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REPRODUCTIVE ENERGETICS OF THE PAINTED TURTLE (*CHRYSEMYS PICTA*)

JUSTIN D. CONGDON AND DONALD W. TINKLE

ABSTRACT: Only 50–70% of the female *Chrysemys picta* in southern Michigan reproduce every year, and approximately 10% produce two clutches in a season. Energy allocation to the largest class of follicles begins at least 10 months prior to egg laying. The average female enters brumation with half of the 222 kJ of an average clutch already in follicles that are approximately 14 mm in diameter. Between emergence in the spring and egg laying, stored body lipids may supply the remaining 50% of the energy required to complete the clutch. The average clutch in the population is 7.6 eggs. Egg material of the painted turtle is high in energy (26.43 J mg⁻¹ dry mass), and each egg contains 29.2 kJ. Egg lipids average 22.3% of the total dry mass and 28.2% of the dry mass of eggs without shells. Hatchlings are 20.7 percent lipid by mass. During development 38% of the total egg lipids are utilized while 62% remain in the hatchling to be utilized as fuel for maintenance and possibly for early growth. Egg size is positively related to body size of the female. Indirect evidence indicates that design constraints on the pelvic girdle may limit maximum egg size at a given body size. Levels of stored body lipids are more variable than reproductive output, indicating that painted turtles may fit the “bet hedging” reproductive tactic.

Key words: Reptilia; Testudines; Emydidae; *Chrysemys*; Development; Egg; Lipids; Reproduction

REPRODUCTIVE effort and parental investment are two major components of theories dealing with reproduction. Reproductive effort is the proportion of total resources or energy available to an organism that is allocated to reproduction (Congdon et al., 1982; Dobzhansky, 1950; Fisher, 1930; Hirshfield and Tinkle, 1975; MacArthur and Wilson, 1967; Pianka, 1970; Vitt and Congdon, 1978; Williams, 1966a,b). Parental investment refers to how total reproductive output of an organism is allocated among individual offspring (Brockelman, 1975; Congdon et al., 1978, 1981; Kaplan, 1980; Kaplan and Salthe, 1979; Smith and Fretwell, 1974; Stewart, 1979; Trivers, 1972; Trivers and Willard, 1973; Wilbur, 1977). Both of these concepts are based on the assumption that energy available to an organism is finite, and thus energy allocated to reproduction results in a concomitant reduction in the allocation of energy or resources to other compartments of the energy budget or to other offspring.

Two major selective factors, namely resource availability and demographic en-

vironment (see Stearns, 1976, 1977), are believed to be important in determining levels of reproductive effort and investment per offspring. According to the theory of *r*- and *K*-selection, life history traits such as early maturity, high fecundity, small offspring, short life expectancy, and high reproductive effort should be characteristic of species with high per capita resource availability. Alternative traits would be found in species with low per capita resource availability (Dobzhansky, 1950; MacArthur and Wilson, 1967; Pianka, 1970, 1972).

The demographic environment has been considered important in shaping life histories (Hirshfield and Tinkle, 1975; Murphy, 1968; Stearns, 1976, 1977; Williams, 1966a,b). Williams (1966a,b) discussed the role of the demographic environment in shaping life histories. He used the concept of reproductive value (Fisher, 1930) and predicted (1) that species with long lives should have low reproductive effort per breeding season, (2) that species with short life expectancies should have high levels of reproductive effort because they are at high risk,

and (3) that reproductive effort should increase with age in most species. Others have expanded Williams' arguments and implicated other aspects of the role of the demographic environment. For example, in environments with unpredictable juvenile survivorship associated with relatively high adult survivorship, selection can favor low reproductive effort and increased lifespan (Murphy, 1968; Stearns, 1976, 1977). This model, called "bet hedging" (Stearns, 1976), predicts that reproductive effort will be reduced to allow the number of reproductive bouts to increase and maximize the probability of producing offspring during a period of high survivorship of neonates. These characteristics are identical to those predicted to arise due to the effects of *K*-selection.

