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Reproduction in the Western Box Turtle, *Terrapene ornata luteola*

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Optimal egg size theory was tested using reproductive data from the western box turtle, *Terrapene ornata luteola*, obtained from 272 X-rays of 124 different turtles, 72 of which were gravid. Clutch size was positively correlated with maternal body size, but egg width was not related to either maternal length or width or clutch size but was related to maternal mass. Pelvic width was significantly correlated with egg width and maternal body size. Egg size varied little, as predicted by optimal egg size theory. Mean clutch size was 2.70 (n = 77) and mean egg width was 2.66 cm (n = 203); clutch size is smaller and egg width is larger than for *T. o. ornata*. During the three years of the study, two years had unusually wet springs, and egg production was high; one year had a dry spring, and a smaller proportion of females produced eggs; but mean clutch and egg sizes were not significantly different from other years. These data indicate that spring rains may increase the proportion of females laying eggs in the summer, and in years with dry springs, turtles may defer laying eggs completely, rather than reducing annual output.

TURTLES are long-lived, iteroparous tetrapods (Wilbur and Morin, 1988). They are excellent organisms for the study of reproductive output and the trade-off between offspring size and number (Elgar and Heaphy, 1989). This is because there is no parental care other than the provision of nutrition for hatchlings in the egg yolk (see references in Congdon and Gibbons, 1990), which is relatively easy to quantify.

Optimal egg size models assume that resources available for reproduction are limited. They predict that most variation in reproductive output within a population due to environmental conditions will be in clutch size rather than egg size, because egg size has been optimized by natural selection (Smith and Fretwell, 1974; Brockelman, 1975). If this is true in turtles, a positive relationship would exist between clutch size and clutch mass, and variation in egg size would be less than variation in clutch size. Because of limited energy for reproduction, however, some trade-off between clutch size and egg size is expected (Smith and Fretwell, 1974). According to Elgar and Heaphy (1989), there is a negative correlation across turtle genera between clutch size and egg mass, after the effects of body size are removed. A complete trade-off between clutch size and egg mass does not occur, however, because there is a positive relationship between size-adjusted clutch size and clutch mass.

Other factors and constraints may be operating to complicate the relationship between clutch size, egg size, and body size in turtles. The size and shape of an egg may be limited by the size of the pelvic aperture of the female turtle (Congdon and Gibbons, 1987; Long and Rose, 1989). Small turtles with small pelvic apertures may produce elongated eggs to reach the minimum egg size necessary to produce viable offspring (Long and Rose, 1989). Therefore, when considering clutch and egg size relationships, it is necessary to test whether pelvic constraints are operating in a population of turtles under study. In addition, the effects of proximate ecological factors on clutch and egg size, such as the amount of food available in a given year, are rarely considered. Optimal egg size models predict that egg size remains relatively constant but that clutch size would decrease under low food conditions and increase with abundant food availability.

The reproductive output and life-history strategy of *Terrapene ornata luteola*, the western or desert box turtle, is of interest because the harsh and unpredictable environmental conditions in which it lives are expected to have major effects on reproductive patterns. Little is known about reproduction of this subspecies, which lives in arid grasslands and deserts of the southwestern United States and northern Mexico. More is known about the ornate box turtle, *T. o. ornata*, the only other subspecies. It occurs mainly in prairie and forest habitats from Indiana to Texas and west to Colorado and eastern New Mexico (Legler, 1960). Ornate box turtles are omnivorous but eat mostly insects (Legler, 1960); western box turtles are also omnivorous (Norris and Zweifel, 1950; pers. obs.), but the percentage of animal matter in their diet is unknown. Both subspecies, but particularly *luteola*, live in more arid habitats than the eastern box turtle, *Terrapene carolina* (Ernst et al., 1994). *Ter-*

rapene o. luteola is considered by some to be relictual, on its way to extinction because of the increasing aridity of its range (Milstead and Tinkle, 1967).

