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Optimal egg size in a suboptimal environment: reproductive ecology of female Sonora mud turtles (*Kinosternon sonoriense*) in central Arizona, USA

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Abstract. We studied the reproductive ecology of female Sonora mud turtles (*Kinosternon sonoriense*) at Montezuma Well, a chemically-challenging natural wetland in central Arizona, USA. Females matured between 115.5 and 125 mm carapace length (CL) and 36-54% produced eggs each year. Eggs were detected in X-radiographs from 23 April-28 September (2007-2008) and the highest proportion (56%) of adult females with eggs occurred in June and July. Clutch frequency was rarely more than once per year. Clutch size was weakly correlated with body size, ranged from 1-8 (mean = 4.96) and did not differ significantly between years. X-ray egg width ranged from 17.8-21.7 mm (mean 19.4 mm) and varied more among clutches than within. Mean X-ray egg width of a clutch did not vary significantly with CL of females, although X-ray pelvic aperture width increased with CL. We observed no evidence of a morphological constraint on egg width. In addition, greater variation in clutch size, relative to egg width, suggests that egg size is optimized in this hydrologically stable but chemically-challenging habitat. We suggest that the diversity of architectures exhibited by the turtle pelvis, and their associated lack of correspondence to taxonomic or behavioral groupings, explains some of the variation observed in egg size of turtles.

Keywords: clutch size, *Kinosternon sonoriense*, optimal egg size, Sonora mud turtle, reproduction.

Introduction

Organisms occupying different habitats often exhibit variation in reproductive output as a result of differences in resource quality and availability that can affect body size, clutch size, clutch frequency and egg size. Due to harvest and processing limitations, finite resources are presumably available for an individual to allocate energy to the competing compartments of growth, maintenance, storage and reproduction (Congdon, Dunham and Tinkle, 1982). Females must allocate resources to reproduction within the constraints of: 1) the proportion of total energy allocated to reproductive output, 2) the amount of energy to be allocated to each offspring (parental investment), and 3) the number of offspring that can be produced with the energy available, after accounting for the energy allocated per offspring (optimal egg size: OES). Substantial bodies of theory have emerged to understand these allocations as reviewed by Congdon (1989). The constraints imposed by the various allocations are not independent (Roosenburg and Dunham, 1997). Natural selection is predicted to cause females to produce the maximum number of young possible only after allocating an optimal resource level to each that enhances survivorship, in turn maximizing the lifetime reproductive success of a female. It is the expected fitness of the female and her surviving offspring (offspring fitness is determined by parental investment), not strictly

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the number of offspring produced, that is optimized by natural selection (Trivers, 1972; Smith and Fretwell, 1974; Brockelman, 1975).

We studied the reproductive ecology of a population of Sonora mud turtles, *Kinosternon sonoriense*, a small-bodied species, at Montezuma Well, Arizona, USA. The study site is a unique natural wetland that provides a hydrologically stable, but chemically-challenging environment (Blinn, 2008), both uncharacteristic of habitats typically occupied by this species (Hensley et al., 2010) that tend to be ephemeral and without high levels of dissolved CO_2 and arsenic. Since OES has been suggested for *K. sonoriense* (Rosen, 1987; van Loben Sels, Congdon and Austin, 1997), an objective of our study was to confirm the existence of the phenomenon in this unusual environment. Although the species is one of the least-studied turtles in the United States (Lovich and Beaman, 2008; Ernst and Lovich, 2009), data on reproductive ecology are available from other locations, providing an opportunity for comparison with populations living in more typical habitats.

Despite the theoretical foundation for OES, not all turtles conform to predictions. In many turtles, egg size varies with body size of the female. In others, both egg size and clutch size increase with female body size, again, in contradiction to OES theory (Clark, Ewert and Nelson, 2001; Naimi et al., 2012; Ryan and Lindeman, 2007), even when egg size appears to be unconstrained by pelvic aperture width (PAW) (Iverson and Smith, 1993). The interaction of morphological and other factors on egg size in turtles leads to five basic responses (fig. 1): 1) egg width is constrained/not optimized, 2) egg width is unconstrained/optimized, 3) egg width is unconstrained and optimized only in the largest females (threshold size-constrained), 4) egg width is unconstrained/not optimized by pelvic aperture width (e.g., see fig. 3 in Iverson and Smith, 1993), but constrained by some other non-morphological factor, or 5) egg width is constrained and requires

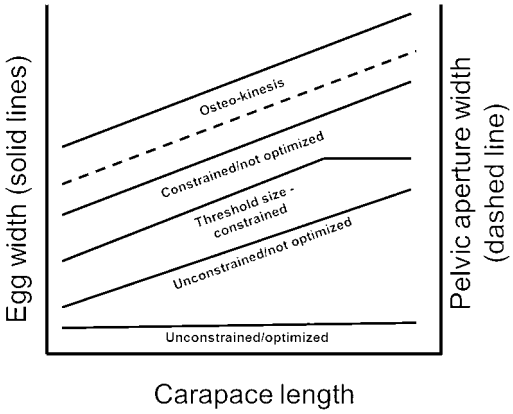

Figure 1. Responses of egg width to pelvic aperture width (shown by solid line scenarios) in various turtle species. Line labels refer to the line immediately above. The dashed line shows the expected relationship between carapace length and pelvic aperture width. The unconstrained/not optimized response suggests a constraint due to something other than pelvic aperture width since egg size increases with body size but the largest egg is still smaller than the smallest pelvic aperture (refer to text for details).

osteo-kinesis for oviposition (Hofmeyr, Henen and Loehr, 2005).