Thus, as pointed out by Wilbur et al. (1974), similar life history traits are predicted under very different selective forces. For example, a comparison of two species with low reproductive effort will not distinguish between demographic environment or resource level as the major selective factors. However, if the underlying stored lipids are monitored, it may be possible to identify the selective force. In a competitive environment where resources are limiting (*K*-selection), storage levels should not react dramatically, compared to reproductive output, in response to an increase in resource availability. In contrast, in environments where juvenile mortality is high and unpredictable (bet hedging) an increase in resources should cause an increase in stored lipids rather than an increase in reproductive output, because an increase in fitness associated with increased reproduction is not predictable.

Organisms with total reproductive output that is similar may allocate different amounts of resources to each offspring. How organisms might vary allocation per offspring in response to resource availability, the competitive environment, and predation has been explored (Batesman, 1948; Brockelman, 1975; Congdon

et al., 1978, 1981; Kaplan, 1980; Kaplan and Salthe, 1979; Smith and Fretwell, 1974; Stewart, 1979; Trivers, 1972; Wilbur, 1977). Most models assume that, within a population, investment per offspring has been optimized and thus the response to short term environmental changes in resources among adults will be in offspring number (Brockelman, 1975; Smith and Fretwell, 1974). While the relationship of clutch size to body size in reptiles has been well documented, the relationship between egg size and female size within populations is not well known.

This report deals with the energetics of reproduction in the midland painted turtle (*Chrysemys picta*) in southeastern Michigan. Data are presented on follicular development, clutch size, clutch frequency, egg size and components, use of egg lipids during development, the relationship of egg size to body size of females, and use of stored body lipids by adults during the period from emergence in spring until eggs are laid in June.

Because a total energy budget for the painted turtle is beyond the scope of this paper (see Congdon et al., 1982), the following limited hypotheses about reproductive energetics of the painted turtle were developed based on the theoretical considerations discussed above:

(1) If egg or offspring size has been optimized there should be little variation in egg size among individuals and no relationship of egg size to body size of females.

(2) If *C. picta* exhibits the "bet hedging" response to environmental variation, there should be less variation in reproductive output compared to variation in underlying lipid stores.

MATERIALS AND METHODS

Adult female turtles were collected from areas near the E. S. George Reserve of the University of Michigan when they emerged from brumation in the spring (early April), during the reproductive season (late May through June), in late

August and early September, and in October. All females were weighed, measured for carapace length (CL) and plastron length (PL), and then frozen for subsequent dissection and lipid extraction. Upon dissection, wet masses were taken of the entire ovaries and liver; all follicles greater than 5 mm were counted and measured (0.1 mm), and some were removed and dried for lipid extraction and energy determinations. Follicles appeared to be developing in sets with similar sizes, so they were assigned to discrete classes if they differed in diameter by 2 mm. Large follicles were the largest class of follicles greater than 10 mm in diameter. Small follicles generally were between 6 and 9 mm in diameter.

Oviductal eggs were counted and measured (0.1 mm), wet masses were recorded (0.01 g), and the eggs were then frozen. Eggshells were removed by slicing around the circumference of frozen eggs with a scalpel and were oven-dried (70 C) to a constant mass (0.1 mg). Unshelled eggs and follicles were freeze-dried to a constant mass (0.1 mg), ground with a mortar and pestle, and then soaked in petroleum ether (15-to-1 ratio of solvent-to-solute) at room temperature for a minimum of 2 days. Solvent and dissolved lipids were vacuum-filtered, the solvent was distilled, and remaining lipids were dried and weighed (0.1 mg).

Some clutches of eggs were separated into two groups. One group was frozen, and the other was incubated on water saturated sand (to prevent reduction in hatchling size due to water stress; Packard et al., 1981) at room temperature (≈ 29 C). Lipids were extracted from the eggs and hatchlings following the procedures described above.

The soma of adult females collected upon emergence in April and in June was separated into body (including the liver) and shell, which was scraped clean of all tissue. Shells were oven-dried and bodies were freeze-dried to a constant mass (0.1 g). Dried bodies were ground with a Wiley Mill®, and total lipids were ex-

tracted from an aliquant sample (≈ 2 g) following the same procedures used for eggs.

Determinations of energy content of freeze-dried eggs and follicles were made using a Philipson micro-bomb® calorimeter (Tinkle and Hadley, 1973, 1975).

We used a non-destructive x-ray technique (Gibbons and Greene, 1979) to determine the number and size of eggs in the oviducts of marked individuals on the George Reserve over 4 years. These data allowed us to explore the relationship of egg size and number to body size of females and of egg size to clutch size, as well as variation of reproductive output among clutches within and among years.