According to Legler (1960), in *T. o. ornata*, ovarian follicles either grew to near maturity in the season preceding ovulation and then remained this way over the winter or grew rapidly between spring emergence from hibernation and ovulation in the spring. Fertilization occurred soon after ovulation, and eggs acquired their shells soon after they entered the oviducts. Eggs were laid from May to July. In August and September, the number of enlarged follicles is very low.

I asked the following questions in my study: (1) When do females lay eggs, and what are the clutch sizes? (2) What is the size at reproductive maturity for females? (3) How long are shelled eggs retained in the body? (4) Do females lay more than one clutch per season, and do they lay every year? (5) Is there a relationship between clutch size or egg size and maternal body size? (6) Is there a trade-off between clutch size and egg size (width)? (7) What rainfall episode (spring or summer), if any, has the greatest effect on turtle reproduction? and (8) Are there life-history differences between the two subspecies of box turtles, presumably because of their living in different habitats?

Materials and Methods

This study was conducted in the McKenzie Flats region of the Sevilleta National Wildlife Refuge, about 85 km south of Albuquerque, in Socorro County, New Mexico. This area is a semiarid grassland habitat at 1600 m elevation on the northernmost fringe of the Chihuahuan desert and at the northern edge of the range of *T. o. luteola*. Vegetation is characterized by blue and black grama (*Bouteloua gracilis* and *B. eriopoda*), dropseed (*Sporobolous* sp.), fluff (*Erioneuron pulchellum*), mule (*Muhlenbergia* sp.), three-awn (*Aristida*) grasses, scattered *Yucca glauca*, assorted cacti (*Opuntia*, *Echinocereus*), snakeweed (*Gutierrezia sarothrae*), and other small shrubs and annuals. Mean annual rainfall in Bernardo, 16.8 km from the study site, is 207 mm, most of it falling during July and August; annual temperatures range from −8 C (mean January minimum) to 35 C (mean July maximum; Owenby and Ezell, 1992). The study site consisted of the area along a 9.3-km dirt road, running approximately north/south.

I began fieldwork at the end of April every year and collected turtles from June through August in 1990 and 1991 and from mid-May until August in 1992. I drove through the study site, finding females on or alongside the road. Each turtle was weighed with a Pesola® scale and measured using dial calipers (straight line carapace length, SLCL; straight line carapace width, SLCW; and plastron length, PL). I used SLCL, SLCW, and mass in subsequent analyses. Each turtle was permanently marked by filing notches into the marginal scutes of the carapace. I placed a flag to mark the exact location of each turtle and put turtles in cardboard boxes, where they were kept from a few hours to seven days (most less than four days) before being returned. Females were x-rayed by a veterinarian once weekly, with a Fischer Veterinary x-ray unit, using the table-top technique with a 91.4 cm focal distance, 300 mA 1/60 second exposure @65 KVP. I used 3M® brand standard veterinary x-ray film. Several turtles were x-rayed on their backs on one plate at the same time. To calibrate size on the radiograph, a quarter was placed on a piece of foam the approximate height above the plate where eggs would be, and the image later measured. I adjusted all measurements accordingly, as in Graham and Petokas (1989). Maximum egg widths to the nearest millimeter were measured from radiographs using dial calipers. Pelvic widths (the shortest distance between the ilia) were only measured from turtles in which the pelvis had been x-rayed symmetrically.

Data on rainfall over the course of the study and for one year before were collected from the Deep Well Meteorological Station Campbell Scientific data logger, located about 300 m to the west of the road. Data from 1990 and 1992 were analyzed separately. Only four clutches were recorded in 1991, and separate analyses were performed on the combined data for all three years. Because three analyses were carried out with the same variables (e.g., clutch size vs SLCL), I made sequential Bonferroni adjustments to all relevant statistics; the significant values reported have this taken into consideration. ANOVAs were conducted to test the differences in body size between all three years. After checking for normality of variables, I used Pearson product-moment correlations to assess the relationship between maternal body size and clutch size, clutch size and mean egg width, and pelvic width, maternal body size, and egg width. I used ANCOVA to test differences betwen regression lines. Partial correlations were conducted between clutch size and egg width; body size (SLCL, SLCW, and mass) was held constant to remove its effect on other variables. I carried out all analyses using the Statistical Analysis Sys-

tems statistical package (vers
SAS Institute, Inc., Cary, NC,

Results

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Results

A total of 124 different individuals were x-rayed during the course of the study (Table 1). In all cases but one, eggs detected in x-rays were clearly visible. In the case where images of eggs were faint, showing the egg shells to be poorly developed, additional eggs were not detected on subsequent films.

