

## Allocation of Reproductive Output: Egg- and Clutch-Size Variation in the Diamondback Terrapin

WILLEM M. ROSENBERG AND ARTHUR E. DUNHAM

A fundamental component of an organism's life history is the allocation of energy available for reproduction into units that will simultaneously produce successful offspring and maximize the lifetime reproductive success of the female. We present five years of data on egg- and clutch-size variation for a single population of the diamondback terrapin, *Malaclemys terrapin*. Clutch size ranged from 4–22 eggs and correlated weakly with female plastron length. Mean egg mass ranged from 6–12 g among clutches. Egg mass did not correlate with female plastron length and female postparturition mass. Consistent with optimal egg size theory, we observed that clutch size varied more than egg size when we considered population averages. However, egg mass correlated negatively with clutch size only during one year. Thus, there was no persistent trade-off between clutch size and egg size. On the other hand, consistent with developmental plasticity, we observed that clutch size and egg size varied simultaneously among clutches of individual females. Thus, neither optimal egg size theory nor developmental plasticity provided an informative explanation for the egg-size variation we observed in terrapins.

OPTIMAL egg size theory (OES) predicts that egg size will be the result of two selective processes. First, selection will favor females that produce the greatest number of progeny. Second, selection will favor larger offspring, assuming that larger offspring have greater fitness (Trivers, 1974; Godfray and Parker, 1991). According to OES, the expected lifetime reproductive success of the female optimizes egg size by maximizing the number of propagules with the minimum amount of resources necessary for viable, successful offspring (Smith and Fretwell, 1974; Brockelman, 1975). An important premise of this model is that the energy available for reproduction is limited, thus resulting in a trade-off between offspring size and number (Smith and Fretwell, 1974; Brockelman, 1975). Elaboration of the OES model led to theoretical studies that evaluated the effect of various biological factors that might influence the evolution of offspring size, including sib competition (Brockelman, 1975; Parker and Begon, 1986), intraspecific competition (Wilbur, 1977; Parker and Begon, 1986), predation (Wilbur, 1977; McGinley, 1989), multiple resources (McGinley and Charnov, 1988), adult survival (Winkler and Wallin, 1987; Shine and Schwartzkopf, 1992; Niewiarowski and Dunham, 1994), neonate survival (Niewiarowski and Dunham, 1994), and environmental heterogeneity (Wilbur, 1977; Parker and Begon, 1986; McGinley et al., 1987). These studies predict differences in clutch and egg size based on contrasting selection pressures. However, they all agree with OES that fluctuation in resources for

reproduction should affect clutch size, whereas egg size within a female should remain relatively constant.

As empirical evidence accumulated, it became apparent that variation in offspring size in many species was not consistent with the predictions of OES. The theory of developmental plasticity was proposed as an alternative explanation for variation in offspring size (Capinera, 1979; Kaplan, 1980; Kaplan and Cooper, 1984). In this model, females in variable environments should exhibit plasticity in the size of their progeny among reproductive bouts, ensuring that a proportion of the offspring will survive across varying environmental conditions. Reproductive attributes of iteroparous organisms living in variable environments should be less canalized as selection favors individuals that have the ability to randomly vary offspring size (Kaplan and Cooper, 1984). Two important assumptions of this model are that environmental heterogeneity favors a range of offspring sizes and that females with the ability to assess current environmental conditions and produce offspring best suited to those conditions would rapidly replace randomly varying females.

Within-individual variation in reproductive traits is seldom reported, but because patterns of variation in offspring size and number within individual females represents another source of variation available to natural selection, it is a critical component of the life history. Additionally, the range of variation in offspring size and number observed within females may differ from the total range of variation in offspring

1  
2

3  
4

size among females, further complicating our interpretation of how selection may act on offspring size. Therefore, data on within-female variation in egg and clutch size are needed, as well as similar data on variation among females. The traditional approach to studying these life-history traits has been to take a cross-section of the population and identify among-individual variation (Dunham et al., 1988). This approach assumes implicitly that selection on reproductive traits reduces within-individual variation without testing the assumption. In this paper, we present five years of data on within- and among-female reproductive output from a single population of the diamondback terrapin, *Malaclemys terrapin*, and discuss how these data relate to OES and developmental plasticity.