RESULTS

Follicular development.—The majority of follicular enlargement generally takes place from late August to October in the year preceding egg laying (Fig. 1). The remaining development to ovulatory size takes place after emergence the following spring. At the point when the turtles enter brumation (October) the average female has a class of enlarged follicles ($\bar{x} = 13.8$ mm diameter; 2 SE = 0.67; $n = 20$) in which each contains one-half of the energy of an oviductal egg (Fig. 2). The average number of enlarged follicles per turtle in the fall sample ($\bar{x} = 7.3$; 2 SE = 0.65; $n = 20$) is not significantly different from the clutch size of 7.6 eggs (Mann Whitney U ; $P > 0.05$). Thus, the large follicles have one-half of the energy for a clutch of eggs 8 months prior to the next nesting season.

The mean number of follicles classified as small during October was 4.8 (2 SE = 0.92; $n = 20$). These averaged 9.6 mm in diameter (2 SE = 0.56; $n = 20$), and therefore contained energy equal to 11% of that in an entire clutch of eggs (Fig. 2).

Clutch frequency.—Turtles containing a substantially greater number of enlarged follicles (≥ 10 mm) than the average clutch size just prior to or during the

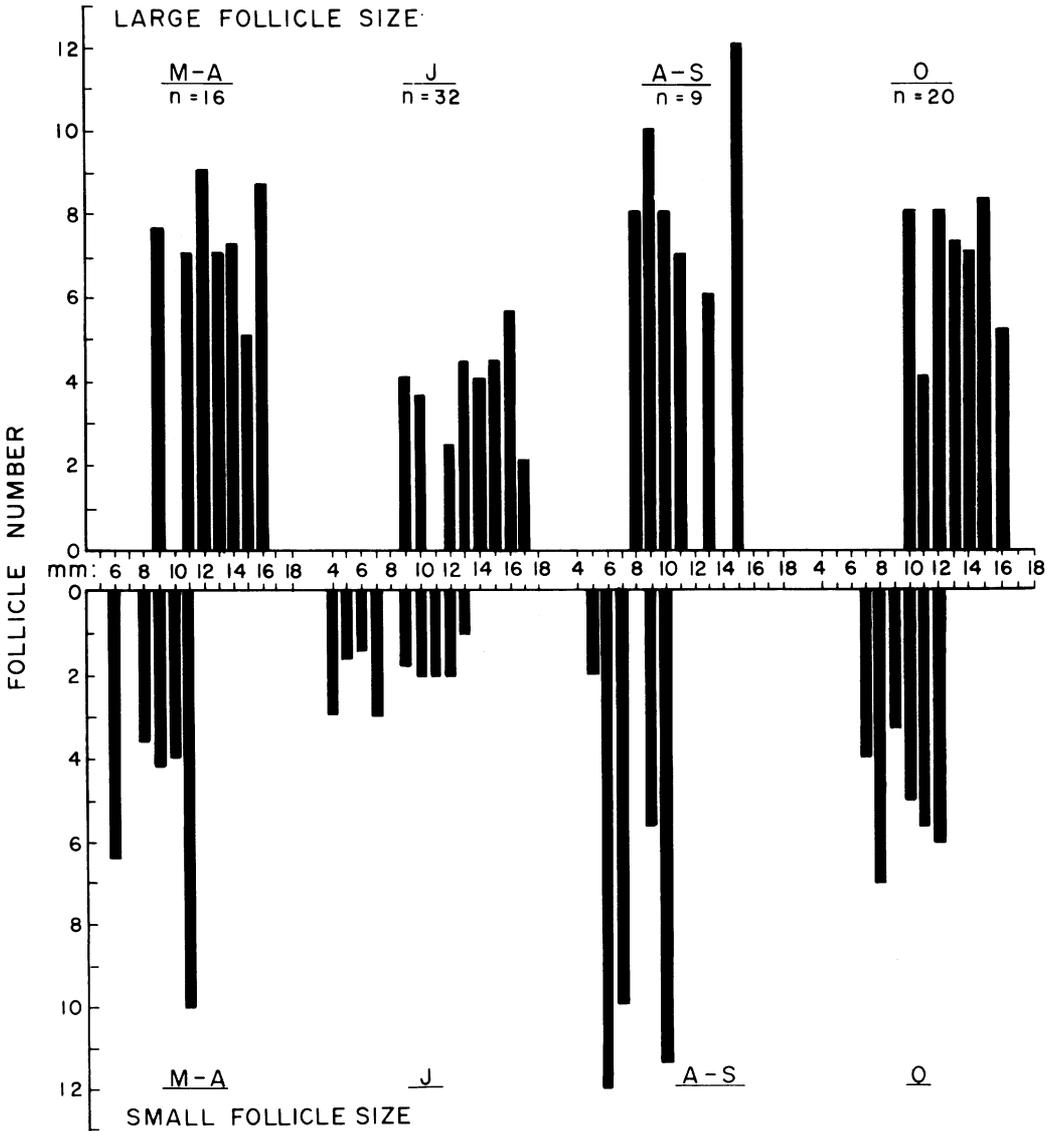


FIG. 1.—The distribution of average follicle sizes over the active season of *Chrysemys picta* in Michigan. See text for an explanation of size classes for follicles. M-A = March and April; J = June; A-S = August and September; O = October.

reproductive season have been presented as evidence for multiple clutches. The data presented here (Fig. 1) show that some of the turtles (36%) in the spring sample had more enlarged follicles than the average clutch size and that the follicles in these turtles were in two