Females were gravid in June and July of 1990 and 1991 and from May through August in 1992 (Table 1). Most females had laid eggs by late July. In 1991, the proportion of females found gravid was much reduced compared with the other two years (Table 1). Body size dimensions of gravid turtles (Table 2) did not differ significantly among years (SLCL: $F_{2,74} = 2.09$, $P = 0.13$; SLCW: $F_{2,74} = 3.06$, $P = 0.053$; body mass: $F_{2,74} = 0.00$, $P = 0.99$). Mean body sizes (± one standard deviation) for 137 females captured in the study area (13 not x-rayed) were SLCL 11.85 ± 0.58 cm (range 10.52–13.93), SLCW 9.88 ± 0.41 cm (range 9.11–11.14), and body mass 430.3 ± 57 g (range 272–590). Only body mass differed significantly between gravid females and all females, gravid females being heavier ($t = -2.185$, df = 207, $P = 0.03$).

Some turtles nested between sequential x-raying. Most nesting seemingly occurred in July, some may have occurred in June (one turtle definitely nested in June), and a few may have nested in August (Table 3).

The smallest gravid female had an SLCL of 10.70 cm, an SLCW of 9.30 cm, and a mass of 327 g. Another female was narrower (SLCW = 9.11 cm) but slightly longer (SLCL = 10.81 cm) and heavier (mass = 349 g). Both females had clutches of two eggs.

Four turtles x-rayed repeatedly were seen to retain eggs in 1990, the minimum time being eight days, the maximum 22 days. These are, of course, minimum estimates of retention, because the eggs may have been formed well before the first radiograph and laid some time after the last. No females were found with eggs in successive x-rays in 1991. In 1992, 11 turtles retained eggs; the shortest retention time was eight days. Nine of them carried eggs for more than 30 days, and the maximum was 50 days. To determine whether egg retention was related to the number of times females were handled, the number of times a retaining female was x-rayed in a season was counted. There seemed to be little relationship to the length of egg retention and number of times a female was x-rayed. For example, the female that retained eggs for 50 days had only been x-rayed twice. Another female that retained eggs for 49 days had been x-rayed three times, and yet another that retained eggs for 48 days had been x-rayed four times before she nested. Of the three turtles that laid eggs late in the season (i.e., August 1992), two had never been x-rayed before; the other had been x-rayed twice previously that year.

Only five turtles were gravid in two years of the three-year study. Clutch sizes in two of the five individuals decreased in the subsequent year of reproduction, and in two it increased, with differences being as many as two eggs. No turtle was found gravid for three successive years. In 1990, turtle 29 had a clutch of two eggs and in 1991 was x-rayed five times throughout the summer and never found to be gravid. She was also x-rayed in June 1992, when she should have been gravid if reproducing that year, but she was not. Five other turtles were found gravid in one year and not gravid in another when x-rayed in June of that year. Another female was found not gravid in June two years in a row. Reproduction may not occur yearly in every individual, but two turtles were found gravid two years in a row. Thus, repeated annual reproduction does sometimes occur.

