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The Effects of Climate on Annual Variation in Reproductive Output in Snapping Turtles (*Chelydra serpentina*).

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1 **The Effects of Climate on Annual Variation in Reproductive Output in Snapping**
2 **Turtles (*Chelydra serpentina*)**

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Abstract

Reptiles are highly dependent on climatic patterns to regulate their behavior and physiology, and studies of the effects of climate on the biology of organisms are increasingly important given expected climate change. Our study examined the effects of climate variation over 15 of the 26 years between 1990 and 2015 on the reproductive output of the Common Snapping Turtle (*Chelydra serpentina* (L., 1758)). Egg mass, clutch size and clutch mass (relative to body size) were significantly higher in years following warmer temperatures in September and October of the year before reproduction, but not related to temperatures in April and May just before reproduction. Of the above life history traits, egg mass varied the least across years, and after warm autumns small turtles (225-285 mm carapace length) increased clutch mass by increasing clutch size but not egg size. In contrast, under the same conditions, large turtles increased clutch mass by increasing egg mass but not clutch size. Our data suggest optimal egg size may vary with female size. Climate change may already have impacted reproductive output in snapping turtles at the site because temperatures during September and October have increased about 0.5 °C each decade for the last 45 years.

Keywords: Common snapping turtle; *Chelydra serpentina*; clutch size; egg size; clutch mass; climate change; annual variation

Introduction

A fundamental question in life history studies is why a particular organism produces the number and size of offspring it does. Optimal egg size (OES) theory predicts offspring size is adapted to maximize maternal fitness in a given environment (Smith and Fretwell 1974). Hence, variation in resource availability to a female should impact her clutch or brood size (and thus, her total clutch or brood mass), rather than her egg size. In turtles, several studies have shown egg size varies less than clutch size (e.g., Elgar and Heaphy 1989; Iverson and Smith 1993), in support of OES theory. However, there is also mounting evidence for substantial annual variability in egg size, clutch size, and clutch mass in turtles (Table 1), including at our long-term field site in western Nebraska. Understanding the correlates of variation in reproductive traits has not been well-studied in turtles, but preliminary evidence suggests climate may be a factor.

To date, only three studies have examined environmental temperature correlates of annual variation in egg size or clutch size (Rowe et al. 2003; Rollinson et al. 2012) or clutch mass (Iverson and Smith 1993; but see Tucker et al. 1998 for flooding impacts) in a turtle. Based on only four years of data for *Chrysemys picta* in Nebraska, Iverson and Smith (1993) found annual variation in body size-adjusted clutch mass tended (though not significantly) to be inversely correlated with March degree days and positively correlated with October temperatures. They suggested warm late autumn temperatures may allow increased resource accumulation, which could be allocated toward the

following year's clutch. They also suggested warmer spring temperatures might decrease the energy available for the clutch due to increased metabolic costs. However, a seven-year study of *C. picta* in Michigan by Rowe et al. (2003) found no annual variation in size-adjusted clutch mass, but significant variation in size-adjusted egg size and clutch size. Unfortunately, they could identify no statistically significant environmental correlate of the variation.

Rollinson et al. (2012) analyzed twelve years of egg size data for *C. picta*, *Chelydra serpentina*, and *Glyptemys insculpta* in Ontario. They demonstrated autumn temperatures (August – October) were positively correlated with egg size in the latter two species, whereas both autumn and spring (30 days before nesting) temperatures were correlated (positively and negatively, respectively) with egg size in *C. picta*. Unfortunately, they did not examine annual variation in clutch size or mass.

One potential mechanism explaining the variability in reproductive output in turtles is via climatic effects on the ovarian cycle. In a typical temperate turtle, the cycle begins with a period of recrudescence from summer to fall, characterized by rapid vitellogenesis, especially in the follicles destined for ovulation the following year (Miller and Dinkelacker 2008; Kuchling 2012). Follicular development is suspended during winter hibernation but resumes during the spring preovulatory (preparatory) period and is completed when fully mature follicles are ovulated in late spring or early summer. Substantial interspecific variation has been described in the relative amount of follicular development occurring in the fall versus the spring (e.g., Rollinson et al. 2012).

