



Optimal offspring provisioning when egg size is “constrained”: a case study with the painted turtle *Chrysemys picta*

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Classic egg size theory predicts that, in a given environment, there is a level of maternal investment per offspring that will maximize maternal fitness. However, positive correlations among egg size and female body size are observed within populations in diverse animal taxa. A popular explanation for this phenomenon is that, in some populations, morphological constraints on egg size, such as ovipositor size (insects) or pelvic aperture width (lizards and turtles), limit egg size. Egg size may therefore increase with female body size due to body size-specific constraints on investment per offspring, coupled with selection towards an optimal egg size. We use 17 years of data from a population of painted turtles *Chrysemys picta* to evaluate this hypothesis. In accordance with our predictions, we find that (1) morphological constraints on egg size are apparent only in relatively small females, similarly (2) egg mass exhibits a strong asymptotic relationship with female body size, suggesting egg mass is optimized only at large body sizes, (3) clutch size, not egg mass, varies with female condition, and (4) clutch size varies more than egg mass across years. Contrary to our predictions, we observe that (5) the egg mass-clutch size tradeoff is not less pronounced at large body sizes. Our data do not fully support the traditional hypothesis, and recent models suggest that this hypothesis is indeed overly simplistic. When the selective environment of a female's offspring is influenced by her phenotype, optimal egg size may vary among maternal phenotypes. This concept can explain correlations among egg size and body size in many taxa, as well as the patterns observed in the present study. In this paradigm, a tight coupling of aperture width (or other ‘constraints’) and egg size may occur in small females, even when such morphological features are not causally related to variation in egg size. In this spirit, we question validity of invoking morphological constraints to explain covariation among egg size and female body size.

Classic egg size theory predicts that, in a given environment, females will divide the energy available for reproduction into eggs of an optimal size (Smith and Fretwell 1974). This idea is sometimes supported (Einum and Fleming 2000), but it is common to observe a great deal of among-female, within-population variation in investment per offspring (McGinley et al. 1987, Roosenburg and Dunham 1997, Hendry et al. 2001). Moreover, such variation is often correlated with the maternal body size (reviewed by Roff 1992: 354–355). This pattern of maternal investment is difficult to frame in the context of the classic model, which predicts that investment per offspring should be relatively conserved among individuals in a population, and variation in the energy available for reproduction should be expressed primarily in terms of offspring number.

Several models have since incorporated the positive correlation among egg size and maternal body size into theoretical framework (Parker and Begon 1986, Congdon and Gibbons 1987, Hendry et al. 2001, Hendry and Day 2003). One popular explanation for this phenomenon is that, in some populations, egg size is constrained by morphological features of female body size, so that in accordance with the classic model, egg size increases with

female body size just until females are large enough to produce eggs of an optimal size (e.g. turtles: Congdon and Gibbons 1987, Long and Rose 1989; lizards: Sinervo and Licht 1991a, Sinervo et al. 1992; snakes: Ford and Seigel 1989; cladocerans: Robertson 1988; sea urchins: Emler 1989). Perhaps the most influential contribution to this body of research comes from the study of three turtle species by Congdon and Gibbons (1987). Using a series of correlations, these authors showed that egg width of two small-bodied species increased with female body size, and that these increases in egg width were tightly coupled with increases in the width of the pelvic aperture, through which eggs must pass during oviposition. In a larger turtle species, they found that egg width and aperture width were not tightly coupled and that the linear slope of egg width on female body size was relatively unpronounced, and only weakly significant. Congdon and Gibbons (1987) argued that this phenomenon represents an adaptive compromise, whereby selection for a larger egg size is opposed by selection for locomotor performance that targets the architecture of the pelvic girdle, and ultimately results in a smaller aperture opening. In this paradigm, as long as egg width is limited, an increase in egg mass may only be

accomplished by means of an increase in egg length, and there are probably functional constraints on egg elongation (Sinervo and Licht 1991b, Ji et al. 2006). Thus, among-species relationships between egg width, aperture width, and female body size provide some evidence that egg size can be constrained in small-bodied turtles, and that the positive correlation between egg size and female body size is due to selection on egg size towards an optimal value. However, this highly influential hypothesis generates specific predictions for population-level phenomena (within species) which have not received much attention.