Clutch sizes ranged from 1–4, with mean clutch sizes (± standard deviation, coefficient of variation) of 2.50 (± 0.82, 33.0%) in 1990, 2.75 (± 0.35, 12.9%) in 1991, 2.70 (± 0.63, 23.3%) in 1992, and a combined mean of 2.68 (± 0.74, 27.6%, a total of 77 clutches, 72 different turtles) for all three years. Clutch sizes were not significantly different between years. I saw no evidence of turtles laying more than one clutch per year, which would entail either detecting different clutch sizes in the same turtle within a year or detecting eggs in an individual, then finding no eggs and later detecting eggs again in the same turtle. It is possible that eggs of two different clutches were mistaken for the same clutch, but the second clutch would have had to have the same number of similar-sized eggs. However, eggs of some turtle species stay in the same position within the turtle (W. Gibbons, pers. comm.), and a comparison of radiographs would reveal whether egg positions had changed. Subsequent radiographs of single individuals were examined to determine whether the eggs were in the same position and therefore probably of the same clutch. In all instances, eggs were in the same position.

Clutch size showed a positive, significant correlation with all measures of size of turtle (Table 2; Fig. 1), except for 1990 measures of SLCL

TABLE 1. NUMBER OF FEMALES X-RAYED AND FOUND GRAVID RELATED TO DATE OF CAPTURE. Totals for the entire year and all years represent the number of different individuals x-rayed (and so do not include repeat x-rays). Numbers in parentheses include turtles x-rayed more than once.

Year	Dates captured	# x-rayed	# gravid	% Gravid	# x-rayed that year and previous year
1990	6–12 June	14	10	71.4	
	19–20 June	11	6	54.6	
	25–26 June	9	4	44.4	
	2–3 July	10	7	70.0	
	10–11 July	10	2	20.0	
	16–17 July	11	0	0	
	23–24 July	8	2	25.0	
	30 July–14 Aug.	26 (31)	0	0	
	Entire season	61 (104)	26	41.9	—
1991	10–12 June	4	2	50.0	
	18–20 June	5	1	20.0	
	24–27 June	4	0	0	
	1–3 July	6	0	0	
	8–11 July	6	0	0	
	15–18 July	12	1	8.3	
	22 July–21 Aug.	25 (37)	0	0	
	Entire season	40 (47)	4	10.0	19
1992	20–21 May	10	9	90.0	
	1–3 June	10	7	70.0	
	7–10 June	16	11	68.8	
	14–17 June	6	4	75.0	
	21–24 June	7	5	71.4	
	28 June–1 July	6	3	50.0	
	6–7 July	3	2	66.7	
	12–14 July	17	11	64.7	
	19–22 July	10	5	50.0	
	26–29 July	17	5	29.4	
	2–5 Aug.	10	1	10.0	
	9–11 Aug.	5	1	20.0	
	16–27 Aug.	16	0	0	
	Entire season	77 (131)	47	61.3	24
	All years	124 (272)	72 (77)	58.1	14

and SLCW. There was no evidence of a tradeoff between clutch size and egg size, from either simple or partial correlations.

Egg width was significantly, positively correlated with maternal body mass in 1992 and all years combined, but the value of r for the latter correlation coefficient is very low ($r = 0.177$; Fig. 2; Table 2). For 1990, correlations were negative and not significant. Egg width is therefore not related to the length or width of the female, but there is some evidence that heavier turtles lay wider eggs. However, pelvic width was significantly correlated with egg width ($r = 0.478$, $df = 85$, $P = 0.0001$ with a slope of 0.31) and maternal body size (SLCL: $r = 0.40$, $df = 32$, $P = 0.019$, SLCW: $r = 0.42$, $df = 32$, $P = 0.014$, body mass: $r = 0.45$, $df = 32$, $P = 0.007$). Slopes and intercepts of egg width and pelvic width against body size were the same (SLCL: slope $F_{1,68} = 2.24$, $P = 0.1395$, intercept $F_{1,68} = 1.62$, $P = 0.2080$; SLCW: slope $F_{1,68} = 2.52$, $P = 0.1174$, intercept $F_{1,68} = 1.89$, $P = 0.1735$; body mass: slope $F_{1,68} = 3.07$, $P = 0.0843$, intercept $F_{1,68} = 1.22$, $P = 0.2739$).