Other non-morphological factors that contribute to egg size variation in turtles include genetic and maternal effects (Rowe, 1994a), locality and year (Rowe, 1994b), clutch number (within a season) (Iverson and Smith, 1993; Harms et al., 2005), and age (Clark, Ewert and Nelson, 2001; Congdon et al., 2001, 2003; Harms et al., 2005; Paitz et al., 2007; Rollinson and Brooks, 2008b). Physiological constraints have also been reported in *Chrysemys picta* where smaller females laid smaller eggs that contained more yolk testosterone while the reverse was observed in larger females from the same population (Bowden et al., 2004). The evidence presented by Rollinson and Brooks (2008a) and Bowden et al. (2004) suggest that there may be a size threshold-constrained response due to other than morphological factors.

In an examination of egg size in three turtle species, Congdon and Gibbons (1987) made two predictions that we test as hypotheses. The first is that egg size in smaller-bodied species of turtles is constrained by PAW, another challenge to OES theory. The second is that in relatively

stable environments, selection reduces variation in egg size. Our data are tested against five constraint/optimization outcomes detailed in a previous paragraph and shown in fig. 1. In addition we test the prediction from OES that clutch size varies more than egg size (width) across a range of female body sizes.

Materials and methods

Our study was conducted at Montezuma Well (elevation 1085 m) and adjacent Wet Beaver Creek in northern Yavapai County, Arizona, near the town of McGuireville. Montezuma Well is a unit of Montezuma Castle National Monument and is protected and managed by the National Park Service. The study area is located in the Verde River Valley of the Central Highlands province of Arizona in a transition zone between the Sonoran Desert Basin and Range province to the south and the Mogollon Rim at the edge of the Plateau Uplands province to the north. The area is arid with mild winters (below freezing at night to 16-21°C during the day) and warm summers with daytime temperatures reaching 38°C or more. Precipitation averages about 30.5 cm/year (Konieczki and Leake, 1997).

Montezuma Well is a large collapsed travertine spring mound with a precipitous shoreline and a narrow littoral zone. The Well is about 112 m in diameter on its longest axis, 0.76 ha in surface area, with a shoreline circumference of 322 m. Mean depth of the well is 6.7 m, with a maximum depth of 17 m (Cole and Barry, 1973). The Well is a unique aquatic ecosystem that supports a distinctive assemblage of 94 aquatic invertebrates, at least six of which are endemic (Blinn and Oberlin, 1995; O'Brien and Blinn, 1999).

Unique features of the Well include: 1) water enters the well from underground springs at a near constant temperature of 24°C (Cole and Barry, 1973); 2) very high dissolved CO_2 concentration of up to 864 mg/l (O'Brien and Blinn, 1999); 3) naturally high arsenic levels (as arsenate) above 100 μg/l (Foust et al., 2004); 4) a highly simplified aquatic food web (O'Brien and Blinn, 1999); 5) endemic species of plants and invertebrates; and 6) absence of fish (Runck and Blinn, 1994) and several major groups of aquatic insects (likely due to the high CO_2 concentration). The native Sonora mud turtle (*Kinosternon sonoriense*) and a small number of non-native turtles (*Trachemys scripta*, *Pseudemys* spp.) occur in the Well. Wet Beaver Creek flows perennially within about 100 meters of Montezuma Well and receives substantial inputs of water from the latter. Water temperatures and discharge rates in the creek vary seasonally, and CO_2 and arsenic levels are lower, especially upstream of the discharge from Montezuma Well. Although it is possible for turtles to move from one habitat to the other, it is rare for them to do so.

We captured 146 mud turtles 240 times with baited hoop traps, basking traps, dip nets and by hand. Each turtle captured was uniquely marked with notches in the margin of the shell, measured for straight-line carapace length (CL) with dial calipers or tree calipers (as dictated by size) accurate to at least 1 mm, and sex was determined using pre-cloacal tail length and plastron shape (Ernst and Lovich, 2009). Females were X-rayed (Gibbons and Greene, 1979; Hinton et al., 1997) on site to determine clutch size, X-ray egg width (XREW) and X-ray maximum pelvic aperture width (XRPAW). Egg width and XRPAW were measured directly from X-radiographs with dial calipers accurate to 0.1 mm. In some female *K. flavescens* pelvic aperture height is a smaller dimension than PAW (Long and Rose, 1989). Although we were unable to obtain measurements of the former dimension from X-radiographs, PAW explains 92.7% of the variation in pelvic aperture surface area in *K. flavescens* making PAW a reasonable estimator of pelvic constraints on egg size in this genus (Long and Rose, 1989). Clutch data were available for 25 females (26 clutches) including seven females from adjacent Wet Beaver Creek. Our decision to combine samples was based on analyses of covariance that demonstrated no significant differences in mean X-ray egg width of a clutch (MXREW) or clutch size between females from Montezuma Well or Wet Beaver Creek after adjusting for body size (CL). This was true whether two females that produced a clutch of one egg (identified as outliers due to Studentized residuals > -3) were included in the analyses or not.