#### MATERIALS AND METHODS

From 1987 to 1991, we studied annual reproduction in a population of diamondback terrapins (*M. terrapin*) in the Patuxent River, a tributary of the Chesapeake Bay. The study site was in Saint Mary's County, approximately 10 km south of Benedict, Maryland. Turtles were captured using a variety of techniques including fyke nets, peeler bank traps, crab pots, and by hand on nesting beaches. All turtles caught in this study were marked using unique combinations of notches cut or drilled in the marginal scutes (Cagle, 1939). We measured straight line plastron length (mm), carapace length (mm), and mass (g) and released all turtles as soon as possible. Mature females were palpated in the inguinal region for the presence of oviducal eggs. Gravid females were painted with a unique number that allowed identification of individuals with minimal disturbance while nesting.

The diamondback terrapin is an excellent species for the investigation of reproductive variation for three reasons. First, terrapins are easy to locate and observe while nesting. In the population studied, females nest primarily on small sandy beaches isolated from each other by salt marsh along the shore of the Patuxent River (Roosenburg, 1994). Second, they show a high degree of nest site philopatry with the same individuals frequently returning to the same beach within and among years. Finally, terrapins in the Patuxent population nest annually and up to three times each nesting season (Roosenburg, 1991). On the other hand, there are two drawbacks to working with terrapins. First, the open nature of their aquatic habitats makes it easy for them to nest undetected; and second, like most emydid turtles, terrapins cannot be aged accurately once they reach maturity.

Two independent sets of egg data were used in our study. The first data set investigated within-clutch, among-female variation in egg size. Ninety clutches were excavated from beaches adjacent to the main study site during 1987–1991. These nests were located by searching for tracks on the nesting beaches and finding the telltale markings of a terrapin nest (Burger, 1977). All the nests used in this study were located and processed within 24 h of oviposition. Eggs were taken to the lab and weighed individually to the nearest 0.1 g on an electronic balance. No information was available on the females that produced these clutches.

The second data set investigated both within- and among-female variation in clutch and egg size. In this data set, information was available for a female and her nest(s). Two nesting beaches were monitored during all daylight hours throughout the nesting season from 1987–1991. Nesting terrapins were watched from observation blinds or from vantage points on the nesting beaches. Unpainted turtles were intercepted after nesting, and their measurements were taken. Paint-marked turtles were allowed to return to the water undisturbed only after positive identification. In all analyses, female postparturition mass was used only from those females that were weighed immediately after oviposition. Within four hours of oviposition, nests were excavated, the eggs were counted, and the clutch was weighed as a whole. Each nest was reburied in its original site and condition. In this data set, average egg mass of a clutch was calculated by dividing clutch mass by clutch size. Clutches were not weighed in 1987 and 1988. However, clutch size data from 1987 and 1988 were included in our analyses.

*Analyses.*—We compared clutch size, egg mass, and clutch mass among years using ANOVA (Statistical Analysis Systems PROC GLM, Rel. 6.03 ed., SAS Institute, Cary, NC, 1988, unpubl.). We conducted path analyses as heuristic tools to develop causal hypotheses about factors contributing to egg-size variation for 1989, 1990, and 1991, independently. Path analysis partitions variation to direct effects between the two variables and identifies the indirect effects of other variables incorporated in the model (Li, 1975). Data were natural log-transformed to reduce the curvilinear relationships among the traits we measured. Correlation analyses identified possible factors affecting reproductive output during 1989–1991. Individual path coefficients were obtained by conducting a multiple regression analysis on the matrix of correlation coefficients of plastron length, female mass,