Snapping turtles (*Chelydra serpentina*) complete nearly all of their follicular development during the fall (White and Murphy 1973; Mahmoud and Alkindi 2008),

which suggests egg size, clutch size, and clutch mass might be determined before the winter and environmental conditions during the autumn might impact reproductive variables. However, White and Murphy (1973) hypothesized enlarged follicles in snapping turtles might serve as an energy reserve in the spring. Also, a female snapping turtle may not ovulate all mature follicles in a given year (e.g., see Dobie 1971 for alligator snapping turtles). Thus, environmental conditions in the spring might also impact egg size, clutch size, and clutch mass.

Our study is the first to examine the environmental correlates of body size – adjusted clutch size, egg mass, **and** clutch mass in a turtle population. We examined variation in reproductive output in the snapping turtle, *Chelydra serpentina*, across 15 years between 1990 and 2015. Based on the research above, we predicted body size – adjusted egg mass, clutch size, and clutch mass would be positively correlated with fall temperatures, and negatively correlated with spring temperatures.

Materials and Methods

Our work focused on nesting females emerging from Gimlet Lake, a shallow, sandhill lake on the Crescent Lake National Wildlife Refuge, Garden County, Nebraska for 15 of the 26 years between 1990 to 2015 during which we observed at least five females (see Iverson and Smith 1993 for a description of study site). Before and during nesting season in most years we walked through the primary nesting area north of the lake from 0600 to 2200 hrs looking for nesting turtles. Females on nesting forays were allowed to nest undisturbed. Once they finished nesting, we captured and individually marked them and recorded maximum carapace length (CL) to the nearest mm with tree calipers and spent body mass (SBM) to the nearest 50g with Pesola scales. The nest was

then excavated; eggs were counted to determine the clutch size, and individual egg mass was measured with an electronic balance (accurate to 0.001g) for at least 15 randomly selected eggs per clutch. Clutch mass (CM) was estimated as the product of clutch size (CS) and mean egg mass (EM). Eggs were reburied immediately in an artificial nest near the original nest site.

In Nebraska, snapping turtles oviposit a maximum of one clutch per year, but our data set (total $N = 205$; $N = 97$ different females) included multiple interannual records for some females (range 1 – 7 captures per female; overall mean for full sample = 1.9/female), with a mean recapture interval of 2.7 years (range 1 – 13; $N = 105$).

Given egg mass, clutch size, and clutch mass all positively correlate with body size (Fig. 1), we standardized the measures in three ways, in part to test the consistency of the three commonly used approaches. First, we used partial correlation analysis to remove the effects of female body size on reproductive variables in two ways. EM, CS, and CM for all females (all years) were each regressed against CL and SBM, and the residuals were saved for further analysis. In addition, despite criticisms of the use of ratios to remove the effects of body size on reproductive variables (e.g., Packard and Boardman 1988), we also included ratio measures of reproductive output in our analysis because of their practical use in the field (unlike residuals), and also for comparison with other turtle studies which used ratios (e.g., Gomez et al. 2015; reviewed for *Chelydra* in Iverson et al. 1997). Our three ratio measures were relative egg mass ($REM = EM / SBM$), relative clutch size ($RCS = CS / SBM$), and relative clutch mass ($RCM = CM / SBM$). We restricted our analysis to the 15 years during which we observed five or more nesting females (mean = 14/yr; 1990, 1993-94, 1998, 2005, 2007-2015).

Climatic data were obtained from the NOAA weather station located approximately 100 m from the primary turtle nesting area. We expected reproductive traits in a given year to vary based on temperatures the previous autumn or the current spring. Therefore, we calculated the mean of the daily minimum and maximum temperatures during September and October of the previous year (SeptOctmean), and in April and May immediately before nesting season (AprMaymean). Statistical analyses were performed using Statview, MS Excel, or R software and we report means $\pm$ 1 SD.

The effects of climatic variables on size-standardized reproductive variables were assessed by regression analysis (with two approaches) and by linear mixed-effects models. First, using the full data set, we calculated the means of each standardized measure of reproductive output by year and then we examined the relationships of the standardized measures with the two independent climatic variables. We acknowledge the approach might bias the results because some females were represented in multiple years; however, given the relatively long mean recapture interval (2.7 years) we could argue most recaptures were independent events.

Second, to account for the potential non-independence of multiple reproductive events by the same female, we reduced our full data set to include only one record per female (our reduced data set; Table 2). For females captured more than once, we included only the second capture in the analysis. We size-standardized the data and then regressed directly with climatic variables (i.e., not graphed by year).