Statistical tests including least squares linear regressions were conducted using SYSTAT software. Following the recommendations of King (2000) we used $\log_{10}$ transformations of data prior to all statistical analysis to improve linearity, remove heteroscedasticity of variances, and facilitate comparisons to other studies. Levels of significance were established a priori at alpha $= 0.05$, but exact probabilities are given when available. MXREW was calculated by summing X-ray egg widths and dividing by the clutch size of each gravid female.

Different authors have used varying criteria for both determining if pelvic aperture width constrains egg width, and for determining the existence of egg size optimization. To test morphological constraints on egg width Congdon and Gibbons (1987) and van Loben Sels, Congdon and Austin (1997) used analysis of covariance (ANCOVA) to compare the slope of the relationship between pelvic aperture width and body size with the slope of the relationship between egg width and body size. Parallel positive slopes imply a constraint. In contrast, Iverson and Smith (1993) showed parallel slopes for the same relationships but the largest egg width was smaller than the smallest pelvic aperture width, so they concluded that there was no morphological constraint on egg size in their population. Different approaches were also used to determine egg size optimization and again, Congdon and Gibbons (1987) used ANCOVA. This time, a significant difference in the slopes (e.g., they were not parallel) indicated optimization of egg width. Ryan and Lindeman (2007) used the criterion of no correlation between egg size and body size to identify the existence of optimization.

To assess the relationship between CL and both XRPAW and MXREW we used ANCOVA with CL as the covariate to test for homogeneity of slopes. Heterogeneity of slopes

comparing XRPAW vs. CL and MXREW vs. CL (Congdon and Gibbons, 1987) and lack of a significant positive relationship between CL and MXREW (Ryan and Lindeman, 2007) would strongly suggest that egg size is optimized across the range of body sizes. Means are followed by ± one SD.

Results

The smallest female with detectable shelled eggs had a CL of 125 mm and the largest female that was X-rayed during the nesting season and never had eggs was 115.5 mm. The percentage of adult females that produced eggs in each year varied from 53.9% (21/39) in 2007 to 35.7% (5/14) in 2008. The proportion of reproductive females did not differ significantly between years (Fisher's exact test, two-tail; $P = 0.352$).

The earliest date at which eggs were detected in females, using X-rays, was 23 April (2008) and the latest date was 28 September (2007). Monthly variation in the percentage of females carrying eggs (when sample size was greater than 1) peaked in June and July (56%, both years combined). Clutch size (including a possible second clutch) ranged from 1-8 eggs with a mean of 4.96 (±1.97) eggs in a sample of 25 females and 26 clutches. Mean clutch size was 4.81 (±2.11) in 2007 and 5.60 (±1.14) in 2008 ($n = 5$) and did not differ significantly between years ($t = -0.801$; df $= 24$; $P = 0.431$). Clutch size frequencies (followed by the number of females in parentheses) were as follows: 1 egg (2), 2 eggs (1), 3 eggs (3), 4 eggs (4), 5 eggs (4), 6 eggs (6), 7 eggs (4), and 8 eggs (2). Clutch size was only weakly correlated with CL ($r^2 = 0.076$, $P = 0.172$) (fig. 2). The two females with a clutch size of one were identified as outliers with Studentized residuals of −2.91 and −3.84. Removing them from the analysis improved the relationship to statistical significance ($r^2 = 0.178$, $P = 0.040$).

At least one female may have produced a second clutch within one year. She was initially X-rayed on 6 June and had 5 eggs. When X-rayed again on 27 July, she had 3 eggs. Although it is possible that she laid two eggs in the intervening period, evidence for splitting clutches has not been reported in this species (see Discussion). However, another female appeared to lay a single egg between 17 June, 2008 and 15 July, 2008 and retained the remainder based on the close correspondence in the location, size, and orientation of the eggs in the radiographs. We cannot rule out the possibility, however, that the July eggs represent a second clutch, and that the location and orientation of the eggs match those of the June clutch by chance. Only one female (CL = 142) was observed to produce a clutch of eggs in both 2007 (7 eggs) and 2008 (6 eggs), however, only three females were captured in both years.

