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Reproductive Output of Ornate Box Turtles (*Terrapene ornata*) in Illinois, USA

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Abstract.—**Reproductive traits in turtles are often positively correlated to body size, with larger females producing more eggs. At northern latitudes, breeding frequency typically decreases, whereas clutch size increases. Given such patterns of variation in reproductive output, population-level data on clutch size and frequency are needed to predict the persistence of remaining Ornate Box Turtle (*Terrapene ornata*) populations. We radiographed and measured female Ornate Box Turtles in Illinois to learn if clutch size is positively correlated to body size and, if so, what is the best measurement to use to approximate body size. We then compared mean clutch size from published accounts across the species range. Of 106 turtles radiographed in Illinois, 36 had visible eggs. Clutch size ranged from 1 to 6 eggs, with a mean of 2.64 and 4.55 at our two most intensively studied sites. We found a modest fecundity advantage in clutch size with female body size. Body size accounted for 38% of clutch size variation. Our results highlight the need for additional studies on Ornate Box Turtle growth and reproduction to guide conservation decisions and better understand life-history constraints.**

Key Words.—body size; clutch size; conservation; Emydidae; fecundity; radiography; Testudines

Introduction

Over half of all turtle and tortoise species are threatened with extinction, making chelonians one of the most threatened groups of vertebrates (Lovich et al. 2018). Enacting conservation measures to address threats and prevent extinction often requires information about the reproductive biology of a species (Cree 1994; Hamann et al. 2010), yet our knowledge of reproduction in most turtle and tortoise species is incomplete. Even in species where basic reproductive information exists, clutch size and frequency can vary clinally, making population-level data valuable (e.g., Tinkle 1961; Christiansen and Moll 1973; Litzgus and Mousseau 2006; Hedrick et al. 2017). Without estimates of reproductive output, it is impossible to project population persistence under varying management scenarios to inform conservation decisions.

For chelonians, calculating fecundity involves clutch size and frequency, which are determined from the proportion of gravid females in the population and the number of clutches produced each breeding season (Gibbons et al. 1982; Frazer 1984). Calculating the number of female offspring an adult female contributes to a population is also dependent on adult female survival, sex ratio at birth, and nest success. Once calculated, fecundity and survival estimates can be used to examine population growth. For most turtles and tortoises, however, we lack crucial data on population vital rates like fecundity (Ernst and Lovich 2009).

When female turtles invest resources in producing eggs, less energy is available for growth. For organisms like reptiles with indeterminate growth, investing energy in reproduction could be costly when fecundity is positively associated with clutch size (Reznick 1985). One way to study this tradeoff in chelonians is by focusing on the relationship between body size and clutch size. The body size/clutch size relationship can explain why larger female turtles produce more eggs in some populations and not others, revealing life-history constraints that shape selection patterns. This relationship, however, can differ between species and populations (Shine and Greer 1991; Iverson et al. 2019) or can be absent altogether (Broderick et al. 2003; Litzgus and Mousseau 2006). There are also latitudinal effects on growth and reproduction. Notably, clutch size increases while breeding frequency decreases at higher latitudes due to shorter nesting seasons and fewer available resources (Iverson 1992).

Reproductive output increases with female body size in most turtle species studied (Iverson et al. 2019). The greater internal volume of larger shells is thought to allow for increased clutch sizes (Dodd 1997). Absent data on internal shell volume, researchers traditionally use morphometric traits such as carapace and plastron length as proxies (e.g., Gibbons et al. 1982; Ryan and Lindeman 2007; Naimi et al. 2012), but other estimates could be more suitable. For example, by using carapace length, height, and width, the volume of the shell can be approximated with a modified formula for the volume of an ellipsoid (Loehr et al. 2004; Zuffi and Foschi 2015). Alternatively, King (2000) outlines the advantages of using the allometric coefficient from log-transformed data, especially because it allows for interspecific comparisons. Multivariate statistical approaches are also well-suited for approximating the size and shape of chelonians (Jolicoeur and Mosimann 1960; Somers 1986; Lutterschmidt et al. 2007), but until now, they have not been used to investigate a relationship to clutch size.