Third, to retain the full data set, we fit six linear mixed-effects models for each of the reproductive variables (EM, CS, and CM) using the lme4 package (Bates et al. 2016) in R 1.1.12 (R Foundation for Statistical Computing, Vienna, Austria). Raw reproductive

variables were z-transformed before analysis. The female identification number was included as a random effect in each model because some females were represented more than once in the full dataset.

Each model predicted a reproductive parameter as a function of spring and/or fall temperatures, and/or decade (1990s, 2000s, 2010s) corrected for CL. The six candidate models for each reproductive variable (RV) were;

Null: $RV \sim \text{random (female) effect};$

CL: $RV \sim CL + \text{random (female) effect};$

Decade: $RV \sim \text{Decade} * CL + \text{random (female) effect};$

Spring: $RV \sim \text{AprMaymean} * CL + \text{random (female) effect};$

Fall: $RV \sim \text{SeptOctmean} * CL + \text{random (female) effect};$

Global: $RV \sim \text{AprMaymean} * CL + \text{SeptOctmean} * CL + \text{random (female) effect}.$

For each reproductive parameter, the six models were ranked based on differences in Akaike's information criterion adjusted for small sample sized (ΔAIC_c) using AICcmodavg in R (Mazerolle 2013), and models were evaluated based on their relative Akaike weights. We also used the effects package (Fox, 2013) to interpret the significant effects in the top models. Finally, we used the piecewiseSEM package (Lefcheck, 2016) to determine the marginal (fixed-effects) and conditional (fixed and mixed-effects) r^2 values to illustrate the fits of the competing models.

Results

Egg mass, clutch size, and clutch mass were all highly correlated with CL (Fig. 1) and BM (data not reported here) in our population, although the relationship varied by body size. For the smallest third of our sample (225-285 mm CL), clutch size increased

with body size, but egg size and clutch mass did not (Table 3), whereas, for the largest third (340-397 mm CL), none of the three parameters varied with body size..

Annual cohort analysis

Annual mean size-standardized egg mass was significantly positively correlated with mean fall temperatures (September-October), whether egg mass was standardized by partial regression with SBM (Fig. 2 A), and by ratio with SBM ($r = +0.54$; $P = 0.045$), and nearly so if standardized by CL ($r = +0.46$; $P = 0.08$). No correlation was found between any of the body size-standardized measures of egg size and mean spring temperatures (April-May) ($r < -0.23$, $P > 0.12$ for all analyses).

Annual mean size-standardized clutch size was significantly correlated with fall temperatures when standardized by partial regression with SBM (Fig. 2 B); or by ratio with SBM ($r = +0.75$; $P = 0.002$), and nearly so when standardized with CL ($r = +0.50$; $P = 0.059$). Standardized clutch size was not correlated with spring temperatures for any method ($r < 0.22$; $P > 0.13$ for all analyses).

Annual size-standardized clutch mass was positively correlated with fall temperatures whether standardized by SBM (Fig. 2 C), CL ($r = +0.54$; $P = 0.039$) or by ratio with spent body mass ($r = +0.74$; $P = 0.002$), but not with spring temperatures ($r < 0.10$; $P > 0.73$ for all analyses).

Reduced data set analysis

For the reduced data set, the results were less conclusive (Table 4). The relationship between standardized egg mass, and mean spring temperatures approached significance only when egg mass was standardized by CL, and no approach indicated significance for fall temperatures (Table 4). For standardized clutch size, mean fall

temperatures approached significance when standardized by either CL or SBM, but no CS analysis suggested a significant relationship with spring temperatures (Table 4). Finally, fall temperatures were significantly correlated with standardized clutch mass, but spring temperatures were not, no matter what standardization technique was used (Table 4).

Mixed model analysis

Our mixed model analysis (Tables 5, 6) demonstrated the fall mean was the best predictor of egg size ($R^2_{\text{mar}} = 0.60$, $R^2_{\text{cond}} = 0.88$), clutch size ($R^2_{\text{mar}} = 0.41$, $R^2_{\text{cond}} = 0.66$), and clutch mass ($R^2_{\text{mar}} = 0.65$, $R^2_{\text{cond}} = 0.81$). The global model for both CS ($R^2_{\text{mar}} = 0.42$, $R^2_{\text{cond}} = 0.67$) and CM ($R^2_{\text{mar}} = 0.65$, $R^2_{\text{cond}} = 0.81$) were marginally less supported ($\Delta\text{AIC}_c = 0.02$ and 0.26 respectively) and thus were competitive models for both variables. Overall, nearly half of the variation observed in reproductive variables was explained by fall mean temperatures alone, with an additional 30% being accounted for by variation within individuals. However, even the minimal support for any effect of spring temperatures on the reproductive variables, as seen in the global models, explained little additional variation in reproductive variables.