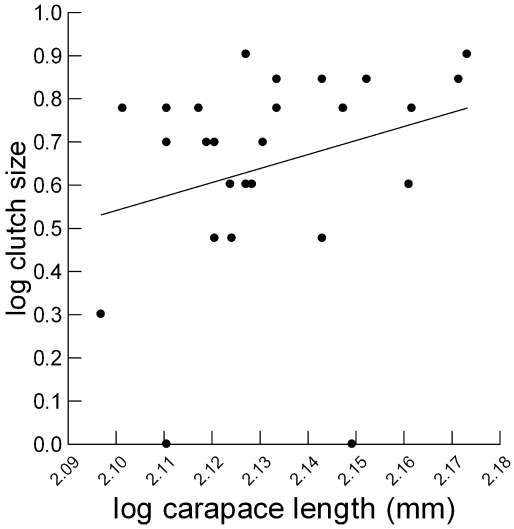

Figure 2. The relationship between clutch size and carapace length in *Kinosternon sonoriense* from Montezuma Well, Arizona, USA. The data include one female that produced a clutch of eggs in both years of the study. Including all $\log_{10}$ transformed data results in a regression equation where $\log_{10}$ clutch size $= -6.269 + 3.243(\log_{10}$ CL). Removing the two outliers (females that produced a single egg clutch) results in the relationship $\log_{10}$ clutch size $= -6.042 + 3.161(\log_{10}$ CL).

Egg width measured from X-radiographs ranged from 17.8-21.7 mm with a mean of 19.4 mm (±0.831). The slope of the regression between MXREW and CL was not significantly different from zero ($r^2 < 0.0001$; $F < 0.0001$; df = 1, 24; $P = 0.999$). Removing one case identified as an outlier (Studen-

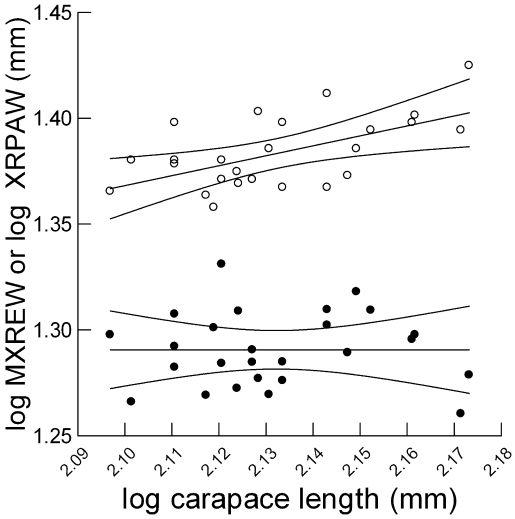

Figure 3. Relationship between carapace length and both mean X-ray egg width (MXREW) (solid circles) and X-ray pelvic aperture width (XRPAW) (open circles) in *Kinosternon sonoriense* from Montezuma Well, Arizona, USA. Linear smoothing functions are shown with accompanying 95% confidence intervals. XRPAW = 12.632 + 0.085(CL). MXREW = 19.631 − 0.001(CL).

tized residual = 2.945) changed the results only infinitesimally. In contrast, the slope of the regression between XRPAW and CL was significantly different from zero, increasing at a rate of 0.085 mm/1 mm CL ($r^2 = 0.338$; $F = 12.236$; df = 1, 24; $P = 0.002$). Comparing the slopes of these two regression equations (fig. 3) with ANCOVA, using CL as the covariate, we rejected the null hypothesis of homogeneity of slopes as shown by a significant interaction term ($F = 4.605$; df = 1, 48; $P = 0.037$).

Subtracting individual XREW measurements from the XRPAW of the females that produced the eggs generated an estimate of "clearance" ranging from 1.8-8.7 mm (mean = 4.936, ±1.339, $n = 129$). Larger females had larger measures of XRPAW, thus the mathematical difference between XRPAW and MXREW increased when regressed on CL ($r^2 = 0.136$; $F = 3.785$; df = 1, 24; $P = 0.064$). No eggs were larger than the XRPAW of a given female.

The coefficient of variation (CV) for clutch size among females was almost an order of magnitude greater than the CV for individual female MXREW (table 1). Log transformed XREW varied more among clutches than within (ANOVA, $F = 10.305$; df = 24, 104; $P < 0.001$).

Table 1. Variation in clutch size and mean X-ray egg width per clutch (MXREW) in mm for female *Kinosternon sonoriense* from Montezuma Well, Arizona, USA.

Variable	*n*	Min	Max	Mean	SE	CV
Clutch size	26	1	8	4.962	0.386	0.397
MXREW	26	18.214	21.433	19.542	0.154	0.040

Discussion

Given the paucity of published literature on *K. sonoriense* relative to other turtle species in the United States (Ernst and Lovich, 2009), it is perhaps surprising that so much information is available on its reproductive ecology (table 2). In his thesis, Rosen (1987) reviewed geographic variation in female reproduction among several populations in Arizona, including Montezuma Well and Wet Beaver Creek. He reported that egg width varied among populations and was weakly correlated with female size, unlike our results where the relationship between egg size and CL was not significantly different from zero. Rosen's result suggests a small constraint on egg size across a range of body sizes. Nevertheless, he concluded that egg size is generally optimized in Arizona *K. sonoriense*, but that the optimum occurs at different egg sizes among populations. Rosen also noted that populations exhibited significantly different pelvic aperture widths (PAW) after adjusting for body size. van Loben Sels, Congdon and Austin (1997) also suggested that egg size was optimized in a population of *K. sonoriense* in southern Arizona even though egg size increased with female size at a statistically significant rate, again, in contrast to our findings. In their study, the slopes of the relationships between body size and both egg width and XRPAW were different even though egg width increased with body size.