We studied female Ornate Box Turtles (*Terrapene ornata*) in Illinois, USA, to (1) learn the average clutch size and proportion of gravid females; (2) determine the relationship between clutch size and body size; (3) find the metric of body size best explaining clutch size; and (4) investigate latitudinal effects on reproductive output. As a threatened species in Illinois (Illinois Endangered Species Protection Board 2015), population-level data about reproductive output are valuable for conservation managers because they can be used to determine the viability of remaining isolated populations. Although clutch size has been studied in the USA in Kansas (Brumwell 1940; Legler 1960), Nebraska (Converse 1999; Converse et al. 2002), New Mexico (Nieuwolt-Dacanay 1997; Germano 2014), South Dakota (Quinn et al. 2014), and Wisconsin (Doroff and Keith 1990), there are no published data for populations in Illinois. Our results provide the first estimates of reproductive output for Ornate Box Turtles at the northeastern edge of their distribution.

Materials and Methods

Study sites.—We studied Ornate Box Turtles intensively at two sites in northern Illinois, USA, one in Carroll County and the other in Ogle County. Surveys took place May–June 2018 and 2019, and 9–13 June 2020. In 2019, we collected data on turtles from five additional sites, including in Lee, Iroquois, and Jasper counties, resulting in seven study sites within remnant prairie in northwestern and east-central Illinois (Fig. 1).

Surveys and morphological data.—We located female turtles using visual encounter surveys and wildlife detector dogs. In 2018 and 2019, we surveyed sites visually during the last two weeks of May and the first week of June. In 2020, we used wildlife detector dogs for 3 d in Ogle County and 2 d in Carroll County. We carried out visual encounter surveys during this time of year based on Tucker et al. (2014), who noted Ornate Box Turtles nesting in northern Illinois between 8 and 20 June. Wildlife detector dogs are highly effective at locating box turtles (Kapfer et al. 2012; Boers et al. 2017) but in 2019 they were not available for use during the limited window between egg calcification and nesting. Therefore, we used detector dogs in early May 2019 to locate turtles for radio transmitter attachments. We used transmitters from Holohil Systems (RI-2B, Carp, Ontario, Canada) and attached them to 18 females after dogs located them. We then relocated radio-tagged turtles at the end of May when eggs were likely to be calcified.

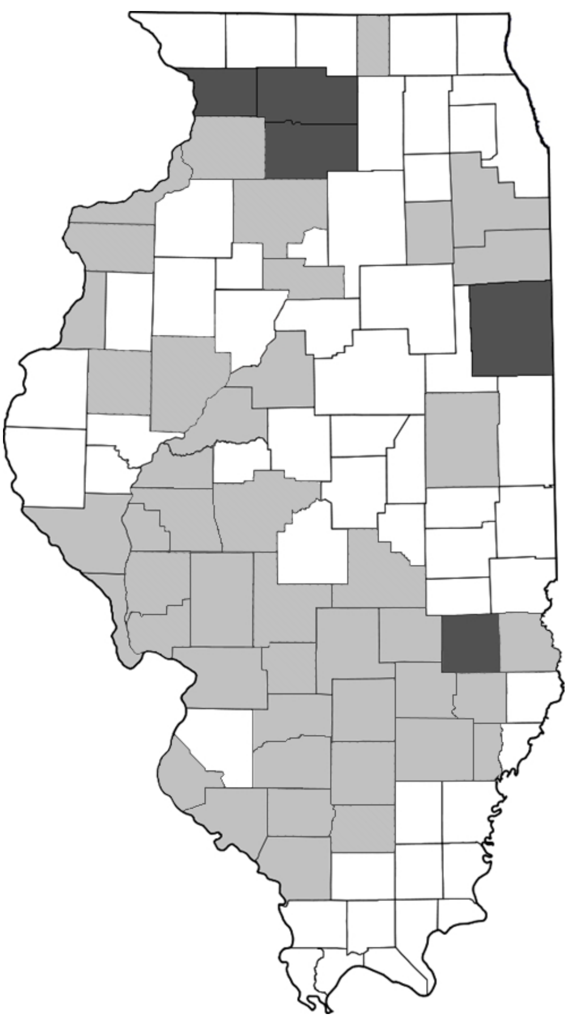

Figure 1. Ornate Box Turtle (*Terrapene ornata*) distribution in Illinois, USA. Dark gray counties were sampled for our study and light gray counties have records of occurrence. Map adapted from the Illinois Natural History Survey (Available from https://www.inhs.illinois.edu/collections/herps/data/ilspecies/te_ornata/. [Accessed 29 July 2019]).