For EM, the effect of fall temperatures was positive, though minimal, but varied with the female body size (Fig. 3). Small females laid smaller eggs and their egg size did not vary with fall temperatures (see also Table 3). However, egg size in larger females increased with warmer fall temperatures.

Clutch size was also positively related to fall temperatures (Fig. 3), but the body size effect was the opposite of that found for egg mass. Warmer temperatures in the fall were strongly positively correlated with clutch size in small females, but large females

exhibited no change in clutch size in warmer years (see also Table 3). Clutch mass likewise exhibited a strong positive correlation with fall temperatures, but increases in clutch mass with temperatures were most evident in smaller females (Fig. 3; Table 3).

Discussion

Our study is the first to examine environmental temperature correlates of annual variation in body-size adjusted egg size, clutch size, and clutch mass simultaneously in any turtle population. Spring temperatures did not impact the reproductive variables examined, but fall temperatures did. Only one other study has examined climatic correlates with relative egg mass in a turtle (Rollinson et al. 2012), and it also found no effects of spring temperatures on egg mass for snapping turtles in Ontario. However, as in our study, they demonstrated a significant positive effect of fall temperatures on standardized egg mass.

No previous study has examined ambient temperature correlates of body size-adjusted clutch size or clutch mass in a turtle population. Our data suggest, as for egg size, fall temperatures positively influence both clutch size and clutch mass in the following summer in snapping turtles, but spring temperatures had no effects on the reproductive variables examined.

Theoretical models suggest offspring size should be optimized with respect to maternal fitness, and hence, somewhat invariant (e.g., Smith and Fretwell 1974). In most turtle species, egg size consistently varies less than clutch size, as predicted by OES theory. However, most turtle species exhibit substantial inter-individual and inter-annual variation in egg size (Table 1), which is in opposition to the predictions of OES theory.

In our snapping turtle population, egg size in small females was relatively invariant, and increased energetic allocations to reproduction (i.e., in years following warm autumns) resulted in substantial increases in clutch size (Fig. 3). On the other hand, large females exhibited little variation in egg size, clutch size, or clutch mass (Fig. 3).

In small turtle species, the interaction between maternal body size and variation in reproductive output could be attributed to constraints imposed by limited pelvic aperture width (e.g., Congdon and Gibbons 1987), but no such physical constraint exists for large-bodied snapping turtles (Janzen and Warner 2009; Hedrick and Iverson, pers. observ.). Indeed, Zug (1971) demonstrated that unlike all other turtles, the ilia of snapping turtles actual diverge dorsally, eliminating any possibility of a pelvic constraint. Without that constraint, OES theory could be invoked to explain the lack of variation in egg size in small females, even among years with highly variable fall temperatures. However, an OES explanation is complicated by the approximately 75% increase in average egg mass from the smallest to the largest turtles in our population (Fig. 1 A). However, Janzen and Warner (2009) provided experimental evidence of strong directional selection for increased egg size in snapping turtles in Illinois; furthermore, selection on egg size maximizes maternal fitness compared to offspring fitness. Thus, increases in egg size with body size in snapping turtles may still reflect selection for OES, except the optimum increases with female body size. Such a conclusion is supported by the reproductive data and analyses available for painted turtles (Iverson and Smith 1993; Rollinson and Brooks 2008; Janzen and Warner 2009; Bowden et al. 2011).

Since follicular development in *Chelydra* is accomplished primarily during the autumn (Mahmoud and Alkindi 2008), the impact of fall temperatures on reproductive

output should not be surprising. However, the pattern could be due to direct temperature effects on the physiology of follicular development, or to indirect effects through local rates of productivity, harvestability, or processability of diet resources (Rollinson et al. 2012). Also, whether the driving mechanism is simply the accumulation of warmth during the active months following oviposition (e.g., July – October), or whether some particular, restricted period during the season is most crucial is not yet clear and demands further study.

Based on our results, one might expect an inverse relationship between latitude and egg and clutch size and mass (warmer southern temperatures driving larger clutch parameters). However, Iverson et al. (1997) could find no such latitudinal pattern in size-adjusted egg mass, clutch size, or clutch mass in a range-wide study of snapping turtles. Further studies on the interactions of climate and reproductive output in snapping turtles across their range may provide an explanation for the apparent lack of latitudinal patterns.