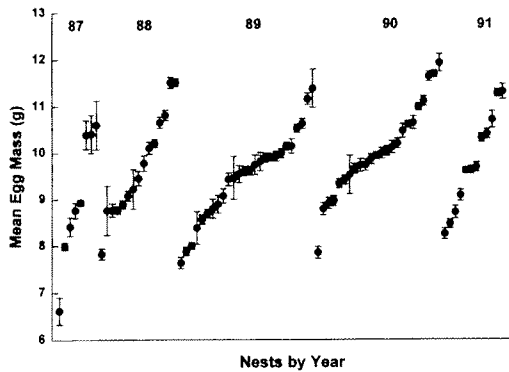


Fig. 1. Mean egg mass,  $\pm 2$  standard errors of 90 clutches collected during the five years of the study for which all eggs within each clutch were individually measured. Nests are arranged by increasing average egg size for each of the five years. The numbers above refer to the year the data were collected.

clutch size, and egg size. A final path analysis pooled data on clutch size, egg mass, and plastron length of the females that were observed nesting more than once during 1989–1991. Multivariate analysis of variance (MANOVA) of clutch size, egg size, and plastron length on mother removed the within-female variation and provided the partial correlation coefficients for a final path analysis. We did not include female postparturition mass in this analysis because this information was lacking for many individuals.

## RESULTS

*Among-female variation in egg and clutch size.*—Egg mass varied little within clutches; however, mean egg mass differed considerably among clutches when eggs were weighed individually (ANOVA,  $F_{82,1080} = 40.94$ ,  $P < 0.0001$ , Fig. 1). Clutch mean egg mass did not differ among years (ANOVA,  $F_{4,79} = 1.28$ ,  $P > 0.05$ , Table 1). The coefficient of variation (CV) for among egg mass was greater than the average CV for among-clutch mean egg mass both within years and for all years combined (Table 1), indicating that egg-mass variation in the population was greater than mean egg-mass variation among clutches. Field determinations of egg mass (clutch mass divided by clutch size) in our second data set assumed that egg size varied little within a clutch. The pattern of within- and among-clutch variation in egg mass from our first data set supports the assumption that our field method was a good estimator of average egg mass (Fig. 1).

Clutch size in terrapins ranged from 5–22

TABLE 1. SUMMARY STATISTICS OF EGG-MASS VARIATION AMONG THE FIVE YEARS OF THE STUDY FOR CLUTCHES THAT HAD EACH EGG WEIGHED (DATA SET 1). Among-egg variation compares egg mass within clutches among years. Among-clutch variation compares mean egg mass of clutches. Letters in parentheses identify means that grouped together based on a Student-Newman-Keuls multiple range test among groups found to be different. ns = nonsignificant differences among means.

Source	n	Mean egg mass(g)	SE	CV
Among egg				
1987	95	10.25 (C)	0.19	18.66
1988	198	9.66 (A)	0.19	12.87
1989	358	9.46 (A)	0.06	11.85
1990	330	10.03 (B)	0.06	10.68
1991	183	9.71 (A)	0.07	10.68
Total	1265	9.78 (A)	0.04	14.27
Among clutch				
1987	7	9.03 (ns)	0.28	10.93
1988	15	9.69 (ns)	0.16	6.26
1989	26	9.49 (ns)	0.16	6.10
1990	24	10.05	0.13	4.70
1991	12	9.79 (ns)	0.11	4.39
Total	83	9.84 (ns)	0.16	6.02

eggs but did not differ significantly over the five years of the study (ANOVA,  $F_{4,499} = 1.88$ ,  $P > 0.05$ , Table 2). However, in 1991, average clutch size increased by about one egg per clutch (12.7 to 13.7). Average egg mass did not change among years (ANOVA,  $F_{2,267} = 2.44$ ,  $P > 0.05$ , Table 2) nor did clutch mass (ANOVA,  $F_{2,269} = 1.52$ ,  $P > 0.05$ , Table 2). Comparisons of the CV for clutch size, egg mass, and clutch mass (Table 2) indicated that clutch size and mass varied almost twice as much as egg mass.