Monthly means of precipitation are shown in Table 4. Although reproduction was greatly reduced in 1991, the amount of rainfall received in the summer and fall of 1990, when turtles might be sequestering resources to put into reproduction the following year, was substantial. In fact, in all three years rainfall was above the long-term average for the area. In 1989, there was less than average rainfall, but July, August, and October were very wet; rainfall figures for

TABLE 2. TURTLE BODY SIZES
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Parameter
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SLCW (cm)
Body mass (g)
Eggs:
Width (cm)
CV (%)
Pearson correlations:
Clutch size versus:
SLCL
SLCW
Body mass
Egg width:
Pearson correlations:
with egg width
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TABLE 2. TURTLE BODY SIZES, ESTIMATED EGG WIDTHS AND CORRELATIONS BETWEEN VARIABLES. Sample sizes are in parentheses and, for turtle sizes, represent the number of different turtles found gravid within a year. Values for body size for Total (all three years) includes the mean values for five turtles found gravid for more than one year. Means ± one standard deviation, SLCL = straight line carapace length, SLCW = straight line carapace width, CV (%) = coefficient of variation. All measurements are in centimeters or grams. Statistical significance indicated by * $P < 0.05$, ** $P < 0.025$, *** $P < 0.001$ without any Bonferroni adjustment; all asterisked values are also significant with sequential Bonferroni adjustment, except for *†, which is not significant after sequential Bonferroni adjustment.

Parameter	1990	1991	1992	Total	Range
Gravid females:	(n = 26)	(n = 4)	(n = 47)	(n = 72)	
SLCL (cm)	12.07 ± 0.64	11.73 ± 0.43	11.79 ± 0.51	11.90 ± 0.57	10.78–12.79
SLCW (cm)	10.08 ± 0.43	9.88 ± 0.41	9.84 ± 0.39	9.92 ± 0.43	9.11–10.86
Body mass (g)	454.20 ± 65.4	448.80 ± 37.9	447.70 ± 55.9	447.30 ± 57.2	327–590
Eggs:	(n = 64)	(n = 11)	(n = 128)	(n = 203)	
Width (cm)	2.64 ± 0.10	2.74 ± 0.08	2.66 ± 0.11	2.66 ± 0.11	2.38–2.90
CV (%)	3.79	3.03	4.14	4.14	
Pearson correlations:					
Clutch size versus:					
SLCL	0.383	—	0.426**	0.342**	
SLCW	0.385	—	0.499***	0.380***	
Body mass	0.441*	—	0.513***	0.445***	
Egg width:	(n = 64)	—	(n = 128)	(n = 203)	
	0.137	—	0.048	0.107	
Pearson correlations:					
with egg width					
SLCL	−0.100	—	0.188	0.034	
SLCW	0.150	—	0.211	0.138	
Body mass	−0.157	—	0.358***	0.177**	
Partial correlations:					
with egg width; the following held constant					
SLCL	0.181	—	−0.025	0.101	
SLCW	0.094	—	−0.047	0.058	
Body mass	0.248*†	—	−0.148	0.021	

this year were included because they may explain the reproductive pattern in 1990. Both 1990 and 1992 had unusually wet springs; these coincide with relatively high proportions of gravid females in those years. In contrast, in 1991, when only a small proportion of females were gravid, the spring was dry.

Terrapene o. luteola had smaller clutch sizes than *T. o. ornata*, which had a mean clutch size of 3.5 (n = 21) in south-central Wisconsin (Doroff and Keith, 1990) and 4.7 (n = 23) in northeast Kansas where ornate box turtles may produce two clutches/year (Legler, 1960). In the latter study, mean egg width was 2.17 cm (n = 42), smaller than the mean width found in this study (2.66 cm). Body sizes of the Kansas population are not significantly different (Mann-Whitney Rank Sum test, $t = 902$, $P = 0.437$) from those of this study (gravid females only, Kansas mean plastron length 12.15 cm [n = 21] and for New Mexico, mean plastron length 12.32 [n = 72]). Body size data were not presented for the Wisconsin population.