Previous studies have standardized measures of reproductive output using partial correlation with carapace (or plastron) length and/or body mass (e.g., Wang et al. 2011; Vásquez Gómez et al. 2015) or by using ratios with (spent) body mass (e.g., Ashton et al. 2007; Ruane et al. 2008; Rasmussen and Litzgus 2010). We examined each approach and found the results to be consistent regarding significance versus non-significance in our analyses. However, correlation coefficients using ratios were usually lower than for the other two methods (e.g., see Table 4). Because CL is more difficult to measure reliably in comparison to SBM, and because our SBM-standardized results more closely matched the more robust mixed-model results, we recommend standardization by SBM for future studies.

Over the past 47 years, mean September – October temperatures have increased significantly at our field site ($r = 0.49$; $P = 0.0004$; average annual increase = 0.053°C); however, mean April – May temperatures have not ($r = 0.16$; $P = 0.28$). Hence, climate change may already have impacted the reproductive output of snapping turtles at our site, although no significant change in SBM or carapace length-adjusted residuals for egg mass ($P > 0.18$), clutch size ($P > 0.32$), or clutch mass ($P > 0.48$) was evident over the course of our study (only 15 years between 1990 and 2015). Our results make it clear that long-term studies (i.e., >15 years), with substantial sample sizes (i.e., > 200) will be necessary to fully understand the impacts of climate on reproductive output in turtles and other long lived species. For example, it remains to be determined whether the net reproductive impacts of warmer autumns (increased output) will be positive or negative regarding overall fitness for snapping turtles (or any other turtle species). The dearth of such long-term studies on other turtle taxa is thus quite troublesome given climate change predictions over the next century (IPCC, 2014).

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Table 1. Evidence for annual variation in egg size, clutch size, and clutch mass in turtles. Only studies standardizing reproductive data by female body size are included. Asterisks indicate studies using egg width as a proxy for egg mass. CY = Cypress.

Taxon	Location	# of Years	Egg Mass	Clutch Size	Clutch Mass	Reference
<i>Sternotherus odoratus</i>	FL	3	-	Yes	-	Gross 1982
<i>Sternotherus odoratus</i>	VA	2	Yes	No	-	Mitchell 1985b
<i>Sternotherus odoratus</i>	SC	4	-	No	-	Gibbons et al. 1982
<i>Sternotherus odoratus</i>	SC	13	Yes*	No	-	Wilkinson and Gibbons 2005
<i>Kinosternon subrubrum</i>	SC	4	-	No	-	Gibbons et al. 1982
<i>Kinosternon subrubrum</i>	SC	13	Yes*	Yes	-	Wilkinson and Gibbons 2005
<i>Chrysemys picta</i>	VA	2	No	No	-	Mitchell 1985a
<i>Chrysemys picta</i>	NE	4	No	Yes	Yes	Iverson and Smith 1993
<i>Chrysemys picta</i>	MI	4	No*	Yes	-	Congdon and Tinkle 1982
<i>Chrysemys picta</i>	MI	6	Yes	Yes	No	Rowe et al. 2003
<i>Chrysemys picta</i>	IL	4	Yes	-	-	Bowden et al. 2011
<i>Chrysemys picta</i>	ON	3	Yes	No	Yes	Schwarzkopf and Brooks 1986

<i>Chrysemys picta</i>	ON	12	Yes	-	-	Rollinson et al. 2012
<i>Deirochelys reticularia</i>	SC	4	-	No	-	Gibbons et al. 1982
<i>Glyptemys insculpta</i>	ON	12	Yes	-	-	Rollinson et al. 2012
<i>Trachemys scripta</i>	VA	4	No	-	-	Mitchell and Pague 1990
<i>Trachemys scripta</i>	IL (3 populations)	3	Yes	Yes	Yes	Tucker et al. 1998
<i>Trachemys scripta</i>	SC	4	-	No	-	Gibbons et al. 1982
<i>Pseudemys floridana</i>	SC	2	-	No	-	Gibbons et al. 1982
<i>Pseudemys floridana</i>	SC	13	No*	Yes	-	Wilkinson and Gibbons 2005
<i>Chelydra serpentina</i>	NE	2	No	No	No	Iverson et al. 1997
<i>Chelydra serpentina</i>	ON	12	Yes	-	-	Rollinson et al. 2012
<i>Chelonia mydas</i>	CY	9	-	No	-	Broderick et al. 2003
<i>Caretta caretta</i>	CY	9	-	No	-	Broderick et al. 2003

Table 2. Average life history parameters for nesting female snapping turtles (*Chelydra serpentina*) at Gimlet Lake, Nebraska. Means are followed by $\pm$ 1SD. Sample size and range appear in parentheses below means. The full sample includes multiple records for many females; the reduced sample includes only one record per female.