Table 2. A comparison of reproductive attributes of female *Kinosternon sonoriense* from various populations in Arizona, USA.

	Montezuma Well (this study)	Chiracahua Mtns. (van Loben Sels et al., 1997)	Arizona (Rosen, 1987)	Quitobaquito (Rosen and Lowe, 1996)	Bradshaw Mtns./ and Maricopa Co. (Hulse, 1982)
Egg production season	April-September	–	May-September	July-September	–
Smallest gravid female	125 mm	106 mm	86 mm	100 mm	93 mm/130 mm
Clutch size	4.96 (1-8)	6.7 (2-11)	3.09-8.12 (1-11; 5.35 for Montezuma Well)	4	2.8(2-4)/5.3(2-9)
% 2nd clutches	4% (see text)	23%	–	–	–
Clutch frequency	2 (see text)	2	1-4 (4 for Montezuma Well)	1.4-1.6	–

Geographic variation in reproductive output of turtles is well-known for many turtle species in the United States (Ernst and Lovich, 2009) and clutch size typically increases with latitude while egg size decreases (Iverson et al., 1993). This same general trend is not clearly reflected in the data presented by Rosen (1987) from central to southern Arizona, but this area constitutes only about half the latitudinal range (but the majority of the elevational range) of the species. van Loben Sels, Congdon and Austin (1997) observed a negative correlation between clutch size and body size-adjusted egg width in *K. sonoriense*, also suggesting that as clutch size increases egg width decreases.

The rarity of multiple clutches observed during our study is perplexing in light of previous observations. Rosen (1987) suggested the potential for multiple clutches (up to four/year) at Montezuma Well and three other Arizona locations at X-ray intervals of 4-7 weeks. The low recapture rate of reproductive females during our study is the only explanation we have for this discrepancy. Similarly, while splitting clutches has not previously been reported in this species (van Loben Sels, Congdon and Austin, 1997; Ernst and Lovich, 2009; Congdon pers. comm.), it has been suggested for the parapatric sister taxon *K. hirtipes* (Iverson et al., 1991; Iverson, 1998). In contrast, egg retention has been reported in various other turtle species (Buhlmann et al., 1995) so it is possible that partial clutches are oviposited and the remaining eggs are retained for a subsequent oviposition event.

Although egg size can be limited by the architectural constraints imposed by PAW in some small-bodied turtles (Congdon and Gibbons, 1987), we found no evidence of this relationship in *K. sonoriense*, itself a small-bodied turtle. The lack of a pelvic constraint on egg size was also reported by Macip-Ríos et al. (2009) for *K. integrum*. In addition, the fact that the slope of the relationship between MXREW and CL was not significantly different from zero suggests that egg size is optimized in our population: larger females could produce larger eggs due to increased clearance but they don't. Based on the scenarios in fig. 1 we conclude that egg width in our study population is unconstrained/optimized. While the pelvic girdle is structurally important for locomotion and support in turtles (Ruckes, 1929; Richmond, 1964; Zug, 1971), our data suggest that PAW itself does not constrain egg size as an architectural byproduct of those functions in *K. sonoriense*. Although we did not measure caudal gaps (another architectural trait known to constrain egg size in turtles) our data show no evidence of any morphological constraints.

The caudal gap, formed between the posterior margins of the carapace and plastron, acts as a second physical barrier to an oviposited egg. In the small-bodied turtle species *Sternotherus*

odoratus, a member of the same family (Kinosternidae) as *K. sonoriense*, caudal gaps were smaller than pelvic aperture height and width in virtually every specimen examined by Clark, Ewert and Nelson (2001). Since the eggs of *S. odoratus*, like those of *K. sonoriense*, are brittle-shelled and cannot be deformed without breaking, plastron and pelvic kinesis must allow for expansion of the caudal gap at oviposition. These types of kinesis are documented for other relatively small turtles with large eggs (Rose and Judd, 1991; Hofmeyr, Henen and Loehr, 2005), the family Kinosternidae, including *K. sonoriense* (Bramble, Hutchison and Legler, 1984), and other unrelated turtle species (Bramble, 1974).

Optimal egg size (OES) theory predicts that variation in reproductive investment should result primarily in variation in clutch size rather than egg size. Our data support this theory in two ways. First, we observed greater variation in clutch size than in MXREW (table 1, fig. 2) as predicted under OES. Second, although MXREW varies more among clutches than within, it remains essentially constant across the wide range of body sizes we observed (fig. 3), whereas the relationship of clutch size to body size was significant after removal of outliers.