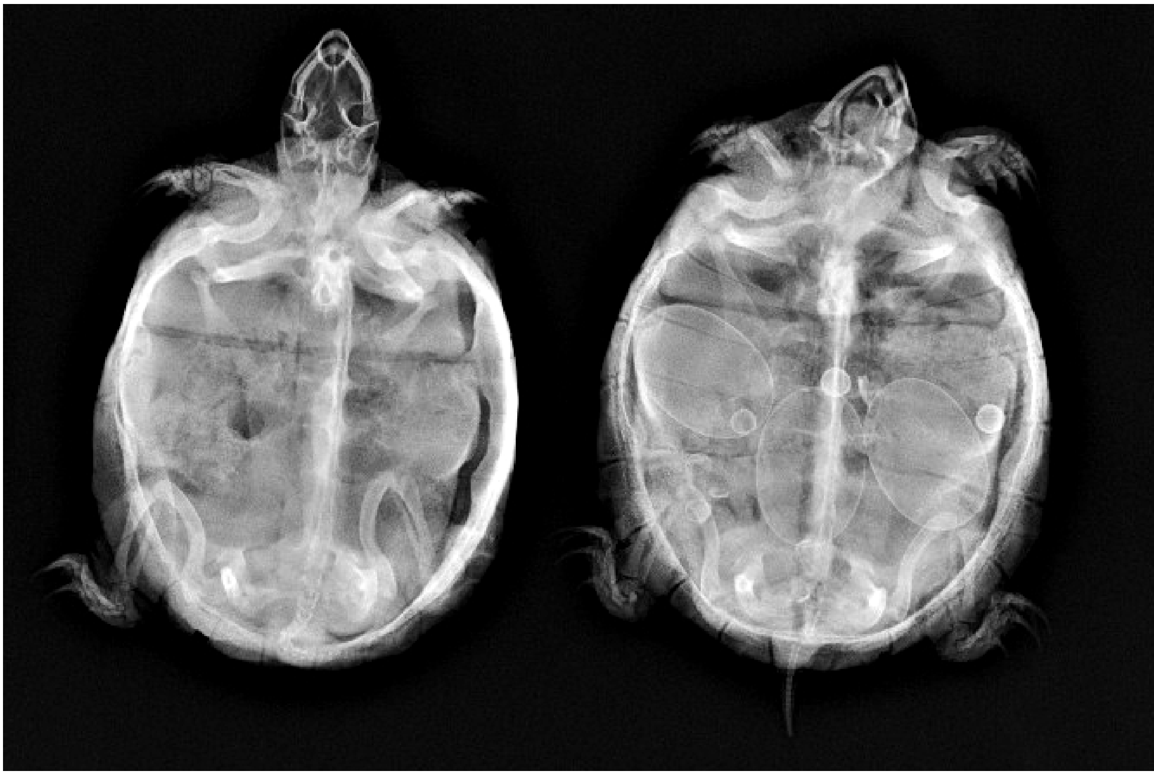

Figure 2. Radiograph of Ornate Box Turtles (*Terrapene ornata*) from Carroll County, Illinois, USA. The female on the right is gravid with three eggs. The smaller spots are likely partially mineralized follicles.

When we located a turtle, we recorded the location with GPS. We held the turtle overnight in a plastic container for either radiography the following day or to attach a radio-transmitter for future relocation. We assigned each turtle a unique identification number (ID) by notching marginal scutes (Cagle 1939). We measured maximum straight-line carapace length, carapace width at the widest point, and maximum shell height to the nearest 1 mm using forestry calipers. We measured the left pectoral scute length to the nearest 0.1 mm with digital calipers. Lastly, we calculated plastron length by summing maximum anterior plastral lobe length and maximum posterior plastral lobe length from the plastral hinge measured to the nearest 0.1 mm.

***Radiography*.—**In 2018 and 2019, we brought turtles to local veterinary clinics near study sites to be radiographed to determine clutch size (Gibbons and Greene 1979; Hinton et al. 1997). In 2020, we radiographed turtles on site using a portable radiography system. We placed turtles with plastron facing up to help immobilize them while radiographing up to five turtles per plate. We noted the locations of individuals on the plate and recorded IDs of each turtle before each radiograph. Veterinarians exposed turtles at 150 mA for 1/20 to 1/10 of a second at 62–65 kV. We examined digital images of radiographs to determine if females were gravid and, if so, the size of clutches (Fig. 2).

