

# Reproductive Output Depends on Body Condition in Spotted Turtles (*Clemmys guttata*)

Jacqueline D. Litzgus<sup>1</sup>, Frances Bolton<sup>1</sup>, and Albrecht I. Schulte-Hostedde<sup>1</sup>

**The body condition of an animal reflects its energetic state such that an animal in good condition has greater energy reserves than one that is in poor condition. Body condition in turn should be positively correlated with fitness because energetic reserves limit the amount of energy that can be allocated to reproduction. Using Spotted Turtles (*Clemmys guttata*) as a model system, and three years of field data from a South Carolina, USA population, we tested the prediction that reproductive output increases with maternal body condition. The effect of body condition on the reproductive output of female turtles was examined at three temporal scales (among clutches, among nesting seasons, and among females) using several variables including clutch frequency, clutch size, and multiple measures of egg size. We predicted that females in good condition will have a higher clutch frequency than those in poor condition; that females in good condition will have larger clutch sizes than those in poor condition; and that females in good condition will have larger eggs than those in poor condition. Among clutches and nesting seasons, we found no relationship between female body condition and reproductive output. Among females over the entirety of the three-year study, we found a positive relationship between body condition and clutch mass and egg size. In addition, females in poor condition and females in good condition both produced larger clutch sizes than females in intermediate condition. Our findings suggest that within a given reproductive bout and within a given reproductive season, energy reserves do not affect immediate reproductive investment. However, over the longer-term, females in good condition have greater reproductive output, which supports the idea of a bet-hedging life history strategy in turtles.**

THE body condition of an animal reflects its energetic state such that an animal in good condition has greater energy reserves than one that is in poor condition (Hayes and Shonkwiler, 2001; Schulte-Hostedde et al., 2001, 2005). Variation in body condition has been associated with male and female fitness components, such as survival and reproductive success, in a variety of taxa including mammals (Schulte-Hostedde et al., 2005; Toïgo et al., 2006), amphibians (Lowe et al., 2006), birds (O'Dwyer et al., 2006), and snakes (Shine et al., 2001). Maternal body condition has a substantial effect on both offspring size and offspring number and therefore is positively correlated with reproductive fitness (Chastel et al., 1995; Dobson and Michener, 1995). Understanding mechanisms and patterns of energy allocation with respect to body condition and life history can provide valuable insights into variation in individual fitness.

Optimal egg size (OES) theory predicts that females should invest surplus energy allocated to reproduction into producing more eggs rather than larger eggs to maximize maternal fitness (Smith and Fretwell, 1974; Brockelman, 1975; Bernardo, 1996). Producing an additional egg is more advantageous than producing larger eggs because investment in an additional offspring provides a larger maternal fitness benefit than investing more heavily in existing individual offspring. Thus, selection should favor an optimally-sized egg rather than a large egg. Alternatively, because offspring survival can increase with offspring size, maternal fitness is expected to increase with increased maternal investment per offspring (Miller et al., 1987; Sinervo and Doughty, 1996; Janzen et al., 2000a). However, energy is limited and life history theory predicts a trade-off

between the number of offspring and the size of those offspring. Thus, natural selection should favor either a large number of small offspring or a few large offspring (Smith and Fretwell, 1974).

Previous studies on turtles have shown that clutch size varies with maternal body size such that larger females produce more eggs than smaller females (Iverson, 1992; Rowe, 1994; Wilkinson and Gibbons, 2005). However, it also has been shown that in some turtles both clutch size and egg size increase with body size (Iverson, 1991; Brooks et al., 1992; Clarke et al., 2001). An increase in egg number may manifest as an increase in clutch frequency (Iverson, 1992), which is an important measure of an individual turtle's reproductive success and thus its fitness (Gibbons, 1982). These findings generally support OES theory if one assumes that larger females have more energy to invest in reproduction than smaller females. In small-bodied turtle species, the relationship between egg size and body size is confounded by the physical constraint imposed by the width of the pelvic girdle aperture and the size of the space between the carapace and plastron through which the eggs must pass during oviposition (Congdon and Gibbons, 1987; Clarke et al., 2001; Wilkinson and Gibbons, 2005). In addition, elevated testosterone levels in younger female turtles may constrain egg size physiologically (Bowden et al., 2004). In large-bodied turtles that do not have a pelvic girdle constraint on egg size, it may be beneficial for female fitness to shunt excess energy into producing larger eggs rather than more eggs. Larger eggs produce larger hatchlings which can have higher survivorship than small hatchlings because larger individuals are better able to cope with the hardships of early life (but see Congdon et al., 1999). For example,

<sup>1</sup>Department of Biology, Laurentian University, Sudbury, Ontario, P3E 2C6, Canada; E-mail: (JDL) jlitzgus@laurentian.ca. Send reprint requests to JDL.