Since 1990, we have been studying a population of painted turtles *Chrysemys picta* in Algonquin Provincial Park, Ontario, Canada. This population exhibits a large range of adult body sizes, and a positive correlation between egg mass and body size has been detected (Schwarzkopf and Brooks 1986). The purpose of this study is to evaluate the merits of the 'constraint hypothesis', whereby egg mass increases with body size because of body size-specific constraints on egg mass, coupled with selection towards an optimal egg size (Congdon and Gibbons 1987, Robertson 1988, Emler 1989, Ford and Seigel 1989). First, using postulates developed by Congdon et al. (1983a; see also Kratochvil and Frynta 2006), we test whether egg mass is constrained in smaller, but not larger females. We expect that if egg dimensions (and hence egg mass) are limited by aperture width (Congdon et al. 1983a, Kratochvil and Frynta 2006), or if egg dimensions are otherwise morphologically constrained (Clark et al. 2001), then (1) egg sphericity (the ratio of egg width over egg length) will increase with body size only until the constraint is relaxed, similarly (2) because egg width is the measure of egg size that is likely constrained, the slope of egg width over body size will be greater than the slope of egg length over body size (Congdon et al. 1983a). Second, we test whether patterns of investment are consistent with the notion that egg mass increases with body size because of selection towards an optimal egg size. We predicted that (3) egg mass would exhibit an asymptotic relationship with female body size, (4) the egg mass-clutch size tradeoff should be less pronounced in larger females, as investment per offspring should be optimized in larger females, (5) clutch size, but not egg mass, should vary with female condition, and (6) within females, clutch size should be more variable than egg mass across years. Predictions 5 and 6 apply to females of all sizes, because under the classic model, maximizing investment per offspring when investment per offspring is limited should yield the highest maternal fitness (Smith and Fretwell 1974).

Methods

Study site

We studied a population of painted turtles from 1990–2006 in Algonquin Provincial Park, Ontario, Canada. The majority of turtles in this population reside in two ponds. Wolf Howl Pond (45°34' N, 78°41' W) is a 1.70 ha black spruce *Picea mariana* bog that is predominantly 1.3 m deep and is bisected into a east and west side by a 4 m high abandoned railway embankment where females nest during

the nesting season. West Rose Lake is about 400 m southeast of Wolf Howl Pond, and the railway embankment runs along its western shore. West Rose Lake is larger in surface area, but it is similar to Wolf Howl Pond in biotic and abiotic components.

Clutch information

Turtles were captured with dipnets from a canoe between late April and early June. Individuals were brought back to a research station where straight-line morphometric measurements were taken with calipers to the nearest 0.01 cm. Maximum plastron length (MPL) was the greatest distance between the anterior and posterior parts of the plastron. Carapace height was the greatest distance between the bottom of the plastron and the top of the carapace. Carapace width was the greatest distance between right and left marginals of the carapace (measured at 90° from MPL measurements). Body mass was measured by placing the turtle in a small plastic bucket and weighing it to the nearest 1 g with a scale. Turtles were permanently marked by filing notches in their marginal scutes (Cagle 1939).

Nesting patrols were initiated when gravid females were detected. Patrols consisted of a minimum of two researchers surveying the railway embankment every 30–40 min. from ~1500 h to at least 2200 h. Turtles were observed nesting, and within 5 h their clutches were excavated and brought back to the research station where egg mass was recorded with an electronic scale to the nearest 0.1 g, and where egg width and length were measured to 0.001 cm using digital calipers. Approximately 20–30% of females in our population lay a second clutch in a given season; this usually occurs two to three weeks after the first clutch is deposited. Eggs in the second clutch are smaller than those in the first clutch (Samson 2003), so only data from first clutches were used in our analyses. We excluded second clutches from our analyses by only considering data from the first 15 days of a given nesting season.

Statistical methodology

We identified 232 females (comprising 1630 clutches) with nesting observations in at least four years between 1990 and 2006. We used average clutch characteristics (e.g. mean egg mass of all eggs in a given clutch) in our analyses, and unless otherwise noted, all models were fit using PROC NLMIXED (SAS ver. 9.1). Testing most of our predictions involved comparing the explanatory power of models where data were fit with a quadratic function to the explanatory power of models where a linear function was fit. Models generally took the form:

$$Y = b(\text{MPL})^2 + b_1(\text{MPL}) + u_i + e_{ij} + c \quad (\text{Model 1})$$

or,

$$Y = b(\text{MPL}) + u_i + e_{ij} + c \quad (\text{Model 2})$$

where Model 1 is the quadratic model and Model 2 is the linear model, and where MPL is maximum plastron length (cm), u_i is the random effect of female, e_{ij} is random error (which is assumed to be normally distributed), c is the intercept, and both b and b_1 are parameters to be estimated.