DISCUSSION

X-radiographs are often considered 100% accurate in revealing shelled eggs (Gibbons and Greene, 1979), but Turner et al. (1986) maintained that radiographs failed to show all eggs in a clutch when the shells were just being developed. In all cases here, when gravid females were x-rayed repeatedly within a year, clutch sizes remained the same.

In western box turtles in Socorro County, New Mexico, there was no evidence that turtles laid more than one clutch per season. Some individuals laid eggs in successive years, and some may have skipped years between reproductive bouts. This is not unusual in long-lived, itero-

TABLE 3. DATES OF NESTING FROM SEQUENTIAL X-RAYING. Nesting had occurred sometime after the first date and before the second date.

Year	Turtle #	Nesting date	
		After	Before
1990	29	7–03	7–11
	39	6–20	8–14
	46	6–26	7–11
	66	7–24	8–14
	114	6–12	7–17
1991	39	6–12	6–26
1992	9	7–07	7–22
	24	6–24	7–22
	75	7–17	7–29
	108	5–21	8–05
	604	6–17	7–22
	613	7–29	8–18
	616	6–10	7–22
	620	7–14	7–29
	664	7–29	8–27
	666	7–14	8–05
	798	7–14	8–05

parous organisms, particularly ectotherms (Bull and Shine, 1979). It also occurred in *T. o. ornata* in Wisconsin, where 57% of female turtles in a two-year period laid eggs (Doroff and Keith, 1990); this figure is close to that of my study (58% over three years).

Retention of shelled eggs inside the female can occur for considerable periods (up to 50 days, but possibly more), and much longer retention times were observed in 1992 than in 1990. Egg retention has been reported in *T. o. ornata* for up to three weeks in Kansas (Legler, 1960). Handling may increase egg retention, but my data do not show this unequivocally.

Clutch size varied both within (Table 2) and

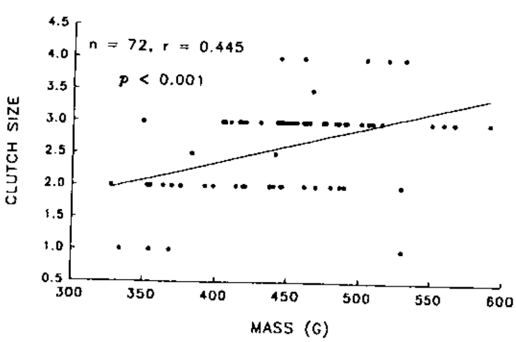

Fig. 1. Clutch size versus body mass of female turtles, all years combined. The mean of the clutches were used for five turtles that laid more than one clutch during the course of the study.

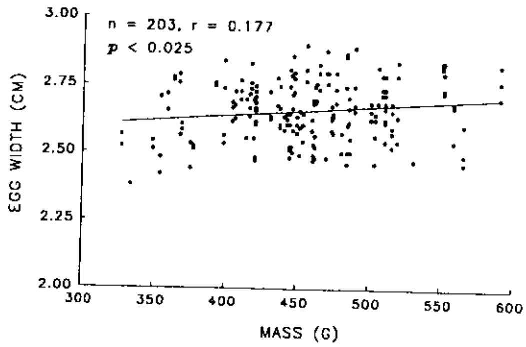

Fig. 2. Estimated egg width versus body mass of female turtles, all years combined.

among individuals (C.V. of 27.6%). Only one of five turtles showed a possible age effect (i.e., turtles increasing clutch size with age).

There was no relationship between clutch size and body size in *T. carolina* (Congdon and Gibbons, 1985), nor for *T. o. ornata* using plastron length as a measure of body size (Legler, 1960). However, when I used plastron length against clutch size for *T. o. luteola*, I also found a nonsignificant relationship, and the regression lines for the two subspecies were significantly different (slope: $F_{1,91} = 39.58$, $P < 0.0001$; intercept: $F_{1,91} = 74.25$, $P < 0.0001$). In *T. o. luteola*, there was no relationship between clutch size and individual egg width and only weak evidence of egg size increasing with body size (only with mass). Egg width did increase with pelvic width, suggesting a possible pelvic constraint on egg size, particulary for smaller females (Fig. 2). Egg lengths are needed to further assess this rela-

TABLE 4. AVERAGE MONTHLY PRECIPITATION (mm) FOR DEEP WELL METEOROLOGICAL STATION, SEVILLETA NATIONAL WILDLIFE REFUGE, NEW MEXICO. * Data lost; reading from Five Points, at the southern tip of the study site.