***Statistical analyses*.—**We used Linear Regression to assess the effect of body size on clutch size. To do so, we first performed a Principal Component Analysis (PCA) using measurements from 183 female Ornate Box Turtles from our study sites. The measurements used in the PCA were carapace length, carapace width, shell height, plastron length, and left pectoral scute length. The Kaiser-Meyer-Olkin (KMO) test of sampling adequacy and Bartlett's test of sphericity suggested a PCA was appropriate for our morphometric data ($KMO = 0.90$; $\chi^2 = 1135.2$, df = 15, $P < 0.001$). Using PCA, we identified a single multivariate approximation of size (PC1), explaining 78% of the variation. We then developed a set of candidate linear models explaining clutch size in 36 gravid individuals using the explanatory variables of either PC1, individual and additive morphometrics, or shell volume estimated as half the volume of an ellipsoid:

$$\text{Shell Volume} = \left(\frac{4}{3} * \pi * \text{CL} * \text{CW} * \text{SH}\right) / 2$$

We assessed homoscedasticity by examining plots of residuals versus fitted values and the assumption of normality with QQ plots. We centered and scaled morphometric data before analysis. Natural log-transformation, as proposed by King (2000), did not improve model fit; however, to allow our results to be comparable to other species and populations, we natural log-transformed data for carapace and plastron length models and report the allometric coefficient. We used Akaike's Information Criterion adjusted for small sample size (AICc) to determine the most parsimonious model in the set with package AICcmodavg (Mazerolle and Linden 2019). We performed all statistical analyses in R (R Core Team 2019).

To investigate the relationship between latitude and clutch size, we used Linear Regression (α = 0.05). First, we compiled clutch size data from all published accounts and then recorded latitude in decimal degrees of study locations (Table 1). Because the relationship did not appear linear, we natural log-transformed both variables. We examined a Cook's Distance Plot and studentized residuals to determine if sites were outliers, deciding it was most appropriate to retain all sites in the regression.

Results

Mean clutch size in Carroll County was 2.64 (95% confidence interval [CI] = 2.24–3.04; range, 1–4; n = 22) and in Ogle County it was 4.55 (95% CI = 3.92–5.17; range, 3–6; n = 11; Table 2). Two individuals at a separate site in Carroll County were gravid with three eggs each, one individual in Lee County was gravid with two eggs, and one individual in Iroquois County was gravid with four eggs (Table 2). No individuals sampled from Jasper County were gravid. Across sites and years, 33.9% (36 of 106) of females were gravid (Table 2). Of twelve recaptured individuals radiographed in different years, only one was gravid both years. In 2018, 54.5% (12 of 22) were gravid, compared to 33.3% (16 of 48) in 2019, and 30.6% (11 of 36) in 2020. Two gravid females radiographed twice in 2018 laid eggs between the radiograph sessions, and we sampled late in 2020, so the true proportion of gravidity could be higher.

We found evidence of a fecundity advantage where larger females produced larger clutches (Fig. 3). The top model showed clutch sizes depended on the multivariate body size component with clutch size increasing at less than the isometric rate with the body size component.

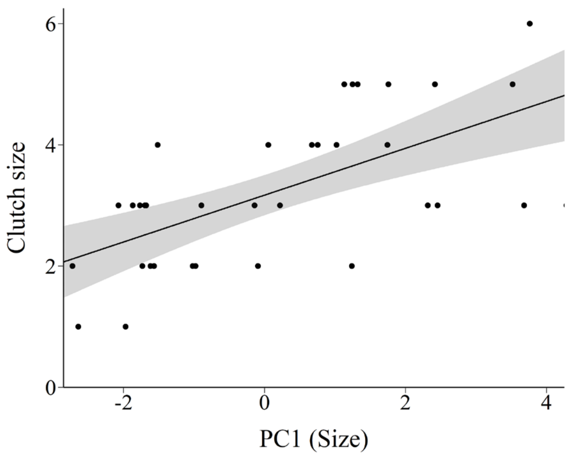

Figure 3. Top model showing the positive relationship between female body size and clutch size in Ornate Box Turtles (*Terrapene ornata*) sampled from Illinois, USA. Gray area is the 95% prediction interval. Points are raw data. The acronym PC1 = Principal Component 1, a multivariate size component from a Principle Component Analysis that used carapace length, carapace width, shell height, plastron length, and left pectoral scute length.