Following Burnham and Anderson (2002), we used Akaike's information criterion (AIC) to select final models. When the difference in AIC between two models (ΔAIC) is >10 , there is strong support for the best model (i.e. the candidate model with the lowest AIC); when ΔAIC is between 4 and 7, the best model has reasonable support, and when $\Delta\text{AIC} < 2$, the explanatory power of the models is equivalent (Burnham and Anderson 2002).

Testing for constraints on egg size (Prediction 1–2)

First, we tested whether a quadratic function or a linear function best described the relationship between egg sphericity and maternal body size, with the expectation that the quadratic model would perform best (Prediction 1). Next, we compared the linear and quadratic slopes of mean egg width and mean egg length as a function of MPL. All data were standardized for this analysis to ensure the slope estimates were comparable. Relationships were modeled as in Model 1 and 2, with the appropriate dependent variables (standardized mean egg width or standardized mean egg length) substituted into the equation. The 95% confidence intervals of the linear slope estimates were then qualitatively compared, with the expectation that the slope of mean egg width over MPL would be greater than that of mean egg length on MPL (Prediction 2).

Investment patterns and classic egg size theory (Prediction 3–6)

We tested whether mean egg mass is best described as a quadratic or linear function of female body size. Mean egg mass was substituted into Model 1 and 2 as the dependent variable, with the expectation that the quadratic model would perform best (Prediction 3). Next, we fit mixed-models to test whether the mean egg mass – clutch size tradeoff was less pronounced in relatively large females. Mean egg mass was modeled both as (Model A) a quadratic effect of MPL and a linear effect of clutch size, and (Model B) a quadratic effect of MPL and a quadratic effect of clutch size. We expected the latter model (Model B) to best predict variation in mean egg mass (Prediction 4), as a linear effect of egg mass on clutch size (after accounting for body size) would suggest that the magnitude (slope) of the egg mass – clutch size tradeoff does not change with female body size.

We tested whether variation in clutch size – but not mean egg mass – is associated with variation in female condition by correlating female body mass with reproductive measures while accounting for female body morphometrics. We identified 114 females (comprising 738 clutch observations) that nested at least three times during the study period and whose body mass was measured at least 10 days (mean = 40.1 days, range = 12–59 days) before oviposition. We used body mass (as opposed to reproductive measures) as the dependent variable in these analyses to minimize multicollinearity among independent variables, and we used PROC MIXED (SAS ver. 9.1) to create two models. In the first model (Model C), female body mass was modeled as a linear function of MPL, carapace height, carapace width, Julian date of body mass measurement, and clutch size, with female as a random effect (i.e. u_i). The

second model (Model D) was equivalent to the first, except mean egg mass was substituted for clutch size. We expected that mean egg mass would not be a significant predictor of body mass (Prediction 5).

Finally, we tested whether among-year variation in clutch size was greater than among year variation in mean egg mass (Prediction 6). We randomly selected four clutch observations from each of 52 females that nested four or more times during the study period (within individuals, all selected observations were within nine years of one-another). We calculated the coefficient of variation (CV) of clutch size and of mean egg mass within these individuals across years. We compared the CV of clutch size to the CV of mean egg mass using a Wilcoxon sign-rank test.

Results

Testing for constraints on egg size (Prediction 1–2)

The quadratic model describing the relationship between egg sphericity and MPL had more support ($\Delta\text{AIC} = 15.1$) than the linear model (Fig. 1). The linear slope of standardized mean egg width on standardized MPL was greater than that of standardized mean egg length on standardized MPL, and quadratic models better predicted variation in both these measures of egg shape (Fig. 2). Prediction 1 and 2 were therefore supported.