The second hypothesis we tested from Congdon and Gibbons (1987) is that egg size variation should be minimized in a stable environment. *K. sonoriense* occupies a wide variety of habitats in the Sonoran Desert region. Within its desert range, it is well-adapted to dealing with temporary aridity in ephemeral streams and other wetlands through estivation and migration (Peterson and Stone, 2000; Hall and Steidl, 2007; Hensley et al., 2010). Montezuma Well represents a somewhat unusual habitat for *K. sonoriense* as a naturally perennial wetland. Although water chemistry presents a challenge to aquatic organisms at the site, the presence of dependable water sustains a large population of turtles in a stable hydrological environment. In contrast, the habitats studied by van Loben Sels, Congdon and Austin (1997) in southern Arizona are the "most permanent streams" and stock tanks in the Chiricahua Mountains, implying that the wetlands are ephemeral. Comparing the slopes of XREW between Montezuma Well and the data presented in van Loben Sels, Congdon and Austin (1997) shows that egg width does not vary significantly with body size in the former, but it does in the latter. This observation appears to support our second hypothesis, especially since the range of egg widths varied by about 5 mm in their study while the range was only 3.2 mm in our study (table 1). Thus, egg width appears to be less variable in a hydrologically stable environment, as predicted.

A critical question is: why do some turtle species exhibit evidence of OES while others do not? In the large-bodied *Graptemys geographica*, Ryan and Lindeman (2007) found evidence in support of a constraint on OES in large females since they increased both clutch and egg size. OES was not observed in the small species *Sternotherus odoratus* (Clark, Ewert and Nelson, 2001), although the authors did observe that scaled residuals of egg size versus female mass were less variable than were those for clutch size as expected under OES theory. Congdon and Gibbons (1987) found that OES was constrained by PAW in small-bodied species including *Deirochelys reticularia* and *Chrysemys picta* but not in the larger species *Trachemys scripta*. Others have suggested that constraints on OES are only observed in relatively small females of *Chrysemys picta* and that egg size is optimized in large females (Rollinson and Brooks, 2008a). While acknowledging that such a "step function" relationship was possible, Ryan and Lindeman (2007) found no evidence for its existence in their analysis of *Graptemys geographica*, a turtle species with large-bodied females. What factors might favor egg size optimization in larger but not smaller females? If female body size influences hatchling survival (the example given is that larger females may nest farther from water in a different environment than smaller females), then there

may be phenotype-habitat matching that drives egg size/hatchling size variation along a body size continuum (Rollinson and Brooks, 2008b; Rowe, 1994b).

We offer a previously underappreciated explanation for some of the variation reported in egg size optimization or constraints in turtles. It is based on recognition of the diversity of morphologies exhibited by this clade of vertebrates (Zangerl, 1969). Given the importance of pelvic and shell architecture in turtle locomotion and shell support, it is likely that structural design constraints also vary widely among species with variation in body plans, mode of locomotion, and adaptations. Indeed, Zug (1971, 1972) noted substantial variation in the osteology and myology of the pelvic girdle of turtles across species, recognizing no less than eight different forms of ilium bone architecture alone. Articulation of the femur to the pelvic girdle also displayed significant variation among species and influenced gait and locomotion. The complex interactions among mechanical, architectural and functional traits of the turtle pelvis and plastron (Angielczyk, Feldman and Miller, 2010) undoubtedly add to the variation observed in egg size of turtles and whether or not egg size is constrained or optimized (Congdon and Gibbons, 1987).

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References

Angielczyk, K.D., Feldman, C.R., Miller, G.R. (2010): Adaptive evolution of plastron shape in emydine turtles. Evolution **65** (2): 377-394.

Blinn, D.W. (2008): The extreme environment, trophic structure, and ecosystem dynamics of a large, fishless desert spring – Montezuma Well, Arizona. In: Aridland Springs in North America – Ecology and Conservation. Stevens, L.E., Meretsky, V.J., Eds, University of Arizona Press, Tucson.

Blinn, D.W., Oberlin, G.E. (1995): Analyses of the Biota in the Aquatic Habitats of Montezuma Castle National Monument. Montezuma Castle National Monument Integrated Inventory and Monitoring Studies. U.S. Department of Interior, National Park Service, Colorado Plateau Research Station, Flagstaff, AZ.

Bowden, R.M., Harms, H.K., Paitz, R.T., Janzen, F.J. (2004): Does optimal egg size vary with demographic stage because of a physiological constraint? Funct. Ecol. **18** (4): 522-529.

Bramble, D.M. (1974): Emydid shell kinesis: Biomechanics and evolution. Copeia **1974**: 707-727.

Bramble, D.M., Hutchison, J.H., Legler, J.M. (1984): Kinosternid shell kinesis: Structure, function and evolution. Copeia **1984**: 456-475.

Brockelman, W.Y. (1975): Competition and fitness of offspring, and optimal clutch size. Am. Nat. **109** (970): 677-699.