discrete classes. These data and the reduction in follicle numbers of all enlarged sizes during the reproductive period (June) suggest that some turtles can produce more than one clutch per year. However, the percent of reproductive females capable of producing more than

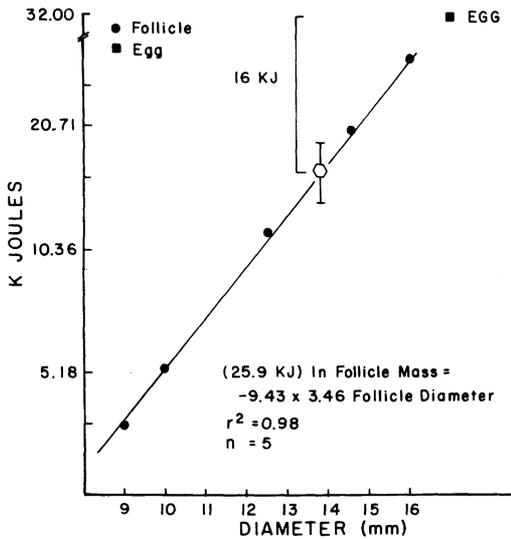


FIG. 2.—The relationship of the energy content of follicles to follicular diameter in *Chrysemys picta*. \circ = mean energy allocated to follicles prior to spring emergence from brumation \pm one standard error of the mean.

one clutch per year cannot be ascertained. Interpretation of follicle counts in determining clutch frequency is hampered because there is no reliable way to determine the point at which an enlarging follicle has a high probability of being ovulated just prior to the next egg laying.

Utilization of body lipid from spring emergence to egg laying.—Total stored body lipids are significantly correlated with adult body size of females (body lipid = $-31.27 + 0.268$ CL; $r^2 = 0.12$; $n = 75$; $P < 0.01$). Therefore, analysis of covariance with body size (CL) as a covariate was used to determine the reduction in body lipids of adult females during the

period from emergence in the spring to the nesting season. Although adjusted mean body lipids were reduced from 7.16 g to 4.10 g over the pre-nesting period the means were not significantly different ($t = 1.50$; $df = 52$; $P > 0.05$). However, we calculated the energy equivalent of the lipid reduction to be 115 kJ, which is equal to 47% of the energy of an average clutch of eggs.

A general description of a female caught in the spring of 1979 is presented as an example of the extreme in lipid storage that can be reached by turtles in this population. This female had 1.24 g of lipid for every gram of lean body tissue and was 26% lipid by total dry mass. Bridge fat-pads were 27.6%, other dissectable fat was 55.4%, and remaining extractable fat was 17.6% of the total mass of body lipids.