Investment patterns and classic egg size theory (Prediction 3–6)

As expected, the quadratic model describing the relationship between mean egg mass and female body size had substantially more support ($\Delta\text{AIC} = 48.1$) than the linear model (Fig. 2A). Interestingly, the quadratic models showed that the inflection point of mean egg mass on MPL

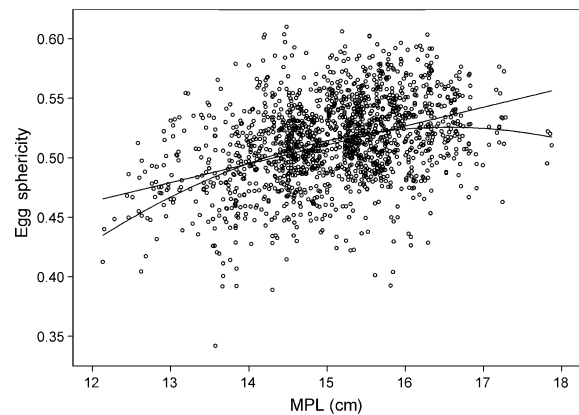


Fig. 1. Quadratic and linear relationships between egg sphericity (the ratio of mean egg width over mean egg length) and maximum plastron length (MPL) of female painted turtles ($n = 232$) laying clutches ($n = 1630$) in Algonquin Park, Canada, between 1990 and 2006. The quadratic model ($\text{AIC} = -7413.6$) is described by the equation $Y = -0.00465x^2 + 0.154x - 0.748$ ($e_{ij} = 0.000017$, $u_i = 0.000067$), and the linear model ($\text{AIC} = -7398.5$) is described by $Y = -0.0158x + 0.273$ ($e_{ij} = 0.000447$, $u_i = 0.000650$). All parameter estimates (not including intercepts) were highly significant ($p < 0.0001$).

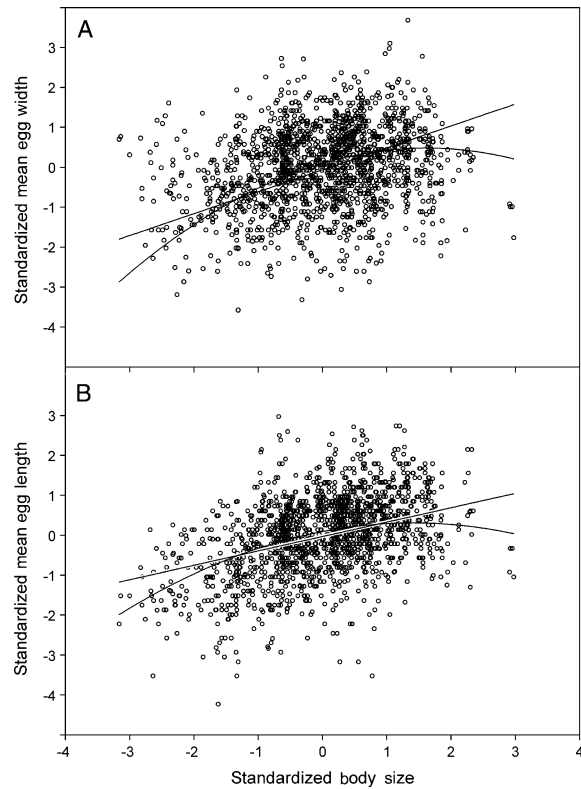


Fig. 2. Quadratic and linear relationships between standardized body size (MPL) of female painted turtles and (A) standardized mean egg width, and (B) standardized mean egg length ($n = 232$ females, 1630 clutches). The linear function for egg width (A) is described by, $Y = 0.546x - 0.0614$ ($e_{ij} = 0.373$, $u_i = 0.456$), and for egg length (B), $Y = 0.361x - 0.0310$ ($e_{ij} = 0.470$, $u_i = 0.506$). The linear slope of egg width over MPL (95% C.I. = 0.463–0.628) was qualitatively greater than that of egg length over MPL (95% C.I. = 0.271–0.451). The quadratic function relating standardized egg width to body size ($Y = -0.147x^2 + 0.475x + 0.102$; $e_{ij} = 0.367$, $u_i = 0.445$) had more support than did the linear function ($\Delta AIC = 27.7$); similarly, the quadratic model for standardized egg length on body size ($Y = -0.110x^2 + 0.310x + 0.0917$; $e_{ij} = 0.466$, $u_i = 0.500$) had more support than the linear model ($\Delta AIC = 12.3$). Parameter estimates (not including intercepts) in all models were highly significant ($p < 0.0001$).

