prevent females from producing eggs of this size. In support of this hypothesis, females in the laboratory that consumed more food during vitellogenesis produced larger eggs (R. M. Pringle & M. J. Angilletta, unpubl. data). Additional studies of food intake in natural environments would confirm that these physiological constraints produce variation in egg size within populations.

Interestingly, we observed a negative relationship between the energy content of an egg and its energy density. This trend was evident within and among the populations, suggesting that the trend stems from a general functional relationship between egg size and energy density. The ubiquity of the trend raises a novel question. Why do females that produce smaller eggs allocate a greater proportion of lipid than protein? Possibly, the greater allocation of lipid is an adaptation to compensate for pelvic constraints on egg size; however, we doubt the validity of this explanation because of our evidence that pelvic constraints do not contribute to variation in egg size within *S. undulatus*. The strongest relationships between egg mass and energy density were observed among females from New Jersey and South Carolina, but egg mass was unrelated to maternal size in these populations. Based on these results, we propose an alternative explanation that could account for the negative relationship between egg size and energy density: a

limitation of lipids. Females of *S. undulatus* use lipids stored during fall and winter to generate eggs during the spring (Derickson, 1976). Lipid is distributed to eggs in the form of lipoproteins, such as vitellogenin and very-low density lipoproteins, and these lipoproteins differ in their ratio of protein to lipid (Thompson & Speake, 2003). If lipids become limiting, females can provision eggs with a greater quantity of vitellogenin, which is richer in amino acids than lipid. The amino acids needed to produce large amounts of vitellogenin can be made available through protein turnover (Hawkins, 1991). Indeed, an increase in protein turnover during reproduction has been observed in other oviparous ectotherms (Bayne, 2004). Thus, the proportion of lipid might necessarily decrease if the need to provision eggs exceeds the ability of females to produce very-low density lipoproteins. Although lipids might be limiting in *S. undulatus*, other species can provide a constant or increasing proportion of lipid with increasing egg size (Booth, 2003). Future tests of this hypothesis (and others) about the cause of variation in egg composition would help to refine evolutionary models of reproductive allocation.

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REFERENCES

- Andrews RM, Mathies T, Qualls CP, Qualls FJ. 1999. Rates of embryonic development of *Sceloporus* lizards: do cold climates favor the evolution of rapid development? *Copeia* **3**: 692–700.
- Angilletta MJ. 1999. Estimating body composition of lizards from total body electrical conductivity and total body water. *Copeia* **1999**: 587–595.
- Angilletta MJ. 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology* **82**: 3044–3056.
- Angilletta MJ, Niewiarowski PH, Dunham AE, Leaché AD, Porter WP. 2004. Bergmann's clines in ectotherms: illustrating a life-history perspective in sceloporine lizards. *American Naturalist* **164**: E168–E183.
- Angilletta MJ, Oufiero CE, Leache AD. 2006. Direct and indirect effects of environmental temperature on the evolution of reproductive strategies: an information-theoretic approach. *American Naturalist* **168**: in press.
- Angilletta MJ, Oufiero CE, Sears MW. 2004. Thermal adaptation of maternal and embryonic phenotypes in a geographically widespread ectotherm. *International Congress Series* **1275**: 258–266.
- Angilletta MJ, Sears MW, Winters RS. 2001. Seasonal variation in reproductive effort and its effect on offspring size in the lizard *Sceloporus undulatus*. *Herpetologica* **57**: 365–375.
- Arnold SJ. 1992. Constraints on phenotypic evolution. *American Naturalist* **140**: S85–S107.
- Bayne BL. 2004. Phenotypic flexibility and physiological tradeoffs in the feeding and growth of marine bivalve molluscs. *Integrative and Comparative Biology* **44**: 425–432.
- Booth DT. 2003. Composition and energy density of eggs from two species of freshwater turtle with twofold ranges in egg size. *Comparative Biochemistry and Physiology Part A* **134**: 129–137.
- Congdon JD, Gibbons JW. 1987. Morphological constraint on egg size – a challenge to optimal egg size theory. *Proceedings of the National Academy of Science of the United States of America* **84**: 4145–4147.
- Congdon JD, Gibbons JW, Greene JL. 1983. Parental investment in the chicken turtle (*Deirochelys reticularia*). *Ecology* **64**: 419–425.
- Derickson WK. 1976. Ecological and physiological aspects of reproductive strategies in 2 lizards. *Ecology* **57**: 445–458.
- Ferguson GW, Talent LG. 1993. Life-history traits of the lizard *Sceloporus undulatus* from two populations raised in a common laboratory environment. *Oecologia* **93**: 88–94.
- Hawkins AJS. 1991. Protein turnover: a functional appraisal. *Functional Ecology* **5**: 222–233.
- Jackson DA. 1993. Stopping rules in principle components-analysis – a comparison of heuristic and statistical approaches. *Ecology* **74**: 2204–2214.
- Leaché AD, Reeder TW. 2002. Molecular systematics of the Eastern fence Lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood and Bayesian approaches. *Systematic Biology* **51**: 44–68.
- Maynard Smith J. 1978. Optimization theory in evolution. *Annual Review of Ecology and Systematics* **9**: 31–56.
- McGarigal K, Cushman S, Stafford S. 2000. *Multivariate statistics for wildlife and ecology research*. New York, NY: Springer-Verlag New York Inc.
- McGinley MA, Temme DH, Geber MA. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *American Naturalist* **130**: 370–398.
- Michaud EJ, Echternacht AC. 1995. Geographic variation in the life history of the lizard *Anolis carolinensis* and support for the pelvic constraint model. *Journal of Herpetology* **29**: 86–97.
- Niewiarowski PH, Angilletta MJ, Leaché A. 2004. Phylogenetic comparative analysis of life-history variation among populations of the lizard *Sceloporus undulatus*: an example and prognosis. *Evolution* **58**: 619–633.
- Parker SL, Andrews RM, Mathies T. 2004. Embryonic responses to oviductal oxygen in the lizard *Sceloporus undu-*