Variable	Full Sample	Reduced Sample
Carapace Length (mm)	321.2 $\pm$ 34.6 (203; 225 – 397)	317.7 $\pm$ 34.3 (96; 234 – 397)
Plastron Length (mm)	253.2 $\pm$ 27.4 (198; 193 – 315)	250.8 $\pm$ 27.0 (95; 202–315)
Spent Body Mass (g)	7256 $\pm$ 1978 (196; 3200 – 12800)	7087 $\pm$ 1969 (95; 3500 – 12800)
Clutch Size	50.8 $\pm$ 11.2 (201; 19 – 79)	50.5 $\pm$ 11.7 (96; 20 – 78)
Egg Mass (g)	11.46 $\pm$ 1.63 (201; 6.93 – 15.14)	11.37 $\pm$ 1.81 (95; 6.93 – 15.14)
Clutch Mass (g)	587.2 $\pm$ 177.4 (197; 196.5 – 1059.4)	577.4 $\pm$ 190.4 (94; 229.0 – 1059.4)
RCSx100	0.73 $\pm$ 0.17 (191; 0.27 – 1.24)	0.74 $\pm$ 0.17 (94; 0.27 – 1.20)
REMx100	0.17 $\pm$ 0.03 (192; 0.10 – 0.30)	0.17 $\pm$ 0.03 (93; 0.11 – 0.30)
RCMx100	8.17 $\pm$ 1.54 (188; 3.07 – 11.68)	8.22 $\pm$ 1.63 (92; 3.07 – 11.68)

Table 3. Relationships between body size (CL, carapace length, in mm) and raw reproductive variables for small females (225-285 mm CL) versus large females (340-397 mm CL) for snapping turtles in western Nebraska. Full data included multiple captures for some females; reduced sample included only one record per female. Bold p-values are statistically significant.

Variable	Sample	N	Small females		N	Large females	
			r	P		r	P
Egg mass	Full	28	-0.07	0.72	68	+0.16	0.19
	Reduced	15	-0.098	0.72	27	-0.15	0.45
Clutch size	Full	28	+0.61	0.007	69	+0.20	0.10
	Reduced	16	+0.51	0.04	29	+0.21	0.28
Clutch mass	Full	27	+0.15	0.43	61	-0.19	0.15
	Reduced	16	-0.18	0.51	27	-0.28	0.15

Table 4. Correlations between body-size standardized reproductive variables and climate measures for the reduced data set of western Nebraska snapping turtles. Correlation coefficients appear above *P* values. Standardization methods are the regression residuals with carapace length (CL res), regression residuals with spent body mass (BM res), and ratio with spent body mass (e.g., REM, RCS and RCM).

Reproductive variable	Method	<i>N</i>	April-May mean temperature	Sept.-Oct. mean temperature
Egg mass	CL res	94	-0.19	+0.14
			<i>P</i> = 0.07	<i>P</i> = 0.18
	BM res	93	-0.13	+0.17
			<i>P</i> = 0.21	<i>P</i> = 0.10
	REM	93	-0.07	+0.02
			<i>P</i> = 0.52	<i>P</i> = 0.87
Clutch size	CL res	95	-0.012	+0.178
			<i>P</i> = 0.91	<i>P</i> = 0.08
	BM res	93	-0.130	+0.169
			<i>P</i> = 0.21	<i>P</i> = 0.10
	RCS	94	-0.025	+0.136
			<i>P</i> = 0.81	<i>P</i> = 0.19
Clutch mass	CL res	93	-0.105	+0.22
			<i>P</i> = 0.32	<i>P</i> = 0.035
	BM res	92	-0.062	+0.25
			<i>P</i> = 0.56	<i>P</i> = 0.016
	RCM	92	-0.089	+0.29
			<i>P</i> = 0.40	<i>P</i> = 0.004

Table 5. Model support for predictions of egg mass, clutch size, or clutch mass for western Nebraska snapping turtles. Highest model weights are in bold. See text for model descriptions.