Month	1989	1990	1991	1992
January	—	3.3	7.2	16.4
February	0	7.8	2.0	7.2
March	5.2	15.0	7.8	16.7
April	0	39.8	0	19.0
May	5.5	21.6	14.1	48.7
June	0	5.5	74.4	5.8
July	56.5	47.0	47.9	33.1
August	34.0	23.9	47.3	42.9
September	5.8	44.1	44.1	23.3
October	30.5	6.1	1.2	20.2
November	0	18.4	32.8	6.3
December	2.9	11.9*	55.9	3.2
Totals	140.4+	244.4	334.7	242.8

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tionship. No trade-off between clutch size and egg size was found in this population. In accordance with optimal egg size models, egg size (C.V. = 4.1%) varied only slightly compared with clutch size (C.V. = 27.6%).

The proportion of females in the samples found with eggs was lower in 1991 compared with 1990 and 1992, which had unusually wet springs. Spring precipitation may affect reproduction that same year, but the number of years of this study is insufficient to confirm this pattern.

Data from other studies on the relationship between reproduction and rainfall are equivocal (for a discussion on aquatic turtles, see Gibbons, 1982; Gibbons et al., 1982, 1983). No relationship between rainfall and reproductive parameters was found in *Testudo hermanni* in Greece and France (Swingland and Stubbs, 1985), nor in *T. graeca* and *T. marginata*, where long-term accumulation of energy is thought to occur (Hailey and Loumbourdis, 1988). In contrast, *Geochelone gigantea* on Aldabra increased mean clutch size, egg mass, and total number of nests in a wet year (Swingland and Coe, 1979). In Mohave desert tortoises, a difference in clutch frequency was attributed to winter rainfall and the net production of vegetation (Turner et al., 1984). In this study, clutch sizes did not change in a year with a dry spring, compared with a year with a wet spring, but most turtles deferred reproduction. It is possible that in New Mexico most resource acquisition for a clutch does occur the previous year (see Congdon and Tinkle, 1982). However, the final decision to lay eggs appears to be made in the spring, after indications that there will be plenty of food for adults to replenish their lipid reserves. Thus, ova may be resorbed (Wilbur and Morin, 1988) in a dry spring, in some females. Deferring reproduction is predicted for iteroparous organisms (Hirshfield and Tinkle, 1975). It appears to occur in Aldabra tortoises, where preovulatory follicles are developed but then resorbed if food resources are limited (Swingland and Coe, 1978).

Mean egg widths in this study are larger than those for *T. o. ornata* in Kansas. However, clutch sizes in *T. o. luteola* were much smaller than in *T. o. ornata*. Some western box turtles did not reproduce every year, as found in ornate box turtles in farmland habitat in Wisconsin (Doroff and Keith, 1990). This is in contrast to ornate box turtles in open woodland/pasture in Kansas that apparently laid eggs yearly, with some even laying two clutches/year (Legler, 1960). South-central Wisconsin is slightly drier that northeast Kansas (795 mm annual precipitation vs 909 mm; Wernstedt, 1972). It is possible that fecundity of box turtles is reduced in desert habitats. In addition, turtles show high variability when studied over several years, and geographic trends can be obscured by local environmental conditions (Gibbons and Greene, 1990).

Optimal egg size theory does describe some, but not all, aspects of egg-laying in the western box turtle. For example, clutch size did not vary with environmental conditions, as predicted. Further research is needed to test the hypothesis that wet springs increase the proportion of females laying eggs in the summer. In addition, the exact cues females use to assess environmental conditions need to be studied. In this subspecies, these conditions may be more critical for egg-laying than in the ornate box turtle, which lives in more mesic habitats.

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