(inflection at MPL = 16.33 cm) was very similar to that of egg sphericity on MPL (inflection at MPL = 16.25 cm).

Little difference was detected among models describing the mean egg mass – clutch size tradeoff (Table 1), despite clutch size exhibiting a linear relationship with MPL (Fig. 2B). The model incorporating quadratic terms between mean egg mass and MPL and between mean egg mass and clutch size (AIC = 2258.5) did not better predict variation in mean egg mass ($\Delta AIC = 1.5$) than the competing linear model (AIC = 2260.0). Moreover, parameter estimates for quadratic terms in the former model were not significant (Table 1). These data suggest that, contrary to Prediction 4, the egg mass – clutch size tradeoff is not less pronounced at large female body sizes.

After controlling for MPL, carapace height, carapace width, Julian date of body mass measurement and random variation among females, we found that clutch size – but not mean egg mass – varied with female body mass (Table 2). Finally, mean within-individual, among-year variation in clutch size (mean $CV \pm SE$: $15.1 \pm 1.04\%$) was significantly greater than variation in mean egg mass ($5.72 \pm 0.431\%$, $Z = -6.11$, $DF = 51$, $p < 0.001$, Wilcoxon sign-rank test). Coefficients of variation of egg mass within clutches were generally low ($3.87 \pm 0.31\%$, range = 0.821%–21.0%), and total growth of individuals in this analysis averaged ($\pm SE$) 0.15 ± 0.025 cm and ranged from 0–0.77 cm; hence, there was little propensity for egg mass to vary within clutches, and it is unlikely that growth over the observation period had any appreciable effect on these findings.

Discussion

Our findings provide some support to the claim that a positive correlation between egg mass and maternal body size in small-bodied turtles is because of body size-specific constraints on egg size coupled with selection towards an optimum value (Smith and Fretwell 1974, Congdon and Gibbons 1987). Egg morphology suggests that egg width is limited in smaller, but not larger females (Fig. 1, 2), and mean egg mass increases with female body size at a

Table 1. Relationships between mean egg mass (the dependent variable), body size (MPL) and clutch size (CS) of painted turtles nesting in Algonquin Park, Canada, between 1990 and 2006 ($n = 232$ females, 1630 clutches). In Model A and B, mean egg mass is modeled as a quadratic function of MPL. In Model A, mean egg mass is modeled as a linear function of clutch size; in Model B, mean egg mass is modeled as a quadratic function of clutch size.

Model	Parameter	Parameter estimate	SE	p
A $Y = a(MPL)^2 + a_1(MPL) + b(CS) + u_i + e_{ij} + c$	Intercept (c)	–35.3	4.92	<0.0001
	a	–0.157	0.0221	<0.0001
	a_1	5.21	0.659	<0.0001
	b	–0.0957	0.00929	<0.0001
	u_i	0.0573	0.00668	<0.0001
	e_{ij}	0.169	0.00649	<0.0001
B $Y = a(MPL)^2 + a_1(MPL) + b(CS)^2 + b_1(CS) + u_i + e_{ij} + c$	Intercept (c)	–35.2	4.91	<0.0001
	a	–0.155	0.0221	<0.0001
	a_1	5.14	0.659	<0.0001
	b	–0.00578	0.00307	0.061
	b_1	–0.00973	0.0464	0.83
	u_i	0.0571	0.00666	<0.0001
	e_{ij}	0.168	0.00648	<0.0001

Table 2. Relationships between female body mass (g) and either clutch size (Model C) or mean egg mass (Model D) while controlling for Julian date of body mass measurement and shell morphometrics. Measurements were taken from female painted turtles ($n = 114$) laying clutches ($n = 738$) in Algonquin Park, Canada, between 1990 and 2006. Clutch size is a significant predictor of body mass (Model C; AIC = 6957.7), but mean egg mass was not (Model D; AIC = 6960.5).