Submitted: 12 April 2007. Accepted: 20 July 2007. Section Editor: S. A. Schaefer.

© 2008 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CH-07-093

large hatchlings have increased locomotor performance (Miller et al., 1987) and thus better abilities to avoid predation (Janzen et al., 2000a, 2000b). However, this idea that “bigger is better” contradicts OES theory, which predicts that individual maternal fitness is enhanced by the production of the greatest number of optimally-sized eggs possible, rather than by the production of bigger eggs. Furthermore, bigger eggs and hatchlings do not always have relatively higher survivorship, and in fact studies of Snapping Turtles (*Chelydra serpentina*) show evidence for stabilizing selection on hatchling body size (Congdon et al., 1999).

To our knowledge, no direct assessments of the relationship between body condition and reproductive fitness have been conducted in turtles despite the fact that turtles are an ideal model organism for such investigations. The shell of turtles can be easily and permanently marked by notching (Cagle, 1939) and so individual turtles can be identified, and their growth and reproduction monitored for their entire lives. The turtle shell also allows the accurate and repeated measurement of carapace and plastron lengths. Reproductive output can be measured non-intrusively using X-rays (Gibbons and Greene, 1979), and nests can be found using radio telemetry. In addition, turtles are generally long-lived (Gibbons, 1987; Ernst et al., 1994) and tend to stay in the same general home range during their lifetime (Kaufmann, 1995; Nieuwolt, 1996; Bernstein et al., 2007), making them easy animals to study over long periods of time. We tested the prediction that reproductive output increases with maternal body condition using Spotted Turtles (*Clemmys guttata*) as a model system, and three years of field data. The effect of body condition on the reproductive output of female turtles was examined at three temporal scales (among clutches, among nesting seasons, and among females) using several life-history variables including clutch frequency, clutch size, and multiple measures of egg size. We predicted that females in good condition would have a higher annual clutch frequency than those in poor condition; that females in good condition would have larger clutch sizes than those in poor condition; and that females in good condition would have larger eggs than those in poor condition. If OES theory is upheld, then we expected that there would be no relationship between body condition and egg size.

## MATERIALS AND METHODS

**Study system and field site.**—Spotted Turtles are semi aquatic and tend to inhabit shallow wetland areas (Lovich, 1988; Ernst et al., 1994). They are easily distinguished from other turtle species by the yellow spots on their black neck and carapace. Spotted Turtles occur in disjunct populations along the coast of eastern North America (Ernst et al., 1994). Populations are declining mainly due to loss of habitat and increased harvesting for the pet trade (Klemens, 2000; Litzgus, 2004). As a result of these threats, Spotted Turtles are considered to be a species at risk throughout their range, and are listed as “endangered” in Canada (Litzgus, 2004). In the South Carolina population studied herein, the active period is between the months of March and October, and the breeding and nesting seasons extend from late March to late June or early July (Litzgus and Mousseau, 2004, 2006). Spotted Turtles aggregate in wetlands to breed in early spring (late March through April; Litzgus and Mousseau, 2004, 2006). After breeding, females leave

wetlands to find nesting areas; these areas include woody debris and rotten logs in the swamp forest (Litzgus and Mousseau, 2004, 2006). Most clutches range in size from two to four eggs, and multiple clutches within a reproductive season have been observed (Litzgus and Mousseau, 2003).

The field site, Francis Beidler Forest, is an approximately 4500-ha National Audubon and Nature Conservancy Sanctuary located in Four Holes Swamp on the Atlantic Coastal Plain of southeastern South Carolina, USA (33°N). The site includes upland pine and mesophytic hardwood forest, seasonally flooded hardwood bottom swamp forest, and cypress–tupelo blackwater swamp forest (see Porcher [1981] for a detailed description of the plant communities).

**Field sampling and data analyses.**—The data used in the following analyses were collected as part of a larger study (Litzgus and Mousseau, 2006). Eleven adult female Spotted Turtles were outfitted with radio transmitters and tracked during the reproductive season (April to July) in 2000, 2001, and 2002 (three field seasons). In addition, females without radio transmitters that were encountered opportunistically during the reproductive season were also assessed for reproductive status. The reproductive status of female turtles was determined by palpation and X-radiographs (Gibbons and Greene, 1979). Turtles were X-rayed at 52 kV peak and 2.5 mA s at a local veterinary clinic. If a female was found to be gravid using X-rays, she was radio tracked and located twice per day: once during the day and again at sundown, until she oviposited. Measurements of female non-gravid body mass were taken using a Pesola spring scale, and carapace length was measured using calipers. Clutch size was determined from X-rays and egg counts at oviposition sites. Nests were excavated and eggs were processed (measured and weighed) and then reburied (see Litzgus and Mousseau [2006] for details). Clutch size data were obtained for females with transmitters and for females encountered opportunistically; however, egg size data were obtained only from nests made by females outfitted with transmitters. To assess female reproductive output, we used a series of variables measured in the field: mean egg mass, mean egg length, mean egg width, clutch mass, and clutch size. Egg volume was calculated using the formula for an ellipsoid,  $V = (\pi/6000) \times LW^2$ , where L is egg length and W is egg width (Iverson and Ewert, 1991).