Buhlmann, K.A., Lynch, T.K., Gibbons, J.W., Greene, J.L. (1995): Prolonged egg retention in the turtle *Deirochelys reticularia* in South Carolina. Herpetologica **51** (4): 457-462.

Clark, P.J., Ewert, M.A., Nelson, C.E. (2001): Physical apertures as constraints on egg size and shape in the common musk turtle, *Sternotherus odoratus*. Funct. Ecol. **15** (1): 70-77.

Cole, G.A., Barry, W.T. (1973): Montezuma Well, Arizona as a habitat. Journal of the Arizona Academy of Science **8** (1): 7-13.

Congdon, J.D. (1989): Proximate and evolutionary constraints on energy relations of reptiles. Physiol. Zool. **62** (2): 356-373.

Congdon, J.D., Gibbons, J.W. (1987): Morphological constraint on egg size: A challenge to optimal egg size theory? P. Natl. Acad. Sci. USA. **84** (12): 4145-4147.

Congdon, J.D., Dunham, A.E., Tinkle, D.W. (1982): Energy budgets and life histories of reptiles. In: Biology of the Reptilia, p. 233-271. Gans, C., Ed., Academic Press, New York.

Congdon, J.D., Nagle, R.D., Kinney, O.M., Van Loben Sels, R.C. (2001): Hypotheses of aging in a long-lived vertebrate, Blanding's turtle (*Emydoidea blandingii*). Exp. Gerontol. **36** (4-6): 813-827.

Congdon, J.D., Nagle, R.D., Kinney, O.M., Van Loben Sels, R.C., Quinter, T., Tinkle, D.W. (2003): Testing hypotheses of aging in long-lived painted turtles (*Chrysemys picta*). Exp. Gerontol. **38** (7): 765-772.

Ernst, C.H., Lovich, J.E. (2009): Turtles of the United States and Canada. 2nd Edition. Johns Hopkins University Press, Baltimore.

Foust, R.D. Jr., Mohapatra, P., Compton-O'Brien, A.M., Reifel, J. (2004): Groundwater arsenic in the Verde Valley in central Arizona, USA. Appl. Geochem. **19** (2): 251-255.

Gibbons, J.W., Greene, J.L. (1979): X-ray photography: A technique to determine reproductive patterns of freshwater turtles. Herpetologica **35** (1): 86-89.

Hall, D.H., Steidl, R.J. (2007): Movements, activity, and spacing of Sonoran mud turtles (*Kinosternon sonoriens*e) in interrupted mountain streams. Copeia **2007**: 403-412.

Harms, H.K., Paitz, R.T., Bowden, R.M., Janzen, F.J. (2005): Age and season impact resource allocation to eggs and nesting behavior in painted turtles. Physiol. Biochem. Zool. **78** (6): 996-1004.

Hensley, F.R., Jones, T.R., Maxwell, M.S., Adams, L.J., Nedella, N.S. (2010): Demography, terrestrial behavior, and growth of Sonora mud turtles (*Kinosternon sonoriense*) in an extreme habitat. Herpetol. Monogr. **24**: 174-193.

Hinton, T.G., Fledderman, P., Lovich, J.E., Congdon, J., Gibbons, J.W. (1997): Radiographic determination of fecundity: Is the technique safe for developing turtle embryos? Chelonian Conserv. Biol. **2** (3): 409-414.

Hofmeyr, M.D., Henen, B.T., Loehr, V.J.T. (2005): Overcoming environmental and morphological constraints: Egg size and pelvic kinesis in the smallest tortoises, *Homopus signatus*. Can. J. Zoolog. **83** (10): 1343-1352.

Hulse, A.C. (1982): Reproduction and population structure in the turtle, *Kinosternon sonoriense*. Southwest. Nat. **27** (4): 447-456.

Iverson, J.B. (1998): Molecules, morphology, and mud turtle phylogenetics (family Kinosternidae). Chelonian. Conserv. Biol. **3** (1): 113-117.

Iverson, J.B., Smith, G.R. (1993): Reproductive ecology of the painted turtle (*Chrysemys picta*) in the Nebraska Sandhills and across its range. Copeia **1993**: 1-21.

Iverson, J.B., Barthelmess, E.L., Smith, G.R., deRivera, C.E. (1991): Growth and reproduction in the mud turtle *Kinosternon hirtipes* in Chihuahua, México. J. Herpetol. **25** (1): 64-72.

Iverson, J.B., Balgooyen, C.P., Byrd, K.K., Lyddan, K.K. (1993): Latitudinal variation in egg and clutch size in turtles. Can. J. Zoolog. **71** (12): 2448-2461.

King, R.B. (2000): Analyzing the relationship between clutch size and female body size in reptiles. J. Herpetol. **34** (1): 148-150.

Konieczki, A.D., Leake, S.A. (1997): Hydrogeology and water chemistry of Montezuma Well in Montezuma Castle National Monument and surrounding area, Arizona. In: U.S. Geological Survey Water Resources Investigations Report 97-4156, p. 49.