Variable	Model	AIC _c	ΔAIC _c	ML	AIC _c WT
Egg mass	Sept.-Oct. mean	353.5	0	1	0.714
	Decade	357.3	3.83	0.147	0.105
	Global	357.6	4.09	0.129	0.092
	CL	357.9	4.45	0.108	0.077
	Apr.-May mean	361.6	8.14	0.017	0.012
	Null	502.5	149	0.000	0.000
Clutch size	Sept.-Oct. mean	451.2	0	1	0.495
	Global	451.2	0.02	0.992	0.490
	Decade	459.4	8.19	0.017	0.008
	CL	460.2	9.00	0.011	0.005
	Apr.-May mean	463.0	11.8	0.003	0.001
	Null	529.8	78.6	0.000	0.000
Clutch mass	Sept.-Oct. mean	347.7	0	1	0.526
	Global	348.0	0.264	0.877	0.461
	Decade	355.3	7.590	0.022	0.012
	CL	360.6	12.91	0.002	0.001
	Apr.-May mean	363.3	15.63	0.000	0.000
	Null	503.7	156.0	0.000	0.000

Table 6. Top model parameter estimates for predicting reproductive output for western Nebraska snapping turtles.

Egg Mass				
			95% C.I.	
	Estimate	S.E	Lower	Upper
$\beta_{\text{Intercept}}$	0.040	0.069	-0.094	0.175
$\beta_{\text{Sept.-Oct mean}}$	0.093	0.033	0.028	0.158
β_{CL}	0.857	0.059	0.742	0.973
$\beta_{\text{Sept.-Oct mean:CL}}$	0.027	0.031	-0.034	0.088
Clutch Size				
$\beta_{\text{Intercept}}$	0.037	0.070	-0.100	0.175
$\beta_{\text{Sept.-Oct mean}}$	0.153	0.048	0.059	0.246
β_{CL}	0.629	0.066	0.499	0.759
$\beta_{\text{Sept.-Oct mean:CL}}$	-0.089	0.046	-0.180	0.002
Clutch Mass				
$\beta_{\text{Intercept}}$	0.048	0.057	-0.063	0.158
$\beta_{\text{Sept.-Oct mean}}$	0.152	0.037	0.079	0.224
β_{CL}	0.824	0.053	0.720	0.928
$\beta_{\text{Sept.-Oct mean:CL}}$	-0.042	0.036	-0.112	0.029

FIGURE LEGENDS

Fig. 1. A) Positive relationship ($P < 0.0001$) between carapace length and egg mass (g; $N = 200$) in Nebraska snapping turtles (*Chelydra serpentina*). For the reduced data set ($N = 94$ different females) $y = 0.041x - 1.631$; $r = 0.79$; $P < 0.0001$. B) Positive relationship ($P < 0.0001$) between carapace length (mm) and clutch size ($N = 199$) in Nebraska snapping turtles (*Chelydra serpentina*). For the reduced data set ($N = 95$ different females), $y = 0.214x - 17.318$; $r = 0.63$; $P < 0.0001$. C) Positive relationship ($P < 0.0001$) between carapace length and clutch mass ($N = 196$) in Nebraska snapping turtles (*Chelydra serpentina*). For the reduced data set ($N = 93$ different females), $y = 4.478x - 840.07$; $r = 0.80$; $P < 0.0001$.

Fig. 2. A) Positive relationship ($r = 0.54$; $P = 0.045$) between mean temperature in September and October in the previous autumn and egg mass – spent body mass residuals in Nebraska snapping turtles (*Chelydra serpentina*). B) Positive relationship ($r = 0.61$; $P = 0.022$) between mean temperature in September and October in the previous autumn and clutch size – spent body mass residuals in Nebraska snapping turtles (*Chelydra serpentina*). C) Positive relationship ($r = 0.66$; $P = 0.010$) between mean temperature in September and October in the previous autumn and clutch mass – spent body mass residuals in Nebraska snapping turtles (*Chelydra serpentina*).

Fig. 3. Predicted variation in mean egg mass, clutch size, and clutch mass in response to changes in mean September-October temperatures ($^{\circ}\text{C}$) for our smallest (225 mm

carapace length), largest (397 mm CL), and median (311 mm CL) Nebraska snapping turtles, based on the top mixed-effects models with the highest Akaike weights. Shaded areas are the 95% confidence limits.

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