We used length-adjusted mass to estimate body condition using one of two techniques. First, where statistically appropriate, we used multiple regressions to examine the effects of non-gravid body mass and carapace length on reproductive output. We interpreted the semi-partial correlation coefficient of body mass as the independent effect of length-adjusted body mass (body condition) on our measure(s) of reproductive output. Where multiple regressions were inappropriate, we used the residuals from a regression of body mass on carapace length as an index of body condition (Schulte-Hostedde et al., 2005). These approaches are statistically equivalent; both use regression to determine size-corrected mass using the same measure of body mass and body size (Schulte-Hostedde et al., 2005). All analyses were conducted on log-transformed data.

We examined the data at three temporal scales. First, we examined reproductive investment per reproductive bout by treating each clutch as an independent sampling unit (among clutches). Second, we examined reproductive investment per nesting season by treating each year for

each female as an independent unit (among nesting seasons) and using the average values for all of the clutches produced in a given season by a female. We also calculated clutch frequency, total clutch mass, and the total number of eggs produced by each female within each nesting season. Finally, we examined reproductive investment over the entirety of the three-year study by treating each female as an independent sampling unit (among females). Data on egg mass and egg size were obtained for the 11 females outfitted with radio transmitters, but not for the two gravid females encountered opportunistically; thus, the analyses for the egg variables were limited to the  $n = 11$  females outfitted with transmitters. Measures of clutch size and total number of eggs produced were available for all captured turtles ( $n = 13$ ). At each scale, we calculated the appropriate average for all clutch variables and female morphometrics. For example, at the *among clutches* scale, we calculated the average of the egg measurements for each individual clutch; at the *among nesting seasons* scale, we calculated the average of all eggs produced in all clutches by each female in each nesting season (year); and at the *among females* scale, we calculated the average for all eggs produced by the female over the three-year study.

## RESULTS

**Among clutches.**—In a given reproductive bout, none of the reproductive variables examined (clutch size, clutch mass, mean egg length, mean egg width, mean egg volume, mean egg mass) were related to maternal body condition (body mass semi-partial  $r < 0.20$ ,  $P > 0.2$  for all variables;  $n = 32$  for clutch size,  $n = 23$  for clutch mass and the egg size variables).