Egg components.—The length of eggs averaged 1.8 times their width (Table 1). Wet mass of eggs averaged 4.14 g (2 SE = 0.44), and eggs were 67% water by mass. Lipids averaged 28.2% (2 SE = 0.68) of the dry mass of eggs without shells and 22.3% of the dry mass of eggs with shells (Table 1). Large follicles and eggs without shells (Table 2) were not significantly different in joules mg^{-1} ($t = 1.24$; $df = 28$; $P > 0.05$). The energy density of eggs with shells was 18% lower than the value for eggs without shells (Table 2), and this corresponds well with the expected reduction in energy content due to energy-poor material in the eggshell (Table 1). An average egg contained 29.2 kJ of energy and the average clutch contained 222 kJ.

Use of egg components during development.—During development approxi-

TABLE 1.—Characteristics of 6 clutches of *Chrysemys picta* eggs ($n = 22$) from southeastern Michigan.

Statistic	Length (mm)	Width (mm)	Egg dry mass (g)			% of dry mass without shell		% of total dry mass		
			Total	Lean	Lipid	Shell	Lean	Lipid	Shell	Lipid
Mean	29.0	16.6	1.322	0.729	0.290	0.302	70.4	28.2	22.9	22.0
2 SE	0.6	0.6	0.074	0.029	0.011	0.020	0.7	0.7	0.6	0.8

TABLE 2.—Energy content (joules mg⁻¹ dry mass) of eggs and follicles of the painted turtle *Chrysemys picta*. N = number of clutches; n = number of determinations.

Subject	Mean	N/n	2 SE
Eggs with shells	21.59	3/12	0.62
Eggs without shells	26.43	2/6	0.72
Large follicles	25.89	8/24	0.47

mately 38% of the egg lipids were used; 62% remained in the hatchling (Table 3). Thus, more than half of the lipids present in the egg are for fueling the hatchling after leaving the egg.

Clutch size and egg size relationships to body size.—Clutch size over 4 years (1978 through 1981) averaged 7.6 (2 SE = 0.31; n = 129), with a minimum of 2 eggs and maximum of 11. Clutch size has been shown to have a slight positive relationship to body size in *C. picta* (Tinkle et al., 1981), so analysis of covariance with CL as a covariate was used to test for differences in clutch size among years. Adjusted mean clutch size for 1981 (\bar{x} = 7.3; 2 SE = 0.60; n = 35) was significantly smaller than the adjusted mean (\bar{x} = 8.2; 2 SE = 0.66; n = 26) for 1978 (t = 2.13; df = 59; P < 0.05), but there were no significant differences among other years. There was no significant difference in adjusted mean egg-width among years.

A phenomenon which is not well documented in turtles is the relationship of egg size to body size, or of egg size to clutch size. The log_e (ln) of total egg dry mass (TEDM) is positively related to ln of egg width (ln of TEDM = -2.714 + 1.073 ln of egg width; r^2 = 0.56; $F_{1,20}$ = 23.8; P < 0.01). Thus, egg width is gen-

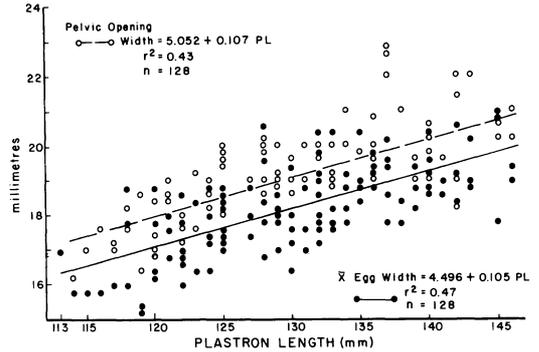


FIG. 3.—The relationship of mean width of eggs and of width of the pelvic opening to plastron length of adult female *Chrysemys picta*.

erally a reliable estimator of TEDM. Utilizing measurements of egg width from our x-ray data we found that egg width increased with female body size (Fig. 3). We also explored the relationship of width of the pelvic opening in relation to carapace length (Fig. 3) and found that it also increased with female body size. The relationship of egg width and width of the pelvic opening to female body size were not significantly different in slope ($F_{1, 126}$ = 1.42; P > 0.05). The relationship of mean egg size per clutch to clutch size was not significant (r^2 = 0.02; n = 129; P = 0.10).

DISCUSSION

The pattern of follicular development observed in these turtles is similar to that in other painted turtles from Michigan (Gibbons, 1968). In October or in April, counts of the largest class of follicles can be used with some reliability to predict clutch size for the following reproductive season. By October the average female

TABLE 3.—Changes in total lean (including shell) and lipid components during development in *Chrysemys picta* eggs from Michigan. Eight eggs and 9 hatchlings were analyzed.