Models with shell volume and univariate components all ranked better than the null (Table 3). Adjusted r^2 showed no model accounted for more than 38% of clutch size variation. For the top model, β_{PC1} was 0.39 (95% CI = 0.22–0.55) and $\beta_{Intercept}$ was 3.17 (95% CI = 2.84–3.50). The allometric coefficient from natural log-transformed regression was 3.18 (95% CI = 1.68–4.68) for carapace length and 3.16 (95% CI = 1.65–4.67) for plastron length, suggesting clutch size increases as a cubic function of length. The smallest gravid female (two eggs) had a carapace length of 94 mm, and the largest gravid female (six eggs) had a carapace length of 126 mm. We did not find latitudinal variation in clutch size ($P = 0.255$).

Discussion

We identified a fecundity advantage in Ornate Box Turtle size. Linear models showed larger Ornate Box Turtles produce larger clutches, though body size

Table 1. Clutch sizes arranged by latitude for Ornate Box Turtle (*Terrapene ornata*) populations reported in literature. We pooled samples from Nebraska, where researchers reported clutch size determined using two different methods (radiographs and nest excavation) in separate sources but sampled at the same site and population.

Location	Latitude	Mean	Range	n	Source
New Mexico	34.3	2.7	1–4	77	Nieuwolt-Dacanay (1997)
New Mexico	34.3	2.9	1–5	39	Germano (2014)
Kansas	39.1	4.7	2–8	23	Legler (1960)
Nebraska	41.8	3.3	2–6	40	Converse (1999); Converse et al. (2002)
Illinois	41.9	4.6	3–6	11	This study
Illinois	42.1	2.6	1–4	23	This study
Wisconsin	43.2	3.5	Max = 7	21	Doroff and Keith (1990)
South Dakota	43.6	4.3	2–5	7	Quinn et al. (2014)

Table 2. The number gravid, the number sampled, and the percentage gravid of female Ornate Box Turtles (*Terrapene ornata*). Data are listed by Illinois (USA) county, site, and year. A and B denote two populations sampled in the same county. One individual at Carroll (A) was recaptured gravid in 2018 and 2019.

County (Site)	Year	# Gravid	# Sampled	% Gravid
Carroll (A)	2018	12	20	60%
Carroll (A)	2019	7	10	70%
Carroll (A)	2020	5	20	25%
Carroll (B)	2019	2	6	33%
Iroquois	2019	1	5	20%
Jasper	2019	0	4	0%
Lee (A)	2019	1	3	33%
Lee (B)	2019	0	2	0%
Ogle	2018	0	2	0%
Ogle	2019	5	18	28%
Ogle	2020	6	16	38%

explained only part of clutch size variation. Our results agree with Nieuwolt-Dacanay (1997) and Germano (2014), who also found a weak positive relationship between body size and clutch size. Although body size explained more variation than in some populations of the Eastern Box Turtle (*Terrapene c. carolina*), where there appears to be no relationship (Congdon and Gibbons 1985; Burke and Capitano 2011), it is not strong enough to suggest a large growth-reproduction tradeoff. Such a tradeoff may be absent if clutch size is only weakly explained by female body size. In addition to body size, turtle clutch size can also depend on abiotic conditions and body condition (Wilkinson and Gibbons 2005; Litzgus et al. 2008). Further research is needed to parse out how abiotic and energetic factors relate to reproductive output and account for the clutch size variation unexplained by body size.

Mean clutch size differed between sites in Carroll and Ogle counties. In Carroll County, mean clutch size was the smallest recorded for the species whereas in Ogle County mean clutch size approached the largest. Reproductive output is influenced by somatic growth because of the positive relationship between body size and clutch size (Congdon and van Loben Sels 1991). Smaller clutches at the site in Carroll County suggest turtles are either on average younger and consequently smaller or growth patterns differ between sites. For example, turtles at Carroll County may grow more slowly or for a shorter duration and thus mature at smaller sizes, resulting in small clutches. Such growth patterns causing variation in size at maturity are known in other chelonians (e.g., Congdon and Gibbons 1983; Rowe 1997; Willemsen and Hailey 1999). Studying if and how food resources differ between sites, especially for juveniles when growth rate is fastest (Bernstein et al. 2018), could help explain the relationship between clutch size and growth.