Clutch size increased with female plastron length; however, the correlation coefficients were small, suggesting that this relationship was weak (Table 3). Additionally, plastron length was uncorrelated with egg size suggesting a lack of pelvic aperture constraint on maximum egg size (Congdon and Gibbons, 1985, 1987; Table 3). Finally, a negative relationship between clutch size and egg size occurred only during 1991, suggesting that energetic or, possibly, body volume constraints resulted in an egg size and number trade-off (Table 3). Our path analyses indicated that the majority of the variation in egg mass was unexplained: 99% in 1989, 94% in 1990, and 93% in 1991. These high residuals suggested that body size (plastron length), body mass, and clutch size did not contribute to egg mass variation in the diamondback. Our second

TABLE 2. VARIATION IN CLUTCH SIZE, EGG MASS (GRAMS) AND CLUTCH MASS (GRAMS) FROM NESTS MEASURED IN THE FIELD (DATA SET 2). Egg mass was calculated as clutch mass divided by clutch size. Clutch-mass data were not taken during the first two years of the study. Values in descending order are mean (one standard error), coefficient of variation, and sample size. There were no significant differences among years in clutch size, egg size, and clutch mass.

Year	Clutch size	Egg mass (g)	Clutch mass (g)
1987	12.78		
	(0.28)		
	21.05		
	91		
1988	12.69		
	(0.27)		
	23.89		
	127		
1989	12.81	10.10	129.68
	(0.29)	(0.11)	(2.95)
	23.29	9.98	21.79
	104	92	92
1990	12.70	9.80	124.21
	(0.28)	(0.14)	(3.04)
	21.83	14.39	24.07
	97	95	97
1991	13.67	9.69	131.27
	(0.31)	(0.15)	(3.09)
	20.64	14.50	21.45
	85	83	83
Total	12.29	9.87	128.21
	(0.13)	(0.08)	(1.75)
	22.39	13.10	22.52
	504	270	272

path analysis on 195 nests by 70 females that nested multiple times had similarly high unexplained variance (97%). Additional regression analyses found no relationship between clutch size and egg mass with either interclutch interval (15 days) or date of nesting (least-squares regression,  $P > 0.05$ ).

*Within-female variation in egg and clutch size.*—The within-female range of clutch size, egg mass, and clutch mass was calculated as the differences between the maximum and the minimum value for an individual female among repetitive nestings (Table 4). Individual female terrapins can vary considerably in clutch size, clutch mass, and average egg mass (Table 4). The within-female CVs for these variables are all similar and large. The mean values for the range of reproductive traits appear low because most females are represented by only two nestings. The range

of egg mass, clutch size, and clutch mass have not been sampled adequately for most females because these range values (Table 4) increased with the number of nestings for each female. A female can vary both the mass of her eggs and size of her clutch simultaneously (Fig. 2). Thus, the conventional trade-off between egg mass and clutch size does not appear to constrain either clutch size or egg size in individual female terrapins.

## DISCUSSION

Diamondback terrapins exhibited a 6–12 g intrapopulation range in average egg mass and a within-individual range of variation up to 3 g. However, egg mass varied little within a clutch. Additionally, egg mass did not correlate with female plastron length and female mass and was negatively correlated with clutch size only in 1991, suggesting that trade-offs and other constraints on egg size were not straightforward. Furthermore, our path analyses did not identify any major factors that potentially contributed to egg-mass variation observed in the Patuxent population. Because our data support certain predictions of both optimal egg-size theory and developmental plasticity, we lack an informative explanation for the egg and clutch size variation we observed in terrapins.

According to OES, variation in reproductive output should result primarily in variation in the number of offspring and secondarily in variation of offspring size (Smith and Fretwell, 1974; Brockelman, 1975). Our data demonstrated that egg and clutch size varied considerably within individual females. Additionally, the trade-off between number and size of eggs was not detectable in terrapins, either within individual females or within the population. However, greater coefficients of variation for clutch size than for egg mass were consistent with OES (Table 2). Similarly, the within-female variation in reproductive output was consistent with developmental plasticity while the summary statistics of reproductive output were not. The contradictory support for the OES and developmental plasticity models suggested that a more mechanistic understanding of reproductive physiology in terrapins is necessary to understand variation in reproductive output.