Statistic	Egg components			Hatchling components		
	Dry mass lean (g)	Dry mass lipid (g)	% lipid	Dry mass lean (g)	Dry mass lipid (g)	% lipid
Mean	1.013	0.270	20.87	0.638	0.170	20.70
2 SE	0.072	0.198	0.03	0.047	0.017	1.22

has half of the total mass and energy of a clutch of eggs already allocated to the largest class of follicles, and some energy is already allocated to the smallest class of enlarged follicles. The smaller class of enlarged follicles may represent allocation of energy to the second clutch of the next nesting season or to a clutch which will be laid in 1.5 years.

In the past, counts of enlarging follicles have been used in conjunction with counts of corpora lutea and oviductal eggs to determine clutch size and frequency in turtles (Cagle, 1950; Christiansen and Moll, 1973; Gibbons, 1968; Moll and Legler, 1971; Powell, 1967; Shealy, 1976). Evidence accumulated from follicle counts suggested that multiple clutches per year are sometimes produced. Ernst (1971) pointed out, however, that despite reports of probable multiple clutches in painted turtles, no second clutches had actually been observed. Moll (1973) echoed this caveat, and Wilbur (1975) emphasized it in his paper on the life table of *C. picta*. It has been estimated that in the population at the George Reserve fewer than 10% of the turtles produce two clutches per year, 30–50% fail to reproduce every year, and 40–60% reproduce once per year (Tinkle et al., 1981). These estimates are low compared to a study of nesting frequency of *C. picta* in the Upper Peninsula of Michigan, where 17% of the observed turtles nested twice and indirect evidence indicated that as many as 33% may have nested twice (Snow, 1980).

As a result of evidence of three frequencies of reproduction (Tinkle et al., 1981) in *C. picta*, the data collected on follicle counts and stored lipids would be expected to be highly variable and difficult to interpret. Lack of a significant difference between lipid storage levels is perhaps due to the high among-individual variability in lipid levels rather than the lack of a distinct lipid utilization and lipid storage periods. The high variability is certainly related to the animal's past history (important in long-lived animals)

and the variation in frequency of reproduction. The levels of stored body lipids in the spring samples and the example presented earlier of a female captured in 1979 which contained 63.5 grams of body fat certainly do not support the contention that most chelonians store very little fat (Pond, 1978).

Lipids comprise 28.2% of the dry mass of the egg (without shell), which is slightly higher than that reported for eggs of *Malaclemys terrapin* without shells (26%) (Ricklefs and Burger, 1977). During development only 38% of the egg lipids were depleted. Thus, most egg lipids are stored by hatchlings for use in maintenance or growth rather than for embryonic development. This suggests that attempts to understand the adaptive value and evolution of turtle eggs, and probably all reptilian eggs, should be made in light of the egg as a two component system.

Present theories dealing with the tradeoff between clutch size and egg or neonate size assume that egg or neonate size has been optimized by natural selection and that increased reproductive expenditure associated with increased body size would be made by increasing egg number rather than egg size (Brockelman, 1975; Smith and Fretwell, 1974). However, the size of painted turtle eggs is positively related to female body size. This relationship, plus the relationship of clutch size to body size (Tinkle et al., 1981), should result in a substantial increase in energy per clutch in larger turtles. An increase in plastron length of females from 115 mm to 150 mm is associated with an average increase in egg size as well as in clutch size (2.1 eggs). This results in about a 61 kJ increase in energy due to a larger clutch, and about a 53 kJ increase due to larger eggs. The total (114 kJ) represents an increase equaling 51% of the energy content of an average clutch. In the painted turtle, the egg size-clutch size tradeoff envisioned by Smith and Fretwell (1974) and Brockelman (1975) does not occur.

With the exception of the viviparous lizard *Gerrhonotus coeruleus* (Stewart, 1979), a positive relationship between egg size and body size has not been documented within a population of reptiles. In some lizards, increased clutch size is associated with increased body size (Carpenter, 1960; Congdon et al., 1978; Dunham, 1980; Newlin, 1976). These relationships suggest that egg or neonate size is generally optimized in lizards.