Model	Parameter	Parameter estimate	SE	p
C	Intercept	-790.4	41.5	<0.0001
	MPL (cm)	64.7	4.05	<0.0001
	Carapace height (cm)	44.0	6.04	<0.0001
	Carapace width (cm)	10.3	6.08	0.0318
	Julian date	-0.373	0.155	0.016
	Clutch size	1.74	0.754	0.021
	u_i	552.8	101.5	<0.0001
	e_{ij}	563.8	32.8	<0.0001
	Intercept	789.2	42.1	<0.0001
D	MPL (cm)	66.7	4.14	<0.0001
	Carapace height (cm)	44.0	6.12	<0.0001
	Carapace width (cm)	9.60	4.81	0.046
	Julian date	-0.383	0.155	0.014
	Mean egg mass (g)	-1.52	1.93	0.43
	u_i	525.5	97.7	<0.001
	e_{ij}	563.9	32.8	<0.0001
	Intercept	789.2	42.1	<0.0001
	MPL (cm)	66.7	4.14	<0.0001

decreasing rate (Fig. 3). This suggests that investment per offspring may be optimized only at large female body sizes. Moreover, the inflection point of egg sphericity on MPL coincided with that of mean egg mass on MPL, and this provides evidence that egg morphology and egg mass are causally linked (Sinervo and Licht 1991b, Rowe 1994) and that investment per offspring may be optimized just at the point where constraints on egg mass are relaxed (Congdon et al. 1983a, Congdon and Gibbons 1987, Kratochvil and Frynta 2006). Finally, as predicted, female condition varied only with clutch size (Table 2), and within individuals, clutch size varied more than mean egg mass across years.

However, we also found that the magnitude (slope) of the tradeoff between mean egg mass and clutch size was similar among small and large individuals (Table 1), and this would not be expected if egg size was optimized (in large females) in accordance with classic egg size theory (Smith and Fretwell 1974, Congdon and Gibbons 1987). Also of note is the wide range of mean egg masses produced by females in this population, even after accounting for body size (Fig. 3A). Such variation does not necessarily undermine classic egg size theory (McGinley et al. 1987), but this finding is puzzling if we assume that each female is optimizing investment per offspring (either in absolute terms or on a body size-specific basis).

Classic egg size theory was developed under the assumption that, in a given environment, there is a predictable relationship between maternal investment per offspring and offspring fitness (Smith and Fretwell 1974). However, the selective environment of eggs or offspring may vary within populations on spatial and temporal scales (Bernardo 1996a, Einum and Fleming 2002, Plaistow et al. 2007), which leads to spatial and temporal variation in optimal egg size (Einum and Fleming 1999, Plaistow et al. 2007). Interestingly, if variation in the selective environment exists and cannot be predicted by the female, then at the population level, a consistent (and relatively large) level of investment per offspring may be favored, especially in iteroparous organisms (McGinley et al. 1987, Schultz 1991, Einum and Fleming 2004). Under these conditions, the

intensity of selection on the optimal strategy of investment may be relaxed (McGinley et al. 1987), and non-adaptive variation in patterns of maternal investment may arise, presumably because females deviating from the optimal strategy would incur only small fitness penalties. This phenomenon could explain the large range of egg sizes produced in the Algonquin population of painted turtles (Fig. 3A), and it would not undermine the theory or predictions of Congdon and Gibbons' (1987) hypothesis.

Alternatively, more recent models have shown that variation in egg size among females in a population may be an adaptive phenomenon if the maternal investment per offspring – offspring fitness function differs predictably among individuals (Parker and Begon 1986, Hendry et al. 2001). Although there are number of reasons this could occur (Plaistow et al. 2007), idiosyncratic fitness functions may be most likely in turtles and other vertebrates if a maternal phenotype, such as body size, influences offspring habitat quality (Hendry et al. 2001, Einum and Fleming 2002, Hendry and Day 2003). That is, maternal 'decisions', such as nest site selection, that are made by virtue of her phenotype may influence or predict the selective environment that will be experienced by her offspring (Bernardo 1996a, Resetarits 1996, Kolbe and Janzen 2001). This concept includes possible density-dependent effects of total energy allocated to reproduction on optimal egg size, whereby clutch size (a maternal phenotype) influences the optimal egg size, and therefore the two traits coevolve (e.g. copepods: Caley et al. 2001; fish: Hendry et al. 2001, Hendry and Day 2003; turtles and birds: Beck and Beck 2005; lizards: Sinervo and Licht 1991b; snakes: Ji et al. 2006). An evolutionary dependence of clutch size and egg size may help explain why we found no difference between small and large females in the egg size – clutch size tradeoff, as classic egg size theory does not consider this evolutionary dependence (Smith and Fretwell 1974).