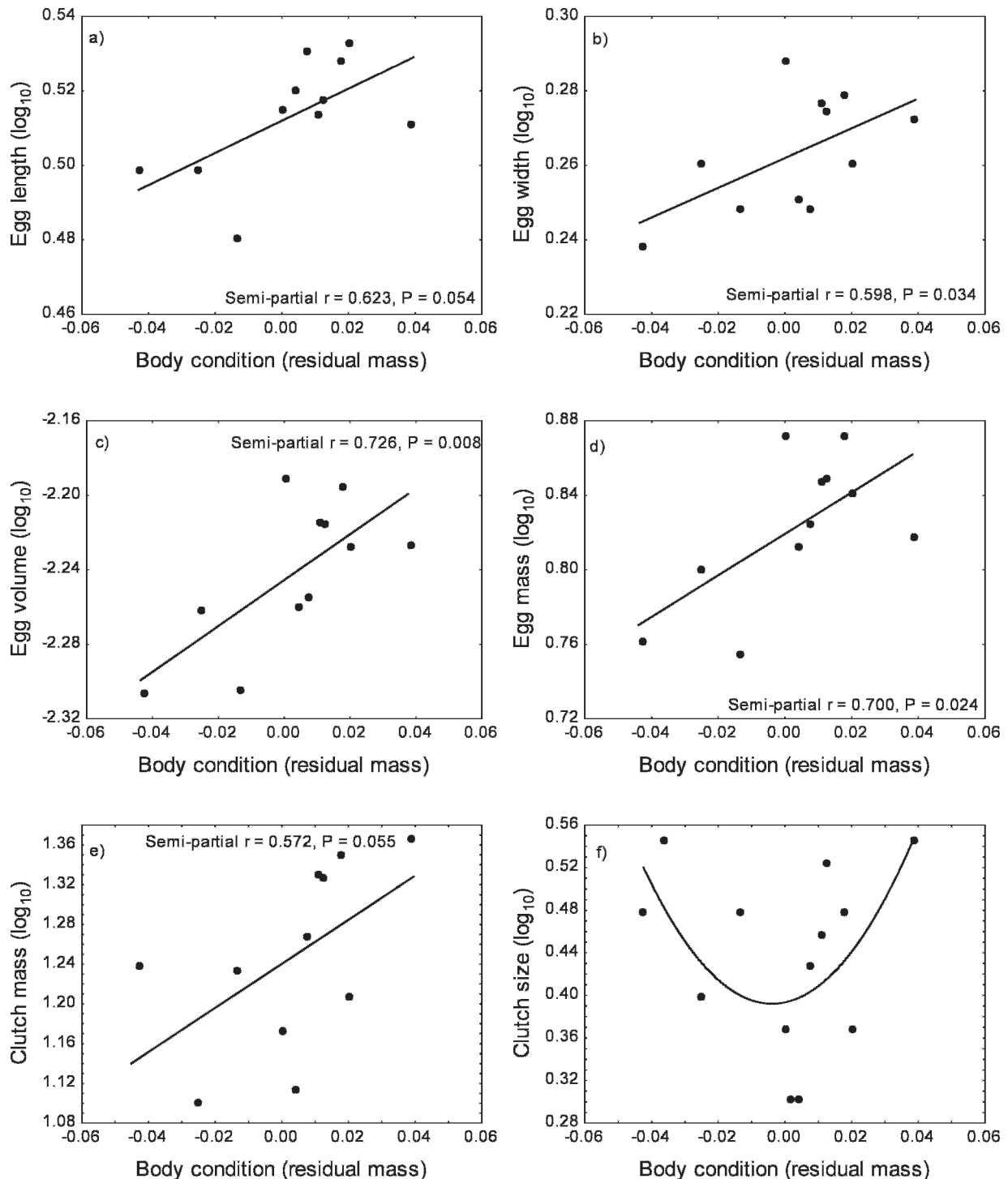
**Among nesting seasons.**—We found no relationship between body condition and any of the reproductive variables (body mass semi-partial  $r < 0.20$ ,  $P > 0.6$  in all cases;  $n = 26$  for clutch size,  $n = 18$  for the other reproductive variables). Clutch frequency, total clutch mass, and the total number of eggs produced were not related to maternal body condition (body mass semi-partial  $r < 0.25$ ,  $P > 0.3$  in all cases;  $n = 26$  for clutch frequency and total number of eggs,  $n = 18$  for total clutch mass). One female did not reproduce in two consecutive field seasons, and one female did not reproduce in one field season. The body condition of these females (calculated as residual mass from the mass–size regression) that did not produce eggs during three field seasons was significantly lower than that of females that produced at least one clutch ( $t = 3.80$ ,  $df = 24$ ,  $P = 0.008$ ).

**Among females.**—All measures of egg size and egg mass, and clutch mass were positively related to maternal body condition (Fig. 1A–E). There was no evidence of a linear relationship between mean clutch size and body condition (body mass semi-partial  $r = -0.06$ ,  $P = 0.85$ ); however, when we fitted a quadratic regression using mean clutch size as the dependent variable and residual body mass (calculated from a regression of non-gravid body mass on carapace length) and (residual body mass)<sup>2</sup>, we found that the quadratic term was significant (semi-partial  $r = 0.60$ ,  $P = 0.04$ ). Females at the extremes with respect to body condition (i.e., those in poor condition and those in good condition) produced larger clutches than those individuals with intermediate values for body condition (Fig. 1F).

## DISCUSSION

The prediction that animals in good body condition will have greater reproductive output than those in poor condition was supported over the longer-term but was not supported over the short temporal scales examined in our study. In contrast to our predictions, we found no relationships between maternal body condition and any measure of reproductive output in Spotted Turtles when comparisons were made among clutches and among nesting seasons. An important caveat to our analysis is the non-independence of the data at the *among clutches* and *among nesting seasons* scales of analysis. Nonetheless, our findings suggest that within a given reproductive bout and within a given nesting season, energy reserves may not affect immediate reproductive investment; that is, proximate factors may not play a major role in determining energy allocated to reproduction measured in terms of egg and clutch size. Instead more ultimate factors, such as the great potential longevity of Spotted Turtles (65–110 years; Litzgus, 2006) may contribute to the pattern we observed over the longer time scale. A single clutch represents a fraction of the lifetime reproductive output of a female Spotted Turtle, and so relationships between body condition and reproductive output may be discernable only at a relatively coarse temporal scale (i.e., encompassing multiple reproductive bouts) rather than at a fine temporal scale. Indeed, over the longer time scale, we found a positive relationship between body condition and clutch mass and all measures of egg size. Females in the poorest condition appeared to forego reproduction completely in some years as indicated by the two females in poor body condition that did not produce any eggs in three field seasons. That female turtles make reproductive decisions based on a longer time scale is consistent with a “bet-hedging” life history strategy (Stearns, 1976; Roff, 1992). In this context, organisms that evolve in environments where egg and hatchling mortality are unpredictable, and where adult mortality is predictable, evolve extreme iteroparity to maximize the probability of successful reproduction in “good years.” Although we did not directly test the effects of environmental variation on body condition and reproductive output, bioenergetic studies of Gopher Tortoises (*Gopherus agassizii*) found that body composition (lipid and nonlipid energy) varied with climate and that this variation caused changes in egg production; the study concluded that the tortoises were hedging their bets by forfeiting body condition to produce a few eggs in stressful environments (Henen, 1997). The long-term advantages of partitioning energy across many reproductive events in terms of life-time fitness outweigh any short term investments (and potential losses) in current reproductive events; thus, it is in a female’s best interests to conserve energy for future reproduction.