Long, D.R., Rose, F.L. (1989): Pelvic girdle size relationships in three turtle species. J. Herpetol. **23** (3): 315-318.

Lovich, J.E., Beaman, K. (2008): Distribution of native turtles in the arid southwestern United States with comments on *Kinosternon sonoriense*: A species presumed to be lost from California's herpetofauna. In: The 2008 Desert Symposium and Field Guide and Proceedings, p. 127-134. Reynolds, R.E., Ed., California State University, Desert Studies Consortium and LSA Associates, Inc.

Macip-Ríos, R., Arias Cisneros, M.L., Aguilar-Miguel, X.S., Casas-Andreu, G. (2009): Population ecology and reproduction of the Méxican mud turtle (*Kinosternon integrum*) in Tonatico, Estado de México. West. N. Am. Naturalist **69** (4): 501-510.

Naimi, M., Znari, M., Lovich, J.E., Feddadi, Y., Ait Baamrane, M.A. (2012): Clutch and egg allometry of the turtle *Mauremys leprosa* (Chelonia: Geoemydidae) from a polluted peri-urban river in west-central Morocco. Herpetological Journal **22**: 43-49.

O'Brien, C., Blinn, D.W. (1999): The endemic spring snail *Pyrgulopsis montezumensis* in a high CO_2 environment: Importance of extreme chemical habitats as refugia. Freshwater Biol. **42** (2): 225-234.

Paitz, R.T., Harms, H.K., Bowden, R.M., Janzen, F.J. (2007): Experience pays: offspring survival increases with female age. Biol. Lett. **3**: 44-46.

Peterson, C.C., Stone, P.A. (2000): Physiological capacity for estivation of the Sonoran mud turtle, *Kinosternon sonoriense*. Copeia **2000**: 684-700.

Richmond, N.D. (1964): The mechanical function of the testudinate plastron. Am. Midl. Nat. **72** (1): 50-56.

Rollinson, N., Brooks, R.J. (2008a): Optimal offspring provisioning when egg size is "constrained": A case study with the painted turtle *Chrysemys picta*. Oikos. **117** (1): 144-151.

Rollinson, N., Brooks, R.J. (2008b): Sources and significance of among-individual reproductive variation in a northern population of painted turtles (*Chrysemys picta*). Copeia **2008**: 533-541.

Roosenburg, W.M., Dunham, A.E. (1997): Allocation of reproductive output: Egg- and clutch-size variation in the diamondback terrapin. Copeia **1997**: 290-297.

Rose, F.L., Judd, F.W. (1991): Egg size versus carapace-plastron aperture size in *Gopherus berlandieri*. J. Herpetol. **25** (2): 248-250.

Rosen, P.C. (1987): Variation in female reproduction among populations of Sonoran mud turtles (*Kinosternon sonoriense*). Unpubl. Thesis, Arizona State University, Tempe.

Rowe, J.W. (1994a): Egg size and shape variation within and among Nebraskan painted turtle (*Chrysemys picta bellii*) populations: Relationships to clutch and maternal body size. Copeia **1994**: 1034-1040.

Rowe, J.W. (1994b): Reproductive variation and the egg size-clutch size trade-off within and among populations of painted turtles (*Chrysemys picta bellii*). Oecologia. **99** (1): 35-44.

Ruckes, H. (1929): Studies in chelonian osteology Part I: Truss and arch analogies in chelonian pelves. Annals of the New York Academy of Sciences **31**: 31-80, pls. IV-VII.

Runck, C., Blinn, D.W. (1994): Role of *Belostoma bakeri* (Heteroptera) in the trophic ecology of a fishless desert spring. Limnol. Oceanogr. **39** (8): 1800-1812.

Ryan, K.M., Lindeman, P.V. (2007): Reproductive allometry in the common map turtle, *Graptemys geographica*. Am. Midl. Nat. **158** (1): 49-59.

Smith, C.C., Fretwell, S.D. (1974): The optimal balance between size and number of offspring. Am. Nat. **108** (962): 499-506.

Trivers, R.L. (1972): Parental investment and sexual selection. In: Sexual Selection and the Descent of Man, 1871-1971, p. 136-179. Campbell, B., Ed., Aldine, Chicago.

Van Loben Sels, R.C., Congdon, J.D., Austin, J.T. (1997): Life history and ecology of the Sonoran mud turtle (*Kinosternon sonoriense*) in southeastern Arizona: A preliminary report. Chelonian Conserv. Biol. **2** (3): 338-344.

Zangerl, R. (1969): The turtle shell. In: Biology of the Reptilia, Vol. 1. Morphology A, p. 311-339. Gans, C., D'bellairs, A., Parsons, T.S., Eds, Academic Press, New York.

Zug, G.R. (1971): Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles. Miscellaneous Publications Museum of Zoology, University of Michigan **142**: 1-98.

Zug, G.R. (1972): Walk pattern analysis of cryptodiran turtle gaits. Anim. Behav. **20** (3): 439-443.

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