- latus* from New Jersey and South Carolina, USA. *Biological Journal of the Linnean Society* **83**: 289–299.
- Parker GA, Begon M. 1986.** Optimal egg size and clutch size: effects of environment and maternal phenotype. *American Naturalist* **128**: 573–592.
- Perrin N. 1988.** Why are offspring born larger when it is colder? Phenotypic plasticity for offspring size in the cladoceran *Simocephalus vetulus* (Müller). *Functional Ecology* **2**: 283–288.
- Roosenburg WM, Dunham AE. 1997.** Allocation of reproductive output: egg- and clutch-size variation in the diamond-back terrapin. *Copeia* **2**: 290–297.
- Schmidt-Nielsen K. 1997.** *Animal physiology*. Cambridge: Cambridge University Press.
- Shanbhag BA, Prasad BSK. 1993.** Follicular dynamics and germinal bed activity during the annual ovarian cycle of the lizard, *Calotes versicolor*. *Journal of Morphology* **216**: 1–7.
- Sibly R, Calow P. 1983.** An integrated approach to life-cycle evolution using selective landscapes. *Journal of Theoretical Biology* **102**: 527–547.
- Sinervo B. 1990.** The evolution of maternal investment in lizards: An experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* **44**: 279–294.
- Sinervo B. 1999.** Mechanistic analysis of natural selection and a refinement of Lack's and Williams's principles. *American Naturalist* **154**: S26–S42.
- Sinervo B, Licht P. 1991.** Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. *Science* **252**: 1300–1302.
- Smith CC, Fretwell SD. 1974.** The optimal balance between size and number of offspring. *American Naturalist* **108**: 449–506.
- StatSoft Inc. 2003.** *STATISTICA (data analysis software system)*, Version 6. Available at: <http://www.statsoft.com>.
- Taylor PD, Williams GC. 1984.** Demographic parameters at evolutionary equilibrium. *Canadian Journal of Zoology* **62**: 2264–2271.
- Thompson MB, Speake BK. 2003.** Energy and nutrient utilization by embryonic reptiles. *Comparative Biochemistry and Physiology Part A* **133**: 529–538.
- Tinkle DW, Dunham AE, Congdon JD. 1993.** Life-history and geographic variation in the lizard *Sceloporus graciosus* – a long term study. *Ecology* **74**: 2413–2429.
- Van Noordwijk AJ, DeJong G. 1986.** Acquisition and allocation of resources – their influence on variation in life-history tactics. *American Naturalist* **128**: 137–142.
- Warner DA, Andrews RM. 2003.** Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biological Journal of the Linnean Society* **76**: 105–124.
- Yampolsky LY, Scheiner SM. 1996.** Why larger offspring at lower temperatures? A demographic approach. *American Naturalist* **147**: 86–100.