Interestingly, we found a nonlinear relationship between maternal body condition and mean clutch size when the data were analyzed across all three years of the study (Fig. 1F). Female Spotted Turtles in poor body condition appeared to produce a large number of small eggs, whereas females in good condition appeared to produce a large number of large eggs. Females in intermediate body condition produced small clutches of medium-sized eggs. Females in good body condition may be able to afford to do everything well, while females in poor condition appear to be maximizing the number of eggs produced. This finding supports the “terminal investment hypothesis,” which



**Fig. 1.** Relationships between maternal body condition and various measures of reproductive output in Spotted Turtles (*Clemmys guttata*) over three years in a South Carolina, USA population. All measures of egg size [a] mean egg length; [b] mean egg width; [c] mean egg volume; [d] mean egg mass) and clutch mass [e] were positively related to body condition. Mean clutch size was related to body condition in a quadratic fashion. Females in poor body condition and females in good body condition produced more eggs per clutch than females in intermediate body condition (clutch size =  $0.3925 + 0.6198$  (residual mass) +  $85.9957$  (residual mass)<sup>2</sup>,  $P < 0.05$ ). Each closed circle represents an individual female.

predicts that individuals should invest more in current reproduction if they are less likely to survive to future reproductive events (Williams, 1966; Part et al., 1992; Weladji et al., 2002). Survival to future reproductive events may be limited by poor body condition, as we suggest here for Spotted Turtles, and/or increasing age. In contrast, in a study on reproduction in the Mud Turtle *Kinosternon subrubrum*, older females did not have larger clutch sizes or higher clutch frequency compared to younger females

(Wilkinson and Gibbons, 2005); these findings do not support the terminal investment hypothesis.

Our data both support and refute the OES model. Optimal egg size theory predicts that females should invest surplus energy allocated to reproduction into producing more eggs rather than larger eggs to maximize maternal fitness (Smith and Fretwell, 1974; Brockelman, 1975; Bernardo, 1996). Analyses of the relationships between body condition and short-term reproductive investment indicate that female

Spotted Turtles do not adjust egg size when they have extra energy (supports theory), but neither do they adjust clutch size (refutes theory). Over the longer-term, Spotted Turtles increased both clutch size and egg size (Fig. 1) when they had excess energy stores, a finding that does not support the OES model. The tradeoff between size and number of eggs predicted under OES theory has been examined in several chelonians, and the results are conflicting; to date, no single general pattern is evident. Some studies have shown support for the theory (Elgar and Heaphy, 1989; Rowe, 1994), whereas other studies have shown little or no support for the theory (Iverson et al., 1997; Roosenburg and Dunham, 1997; Booth, 1998). The lack of a common pattern may be because the previous studies (Litzgus and Brooks, 1998; Valenzuela, 2001; Lindeman, 2005) have done their analyses based on the assumption that a larger body size is indicative of good body condition; thus, these studies have used body size as a proxy for energy reserves. Indeed, in the Spotted Turtle population examined herein, clutch size and egg size are independent of body size per se (Litzgus and Mousseau, 2006). Female body size influences reproductive output such that larger-bodied turtles tend to produce larger and/or heavier clutches of eggs (Iverson, 1992; Rowe, 1994), but whether larger body size means greater energy available for reproduction is undetermined. Our study was a more direct test of OES theory because we examined the relationship between body condition, independent of body size, and clutch size and egg size, and found that the model was not upheld among females over the three-year period of study. Three years is a relatively short period of time in a Spotted Turtle's potential lifespan (Litzgus, 2006), thus future studies should examine the relationship between body condition and reproductive output over a longer time span.