Interestingly, if the maternal phenotype influences the selective environment of her offspring, then extreme caution should be used when invoking morphological constraints to explain why egg size increases with maternal body size, even

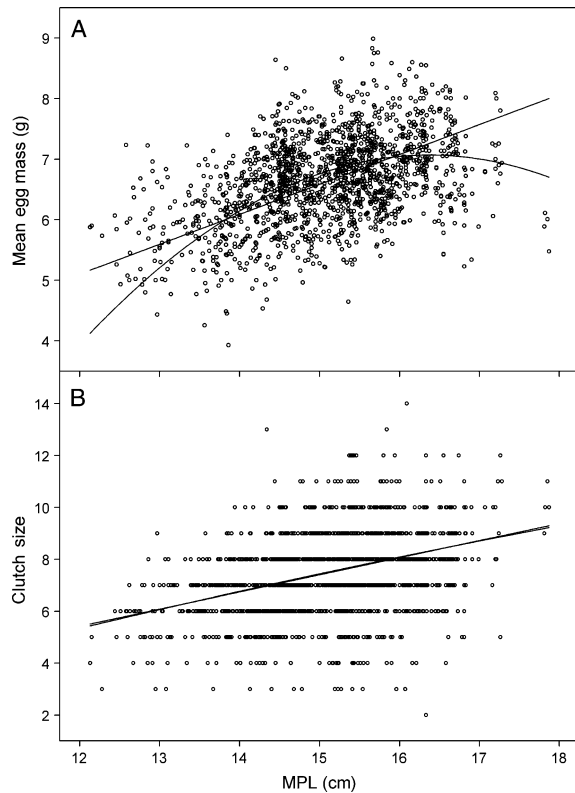


Fig. 3. Quadratic and linear relationships between body size (MPL) and (A) mean egg mass and (B) clutch size of female painted turtles ($n = 232$) laying clutches ($n = 1630$) in Algonquin Park, Canada, between 1990 and 2006. For mean egg mass (A), the quadratic model ($AIC = 2361.2$) is described by the equation $Y = -0.164x^2 + 5.35x - 36.8$ ($e_{ij} = 0.176$, $u_i = 0.276$), and the linear model ($AIC = 2409.3$) is described by $Y = 0.494x - 0.826$ ($e_{ij} = 0.182$, $u_i = 0.279$). All parameter estimates (not including intercepts) were highly significant in these models ($p < 0.0001$). For clutch size (B), the linear model ($AIC = 5458.8$) is described by the equation $Y = 0.653x - 2.43$ ($e_{ij} = 1.31$, $u_i = 0.849$; all parameters $p < 0.0001$, not including the intercept), but the quadratic model ($AIC = 5460.7$) did not produce significant parameter estimates. The explanatory power of competing clutch size models was equivalent ($\Delta AIC = 1.9$), probably owing to the similarity of the quadratic and linear slopes.

if a tight coupling of a morphological feature (e.g. aperture width) and egg size is observed. For example, larger turtles may be less susceptible to adult depredation during oviposition than smaller females (Tucker et al. 1999), and the chance of nest depredation may decrease with increasing distance from water bodies (Kolbe and Janzen 2002, Spencer and Thompson 2003, Marchand and Litvaitis 2004; but see Congdon et al. 1983b, Burke et al. 1998). Large females may therefore attempt to avoid total reproductive failure by venturing far from a water body to deposit their clutch (Harms et al. 2005, Paitz et al. 2007). Thus, a greater maternal investment per offspring in large *C. picta* may be related, at least in part, to the amount of energy required by hatchlings for a relatively long migration to water (Kraemer and Bennet 1981). Size-dependent depredation of hatchlings may also occur during hatchling migration (Janzen et al. 2000), so in conjunction with distance of the nest to water, this would also select for a