Table 3. Adjusted Akaike Information Criterion (AICc) table of linear models explaining Ornate Box Turtle (*Terrapene ornata*) clutch size by body size. Results are sorted by AICc. Acronyms are *K* = number of parameters, PC1 = Principal Component 1, which is a multivariate body size component, CL = carapace length, PL = plastron length, CW = carapace width, and SH = shell height. Shell volume was calculated with a modified formula for half the volume of an ellipsoid.

Model	*K*	AIC_c	ΔAIC_c	Weight	r^2	*P*
Eggs~PC1	3	105.17	0.00	0.48	0.38	<0.001
Eggs~Volume	3	107.94	2.77	0.12	0.33	<0.001
Eggs~CL	3	108.19	3.02	0.11	0.33	<0.001
Eggs~CL+SH	4	108.88	3.71	0.07	0.34	<0.001
Eggs~PL	3	109.53	4.36	0.05	0.30	<0.001
Eggs~PL+SH	4	109.68	4.51	0.05	0.33	<0.001
Eggs~SH	3	109.91	4.74	0.04	0.30	<0.001
Eggs~CW+SH	4	110.62	5.45	0.03	0.31	<0.001
Eggs~CW+SH+CL	5	111.50	6.33	0.02	0.33	0.001
Eggs~CW	3	111.58	6.41	0.02	0.26	<0.001
Global	6	114.39	9.22	0.00	0.30	0.003
Null	2	121.27	16.10	0.00	--	--

Iverson (1992) showed clutch frequency in turtles has an inverse relationship with latitude. Such latitudinal patterns of clutch frequency are due to the restricted nesting season in colder climates (Gibbons 1983). Because Illinois spans a large latitudinal gradient (36.9894°–42.5116°), southern populations in the state could be capable of producing two clutches per year even if northern populations do not. In a Nebraska population, Converse (1999) confirmed double-clutching in one of 25 females. In Kansas, Legler (1960) found 33% of dissected females had enlarged follicles, suggesting they could double-clutch in a year; however, enlarged follicles do not mean eggs fully develop or a female lays a second clutch of eggs. Further north in Wisconsin, double clutches have not been observed (Doroff and Keith 1990). If double-clutching does occur in Illinois, it is likely rare and limited to years when there is a longer warm season.

Our estimates of the percentage of females that were gravid should be interpreted as conservative. In 2018, two gravid females had eggs when initially radiographed but not when radiographed one week later, therefore turtles were nesting as early as 24–31 May 2018. As a result, in 2019, we chose to radiograph turtles earlier; however, eggs may not have been calcified and visible on the earliest radiographs. Our results show at least 30.6–54.5% of females were gravid, which is comparable to other published reports. Tucker et al. (2014) found 66.7% of monitored females nested at a site in northwest Illinois. In Wisconsin, 50–63% of females were gravid (Doroff and Keith 1990), and in

South Dakota, 64% were gravid (Quinn et al. 2014). In New Mexico, 31.3–44.4% (Germano 2014), and 58.1% of females were gravid (Nieuwolt-Dacanay 1997). Our data can be used in fecundity calculations to improve and predict population trends for the species.

Various size measurements have been used to explore the relationship between body size and clutch size in chelonians. Often carapace length and plastron length are analyzed, and our results show both are adequate for approximating clutch size in Ornate Box Turtles. Other approximations of body size may perform better, however. For a population of Eastern Box Turtles in Virginia, carapace width and shell height explained clutch size, whereas carapace length did not (Wilson and Ernst 2005). In European Pond Turtles (*Emys orbicularis*), shell height was a better predictor of clutch size than either carapace length or width (Zuffi et al. 1999). The top model in our study showed the multivariate size component PC1 as the best explanatory variable, which was composed of carapace length, carapace width, shell height, plastron length, and left pectoral scute length. When reducing morphometric variables to principal components, PC1 typically represents body size, and PC2 represents body shape and random variation (Somers 1986). Measuring shell angles or other aspects of shell shape could produce a PC2 useful for analyses of body size, growth, and reproductive output. Future studies of growth and reproduction in chelonians should consider using multivariate approximations of body size when enough morphometric data are available.