Body condition (as measured by residual mass) has been used in studies of squamates and turtles in a number of contexts. In the case of squamates, body condition is assumed to represent fat reserves and thus affect survival (Shine et al., 2001; Husak, 2006) and reproductive success (Blouin-Demers et al., 2005). In the case of turtles, direct measurements of energy reserves through lipid extractions have been conducted in hatchling Painted Turtles (*Chrysemys picta*; Packard and Packard, 2001), but this approach requires destructive sampling, an approach incompatible with long-term mark-recapture studies. Despite the assumption that body condition reflects energy reserves (Jessop et al., 2004), other sources of variation in body condition have been proposed, including the density of dermal bone of the carapace and the degree of hydration of the body (Will-emsen and Hailey, 2002). In the absence of a validation study, we cannot be certain what body condition represents in Spotted Turtles. Nonetheless, our results indicate that body condition is an ecologically important variable that can have consequences for individual fitness. Future studies that use non-destructive methods to determine body composition such as gas dilution (Henen, 2001), total body electrical conductivity (Scott et al., 2001), and ultrasound scanning (Starck et al., 2001) will help determine whether fat reserves or other sources are responsible for the variation in reproductive output we found.

Few studies have directly examined the relationship between body condition and reproductive output in reptiles. Our novel study using turtles as a model system sheds light on important aspects of life history theory, particularly with respect to tradeoffs in energy allocation between mainte-

nance and reproduction. Thus, our study provides valuable data which can serve as a basis for more long-term investigations of the effect of body condition on reproductive fitness in reptiles.

## ACKNOWLEDGMENTS

FB analyzed the data reported herein as part of her Honours Thesis at Laurentian University under the co-supervision of JDL and AIS-H. Funding for FB's Honours Thesis came from Laurentian University. Field data were collected by JDL while she was a Ph.D. student at the University of South Carolina under the supervision of T. Mousseau. The field work was supported by the National Geographic Society (grant #6630-99), Santee Cooper Power Company, Chelonian Research Foundation, and the South Carolina Wildlife Federation. In-kind support was provided by the Francis Beidler Forest National Audubon Society and Nature Conservancy Sanctuary. We would like to especially thank N. Brunswig (SC State Director, National Audubon Society) for his support of the field project. X-rays were conducted at Westbury's Veterinary Clinic, Summerville, SC (2000 field season), and at the Goose Creek Veterinary Clinic, Goose Creek, SC (2001 and 2002 field seasons). S. DuRant, W. Humphries, and T. Merritt assisted with field data collection. We thank D. Lesbarreres and T. Johnston for providing useful comments on an earlier draft of the manuscript. All research was in compliance with SC-DNR permits and USC Animal Use guidelines (IACUC protocols 1007 and 1219).

## LITERATURE CITED

- Bernardo, J.** 1996. The particular effects of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *American Zoologist* 36:216–236.
- Bernstein, N. P., R. J. Richtsmeier, R. W. Black, and B. R. Montgomery.** 2007. Home range and philopatry in the ornate box turtle, *Terrapene ornata ornata*, in Iowa. *American Midland Naturalist* 157:162–174.
- Blouin-Demers, G., H. L. Gibbs, and P. J. Weatherhead.** 2005. Genetic evidence for sexual selection in black ratsnakes (*Elaphe obsoleta*). *Animal Behavior* 69:225–234.
- Booth, D. T.** 1998. Egg size, clutch size, and reproductive effort of the Australian broad-shelled river turtle, *Chelonia expansa*. *Journal of Herpetology* 32:592–596.
- Bowden, R. M., H. K. Harms, R. T. Paitz, and F. J. Janzen.** 2004. Does optimal egg size vary with demographic stage because of a physiological constraint? *Functional Ecology* 18:522–529.
- Brockelman, W. Y.** 1975. Competition, the fitness of offspring, and optimal clutch size. *American Naturalist* 109:677–699.
- Brooks, R. J., C. M. Shilton, G. P. Brown, and N. W. S. Quinn.** 1992. Body size, age distribution, and reproduction in a northern population of wood turtles (*Clemmys insculpta*). *Canadian Journal of Zoology* 70:462–469.
- Cagle, F. R.** 1939. A system of marking turtles for future identification. *Copeia* 1939:170–172.
- Chastel, O., H. Weimerskirch, and P. Jouventin.** 1995. Influence of body condition on reproductive decision and reproductive success in the blue petrel. *Auk* 112:964–972.
- Clarke, P. J., M. A. Ewert, and C. E. Nelson.** 2001. Physical apertures as constraints on egg size and shape in the common musk turtle, *Sternotherus odoratus*. *Functional Ecology* 15:70–77.