relatively large investment per offspring in these larger females. Finally, larger females have more energy for reproduction and more voluminous body cavities (Congdon and Tinkle 1982, Rollinson and Brooks 2007); accordingly, they produce larger clutches of eggs that require deeper nests (Brooks and Rollinson, unpubl.; see also Iverson et al. 1997). This may simultaneously select for a larger investment per offspring to offset the energy required for hatchlings to emerge from a deeper nest cavity (Kraemer and Bennett 1981). On the other hand, smaller females may oviposit closer to water bodies (Harms et al. 2005) to lessen the chance that they will be depredated while constructing their nest (Tucker et al. 1999). Their hatchlings may not, therefore, experience size-dependent predation during migration, nor would they require a large investment to offset the energetic cost of migration. Moreover, smaller clutches of eggs would not require deep nest cavities, so the energetic cost incurred to emerging hatchlings may be relatively small (Kraemer and Bennett 1981). Interestingly, all of the predictions upheld in the present study lend equivalent support to this hypothesis, and to that of Congdon and Gibbons (1987). However, under the former hypothesis, smaller females may not have a greater fitness if they increased investment per offspring to the levels observed in larger females (Fig. 3A).

If we assume a tight coupling of aperture width and egg width in the above example, as may be the case in the present study (Fig. 1–3), an important evolutionary question arises: is egg size truly ‘constrained’ by aperture width, or would the same positive relationship between egg size and body size exist in the absence of this ‘constraint’? The traditional view (Congdon and Gibbons 1987) suggests an adaptive compromise between selection for a larger egg size, and counter selection targeting the mother’s locomotor ability (selection on pelvic architecture resulting in a smaller aperture width). Although this is altogether possible, the latter view reflects a common expectation that egg size will evolve largely to suit other life history traits. But given that offspring provisioning is often of paramount importance to maternal fitness, an alternative possibility is that aspects of an organism’s life history will evolve largely to meet a particular egg size (Bernardo 1996a, 1996b, Einum et al. 2004, Hofmeyer et al. 2005).

The drawback of most studies evaluating morphological ‘constraints’ on egg size, including the present study, is that they rely on correlation, and phenotypic correlations do not show the direction of causality. For example, if selection favoring a smaller aperture width exists (Congdon and Gibbons 1987), then within populations, selection may be directing aperture width to meet the diameter of a particular egg size that is already optimized as a function of other life history constraints (e.g. body size-specific depredation pressures, the dependence of nest depth on clutch size). We may therefore observe an encroachment of aperture width on egg width at small female body sizes, even though aperture width is not causally related to variation in egg size. In support of this, most populations of small-bodied turtles exhibit a positive correlation between female body size and egg size in the absence of tight correlations among aperture width and egg width (reviewed by Clark et al. 2001, see also Hofmeyer et al. 2005, Wilkinson and Gibbons 2005), which suggests some mechanism other than aperture width

is the causal basis for this correlation. Indeed, a manipulative study of egg size in lizards has shown that aperture width does impose an upper limit to egg size (Sinervo and Licht 1991a), but mean observed egg sizes in these populations generally did not converge on the upper threshold, and selection did not always favor larger offspring (Sinervo et al. 1992).

In sum, the patterns of maternal investment observed in the present study lend some support to the traditional view in which egg size increases with female body size because of body size-specific constraints on investment per offspring, coupled with selection towards an optimal value (Congdon et al. 1983a, Congdon and Gibbons 1987, Robertson 1988, Emler 1989). However, our findings are also consistent with more recent theories (Parker and Begon 1986, Hendry et al. 2001, Einum and Fleming 2002, Hendry and Day 2003) in which bona fide morphological ‘constraints’ on investment per offspring, such as aperture width, are dubious. We hope to have emphasized the need to simultaneously consider and integrate the evolution of maternal investment with the evolution of other aspects of an organism’s life history (Bernardo 1996a, 1996b, Einum et al. 2004, Plaistow et al. 2007), including maternal behavior (Reserits 1996). When such an approach is adopted, extreme caution must be used when inferring morphological constraints on egg size, as the cause of a correlation between a maternal phenotype and investment per offspring may be far more complex.

Acknowledgements – We thank all field researchers that participated in the project over the years and the staff at the Wildlife Research Station for providing accommodations. We also thank Doug Armstrong for statistical advice and Jackie Porter for improving earlier versions of this manuscript. Research was funded by Natural Sciences and Engineering Research Council of Canada grants to Njal Rollinson, Ron Brooks and the Wildlife Research Station. Animal handling was authorized under protocol number 04R064 which was approved by the University of Guelph Animal Care Committee.

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