We determined Ornate Box Turtle clutch size in Illinois varied between populations and discovered evidence of a body size/clutch size relationship. We also demonstrated larger female Ornate Box Turtles produce larger clutches, which is common in turtle populations (Christiansen and Moll 1973; Iverson et al. 1993; 2019). Although body size accounted for part of observed clutch size variation, our results suggest only a weak growth-reproduction tradeoff. Wildlife managers can use the data we present on clutch size and gravidity for calculating fecundity and, along with estimates of other vital rates like survival, determine population trends for the species.

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Appendix 1. Morphometrics and egg counts for 36 female Ornate Box Turtles (*Terrapene ornata*) from four sites in Illinois, USA, used for linear regression of body size and clutch size. Measurements are in millimeters. Abbreviations are CL = carapace length, PL = plastron length, CW = carapace width, SH = shell height, PC1 = Principal Component 1, a multivariate body size component. Two gravid females were excluded from analysis because no measurements were taken (one individual from Carroll County A and one from Iroquois County). Additionally, a female at Carroll A was gravid with three eggs both years and so is only included in the table once.

Date	County (Site)	Eggs	CL	PL	CW	SH	PC1	Volume (cm^3)
24 May 2018	Carroll (A)	1	96	99.72	86	51	-2.640	882
24 May 2018	Carroll (A)	2	100	104.37	89	54	-1.734	1007
24 May 2018	Carroll (A)	1	100	100.66	89	48	-1.971	895
29 May 2018	Carroll (A)	2	100	106.31	92	53	-0.979	1021
29 May 2018	Carroll (A)	3	100	100.87	89	51	-2.073	951
30 May 2018	Carroll (A)	2	98	99.18	88	50	-2.724	903
30 May 2018	Carroll (A)	2	105	107.55	88	53	-1.617	1026
30 May 2018	Carroll (A)	3	112	117.09	95	55	0.220	1226
31 May 2018	Carroll (A)	3	100	103.55	89	50	-1.869	932
31 May 2018	Carroll (A)	2	111	113.08	90	54	-0.095	1130
31 May 2018	Carroll (A)	4	112	113.23	93	57	0.053	1243
5 June 2019	Carroll (A)	4	100	106.36	89	52	-1.516	969
5 June 2019	Carroll (A)	3	102	104.16	87	54	-1.768	1004
5 June 2019	Carroll (A)	3	103	104.42	90	48	-1.679	932
5 June 2019	Carroll (A)	3	103	104.11	89	48	-1.698	922
5 June 2019	Carroll (A)	2	104	109.54	88	55	-1.020	1054
5 June 2019	Carroll (A)	3	107	111.57	93	51	-0.142	1063
12 June 2020	Carroll (A)	2	101	106.63	87	51	-1.567	939
12 June 2020	Carroll (A)	4	111	118.31	101	60	1.744	1409
12 June 2020	Carroll (A)	2	94	98.15	82	55	-2.895	888
13 June 2020	Carroll (A)	3	103	108.2	90	50	-0.895	971
13 June 2020	Carroll (A)	4	114	116.62	97	56	0.755	1297
5 June 2019	Carroll (B)	3	120	120.66	103	61	2.454	1579
5 June 2019	Carroll (B)	3	125	130.54	107	57	3.682	1597
29 May 2019	Lee	2	115	113.04	97	58	1.239	1355
29 May 2019	Ogle	4	108	114.53	93	57	1.020	1199
29 May 2019	Ogle	5	116	119.51	100	63	3.519	1531
29 May 2019	Ogle	3	121	124.38	99	56	2.315	1405
29 May 2019	Ogle	3	125	133.31	101	62	4.283	1639
29 May 2019	Ogle	6	126	126.17	101	58	3.762	1546
9 June 2020	Ogle	5	112	114.55	95	57	1.130	1270
9 June 2020	Ogle	5	114	116.04	96	60	1.320	1375
9 June 2020	Ogle	5	120	123.13	101	62	2.416	1574
10 June 2020	Ogle	4	110	107.64	91	59	0.671	1237
10 June 2020	Ogle	5	113	118	93	55	1.249	1211
10 June 2020	Ogle	5	117	121.49	96	57	1.757	1341