- Congdon, J. D., and J. W. Gibbons.** 1987. Morphological constraint on egg size: a challenge to optimal egg size theory? *Proceedings of the National Academy of Sciences of the United States of America* 84:4145–4147.
- Congdon, J. D., R. D. Nagle, A. E. Dunham, C. W. Beck, O. M. Kinney, and S. R. Yeomans.** 1999. The relationship of body size to survivorship of hatchling snapping turtles (*Chelydra serpentina*): an evaluation of the “bigger is better” hypothesis. *Oecologia* 121:224–235.
- Dobson, F. S., and G. R. Michener.** 1995. Maternal traits and reproduction in Richardson’s ground squirrels. *Ecology* 76:851–862.
- Elgar, M. A., and L. J. Heaphy.** 1989. Covariation between clutch size, egg weight and egg shape: comparative evidence for chelonians. *Journal of Zoology* 219:137–152.
- Ernst, C. H., J. E. Lovich, and R. W. Barbour.** 1994. *Turtles of the United States and Canada*. Smithsonian Institution Press, Washington, D.C.
- Gibbons, J. W.** 1982. Reproductive patterns in freshwater turtles. *Herpetologica* 38:222–227.
- Gibbons, J. W.** 1987. Why do turtles live so long? *BioScience* 37:262–269.
- Gibbons, J. W., and J. L. Greene.** 1979. X-ray photography: a technique to determine reproductive patterns of freshwater turtles. *Herpetologica* 35:86–89.
- Hayes, J. P., and J. S. Shonkwiler.** 2001. Morphometric indicators of body condition: worthwhile or wishful thinking?, p. 8–38. *In: Body Composition Analysis of Animals: A Handbook of Non-destructive Approaches*. J. R. Speakman (ed.). Cambridge University Press, Cambridge, U.K.
- Henen, B. T.** 1997. Seasonal and annual energy budgets of female desert tortoises (*Gopherus agassizii*). *Ecology* 78:283–296.
- Henen, B. T.** 2001. Gas dilution methods: elimination and absorption of lipid-soluble gases, p. 99–126. *In: Body Composition Analysis of Animals: A Handbook of Non-destructive Approaches*. J. R. Speakman (ed.). Cambridge University Press, Cambridge, U.K.
- Husak, J. F.** 2006. Does speed help you survive? A test with collared lizards of different ages. *Functional Ecology* 20:174–179.
- Iverson, J. B.** 1991. Life history and demography of the yellow mud turtle, *Kinosternon flavescens*. *Herpetologica* 47:373–395.
- Iverson, J. B.** 1992. Correlates of reproductive output in turtles (Order Testudines). *Herpetological Monographs* 6:25–42.
- Iverson, J. B., and M. A. Ewert.** 1991. Physical characteristics of reptilian eggs and a comparison with avian eggs, p. 87–100. *In: Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles*. D. C. Deeming and M. W. J. Ferguson (eds.). Cambridge University Press, Cambridge, U.K.
- Iverson, J. B., H. Higgins, A. S. Sirulnik, and C. Griffiths.** 1997. Local and geographic variation in the reproductive biology of the snapping turtle (*Chelydra serpentina*). *Herpetologica* 53:96–117.
- Janzen, F. J., J. K. Tucker, and G. L. Paukstis.** 2000a. Experimental analysis of an early life-history stage: selection on size of hatchling turtles. *Ecology* 81:2290–2305.
- Janzen, F. J., J. K. Tucker, and G. L. Paukstis.** 2000b. Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. *Journal of Evolutionary Biology* 13:947–954.
- Jessop, T. S., J. M. Sumner, C. J. Limpus, and J. M. Whittier.** 2004. Interplay between plasma hormone profiles, sex and body condition in immature hawksbill turtles (*Eretmochelys imbricata*) subjected to a capture stress protocol. *Comparative Biochemistry and Physiology Part A* 137:197–204.
- Kaufmann, J. H.** 1995. Home ranges and movements of wood turtles, *Clemmys insculpta*, in central Pennsylvania. *Copeia* 1995:22–27.
- Klemens, M. W.** 2000. *Turtle Conservation*. Smithsonian Institution Press, Washington, D.C.
- Lindeman, P. V.** 2005. Aspects of the life history of the Texas map Turtle (*Glyptemys versa*). *American Midland Naturalist* 153:378–388.
- Litzgus, J. D.** 2004. Status Report on the Spotted Turtle, *Clemmys guttata*. Committee on the Status of Endangered Wildlife in Canada. Environment Canada, Ottawa, Ontario.
- Litzgus, J. D.** 2006. Sex differences in longevity in the spotted turtle (*Clemmys guttata*). *Copeia* 2006:281–288.
- Litzgus, J. D., and R. J. Brooks.** 1998. Reproduction in a northern population of *Clemmys guttata*. *Journal of Herpetology* 32:252–259.
- Litzgus, J. D., and T. A. Mousseau.** 2003. Multiple clutching in southern spotted turtles, *Clemmys guttata*. *Journal of Herpetology* 37:17–23.
- Litzgus, J. D., and T. A. Mousseau.** 2004. Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): implications for management. *Copeia* 2004: 804–817.
- Litzgus, J. D., and T. A. Mousseau.** 2006. Geographic variation in reproduction in a freshwater turtle (*Clemmys guttata*). *Herpetologica* 62:132–140.
- Lovich, J. E.** 1988. Geographic variation in the seasonal activity cycle of spotted turtles, *Clemmys guttata*. *Journal of Herpetology* 22:482–485.
- Lowe, W. H., G. E. Likens, and B. J. Cosentino.** 2006. Self-organisation in streams: the relationship between movement behaviour and body condition in a headwater salamander. *Freshwater Biology* 51:2052–2062.
- Miller, K., G. C. Packard, and M. J. Packard.** 1987. Hydric conditions during incubation influence locomotor performance of hatchling snapping turtles. *Journal of Experimental Biology* 127:401–412.
- Nieuwolt, P. M.** 1996. Movement, activity, and microhabitat selection in the western box turtle, *Terrapene ornata luteola*, in New Mexico. *Herpetologica* 52:487–495.
- O’Dwyer, T. W., W. A. Buttemer, D. M. Priddel, and J. A. Downing.** 2006. Prolactin, body condition and the cost of good parenting: an interyear study in a long-lived seabird, Gould’s Petrel (*Pterodroma leucoptera*). *Functional Ecology* 20:806–811.
- Packard, G. C., and M. J. Packard.** 2001. Environmentally induced variation in size, energy reserves and hydration of hatchling painted turtles, *Chrysemys picta*. *Functional Ecology* 15:481–489.
- Part, T., L. Gustafsson, and J. Moreno.** 1992. “Terminal investment” and sexual conflict in the collared flycatcher (*Ficedula albicollis*). *American Naturalist* 140:868–882.
- Porcher, R. D.** 1981. The vascular flora of the Francis Beidler Forest in Four Holes Swamp, Berkeley and Dorchester Counties, South Carolina. *Castanea* 46:248–280.