Clutch size and body size are positively related within populations of turtles (Gibbons et al., 1982; Tinkle et al., 1981), but the relationship of egg size to body size in turtles within a population is poorly studied. Tucker et al. (1978) suggested that egg size increased with body size in *C. picta* and that egg width was regulated by the size of the pelvic opening, a morphological trait that may also increase with body size. They also suggested that egg length was more variable than egg width because egg width was determined by the opening of the pelvic canal. Thus, a *C. picta* of a given size could only increase egg size by increasing egg length. We did not find increased variability as represented by the coefficient of variation (CV) of egg length (CV = 6.47; $n = 47$) compared to egg width (CV = 7.39; $n = 47$) in the Michigan population of painted turtles. However, the size of the pelvic canal opening may be limited by the musculature associated with the stresses of terrestrial locomotion, and the pelvic opening in turn may limit egg width in *C. picta*. A constraint such as this would help explain why *C. picta* increases egg size as body size increases. If pelvic opening constrains egg width, then the slopes of the regression lines for pelvic opening width and egg width on female body size should be very close to equal, and this is the case (Fig. 3). The equal relationship of pelvic opening width and egg width to body size of the female provides indirect evidence that the maximum width of the egg may be restricted by pelvic morphology. This restraint might function with natural se-

lection acting on the female to prevent expansion of the pelvic opening to the point where it reduced the efficiency of terrestrial locomotion and selection acting on hatchlings for increased body size.

If *C. picta* represents the "bet hedging" reproductive tactic, then lipid levels of adult females should be more variable than is reproductive output (clutch size). Within the total sample of adult females in the reproductive season the level of stored lipids was more variable (CV = 74.1; $n = 37$) than clutch size (CV = 21.4; $n = 24$). If the comparison is restricted only to females with eggs, the variation in stored body lipids is reduced (CV = 53.8; $n = 24$) but is still higher than the variation in clutch size. The long life expectancy of painted turtles provides the potential to reproduce over many years (Tinkle et al., 1981) in which nest and juvenile survivorships would seem to be both unpredictable and highly variable. Under these conditions lipid reserves could be used to buffer the immediate effects of scarce or abundant resources and thus stabilize the amount of energy allocated to reproduction in a given year.

The timing of allocation of energy to reproduction, the relationship of both clutch size and egg size to body size of females, and the apparent involvement of the stored body lipids in reproduction combine to make reproductive energetics of the painted turtle a complex process. These considerations coupled with varying clutch frequency will make it difficult to place reproductive energetics into a discrete total annual energy budget. Therefore, it may be that reproductive effort in painted turtles, and possibly all long-lived animals, will be best explored in terms of a lifetime energy budget.

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ECOLOGICAL AND EVOLUTIONARY DETERMINANTS OF RELATIVE CLUTCH MASS IN LIZARDS

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ABSTRACT: Relative clutch mass (RCM) is identified as an important life-history characteristic in lizards. Differential survivorship of females carrying clutches of eggs should partially determine RCM, and foraging mode and predator escape tactics play important roles in selection for a given RCM. RCM may vary within a population due to variation in resource availability or among populations of a species due to resource availability or geographic variation in escape tactics. Within species that forage widely, RCM is relatively low. RCM tends to be relatively high in species using the sit-and-wait foraging tactic. RCM variation in the latter group correlates with the manner in which crypsis is manifested. Where a streamlined morphology is advantageous (thin branch mimics or fossorial species), RCM may be low. Where crypsis does not involve a streamlined morphology, RCM tends to be high. Energetic costs associated with changes in RCM and variation in predation rates were estimated with a model of the daily net energy-intake of a lizard. Increasing RCM and/or predation intensity on gravid females reduces daily net energy-intake of wide foragers, but has little effect on species which are sit-and-wait foragers.

Key words: Reptilia; Sauria; Energetics; Life history; Reproduction

IN recent years, the adaptive nature of life histories has been of central interest to evolutionary ecologists. Numerous theoretical studies have attempted to identify environmental or demographic characteristics important in molding life histories and to predict the life-history "strategy" which should result under a given set of conditions. The demographic environment (Cole, 1954; Gadgil and Bossert, 1970; Williams, 1966), the position of a species in respect to resources (*r*- and *K*-selection; Gadgil and Solbrig, 1972; MacArthur and Wilson, 1967; Pian-