- Roff, D. A.** 1992. *The Evolution of Life Histories; Theory and Analysis*. Chapman and Hall, New York.
- Roosenburg, W. M., and A. E. Dunham.** 1997. Allocation of reproductive output: egg- and clutch-size variation in the diamondback terrapin. *Copeia* 1997:290–297.
- Rowe, J. E.** 1994. Reproductive variation and the egg size–clutch size trade-off within and among populations of painted turtles (*Chrysemys picta bellii*). *Oecologia* 99:34–44.
- Schulte-Hostedde, A. I., J. S. Millar, and G. J. Hickling.** 2001. Evaluating body condition in small mammals. *Canadian Journal of Zoology* 79:1021–1029.
- Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling.** 2005. Restitution of mass–size residuals: validating body condition indices. *Ecology* 86:155–163.
- Scott, I., C. Selman, P. I. Mitchell, and P. R. Evans.** 2001. The use of total electrical conductivity (TOBEC) to determine body composition in vertebrates, p. 127–160. *In: Body Composition Analysis of Animals: A Handbook of Non-destructive Approaches*. J. R. Speakman (ed.). Cambridge University Press, Cambridge, U.K.
- Shine, R., M. P. LeMaster, I. T. Moore, M. M. Olsson, and R. T. Mason.** 2001. Bumpus in the snake den: effects of sex, size, and body condition on mortality of red-sided garter snakes. *Evolution* 55:598–604.
- Sinervo, B., and P. Doughty.** 1996. Interactive effects of offspring size and timing of reproduction on offspring reproduction: experimental, maternal, and quantitative genetic aspects. *Evolution* 50:1314–1327.
- Smith, C. C., and S. D. Fretwell.** 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499–506.
- Starck, J. M., M. W. Dietz, and T. Piersma.** 2001. The assessment of body composition and other parameters by ultrasound scanning, p. 188–210. *In: Body Composition Analysis of Animals: A Handbook of Non-destructive Approaches*. J. R. Speakman (ed.). Cambridge University Press, Cambridge, U.K.
- Stearns, S. C.** 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51:3–47.
- Toïgo, C., J.-M. Gaillard, G. Van Laere, M. Hewison, and N. Morellet.** 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography* 29:301–308.
- Valenzuela, N.** 2001. Maternal effects on life-history traits in the Amazonian giant river turtle *Podocnemis expansa*. *Journal of Herpetology* 35:368–378.
- Weladji, R. B., A. Mysterud, O. Holand, and D. Lenvik.** 2002. Age-related reproductive effort in reindeer (*Rangifer tarandus*): evidence of senescence. *Oecologia* 131:79–82.
- Wilkinson, L. R., and J. W. Gibbons.** 2005. Patterns of reproductive allocation: clutch and egg size variation in three freshwater turtles. *Copeia* 2005:868–879.
- Willemsen, R. E., and A. Hailey.** 2002. Body mass condition in Greek tortoises: regional and interspecific variation. *Herpetology Journal* 12:105–114.
- Williams, G. C.** 1966. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton University Press, Princeton, New Jersey.