We view life history as a time-ordered sequence of age-specific allocation processes that are based on the physiological state of the organism, environmental conditions, resource availability, and expected offspring and adult survival. Within this context, a life history is a set of rules that specifies three classes of allo-

TABLE 3. CORRELATION MATRICES OF NATURAL LOG-TRANSFORMED PLASTRON LENGTH, BODY MASS, CLUTCH SIZE, AND EGG MASS. (A) Above the diagonal are the coefficients for 1989; below the diagonal are the coefficients for 1990. (B) Above the diagonal are the coefficients for 1991; below the diagonal are the partial correlation coefficients corrected for within female effects combined for all years of the study. Body mass was not used in this analysis due to low sample sizes. The numbers below the correlation coefficients are the sample sizes for each comparison.

	Plastron length	Body mass	Clutch size	Egg mass
<b>A</b>				
Plastron length		0.783*	0.350*	0.108
		48	94	92
Body mass	0.885*		0.152	0.133
	54		48	47
Clutch size	0.223**	0.165		0.045
	97	54		92
Egg mass	0.046	0.164	0.198	
	95	52	95	
<b>B</b>				
Plastron length		0.748*	0.380*	-0.050
		64	84	82
Body mass			0.256**	-0.065
			63	62
Clutch size	0.176**			-0.345*
	195			83
Egg mass	-0.202**		-0.107	
	195		195	

\*  $P < 0.001$ , \*\*  $P < 0.05$ .

cation decisions: the allocation of time; of net assimilated energy (NAE); and of energy available to reproduction (Dunham et al., 1989; Dunham, 1993). Three allocation processes are involved in reproduction: (1) the amount of NAE to be invested in reproduction; (2) the number of offspring to be produced; and (3) the quality or size of those offspring (Congdon et al., 1982; Congdon, 1989). In general, these allocations are not independent (Dunham et al., 1989; Niewiarowski and Dunham, 1994). The rules that determine allocation decisions are fixed and heritable, and thus selection should favor a set of rules that maximizes expected lifetime reproductive success over the range of environmental variation experienced

by the individuals comprising a population (Dunham et al., 1989).

This allocation approach led us to the following interpretations of egg- and clutch-size variation in terrapins. First, because egg mass varies little within a clutch, resources available to egg production appear to be allocated in a uniform manner to the maturing follicles that comprise the next clutch. Terrapins can have as many as five size classes of follicles present in the ovary at one time (WMR, pers. obs.), suggesting that allocation of vitellogenin to several sets of follicles occurs simultaneously. Because turtles produce vitellogenin both in the fall following the nesting season and in the spring just prior to nesting (Licht, 1983), we suggest that vitellogenin deposition may vary seasonally: fall vitellogenin may be allocated to follicles in general, whereas spring vitellogenin may be allocated to specific set(s) of maturing follicles contributing to the next clutch(es). The timing and manner in which vitellogenin deposition occurs in species that simultaneously mature several sets of follicles is not well understood and requires further study.

Second, egg mass variation among clutches within a female suggests that the decisions that determine clutch size and egg size may be decoupled. For example, clutch size may be deter-

TABLE 4. SUMMARY STATISTICS FOR THE RANGE OF VARIATION OF REPRODUCTIVE TRAITS WITHIN FEMALES FOR WHICH TWO OR MORE NESTING EVENTS WERE OBSERVED (MAXIMUM-MINIMUM VALUE FOR EACH FEMALE WITH MULTIPLE OBSERVED NESTINGS). Data were pooled among years. Egg and clutch mass in grams.

Variable	n	Min	Max	Mean	SE	CV
Egg mass	68	0.00	3.00	1.18	0.09	63.95
Clutch size	87	0.00	12.00	3.14	0.23	69.27
Clutch mass	70	1.00	95.00	31.47	2.37	62.90

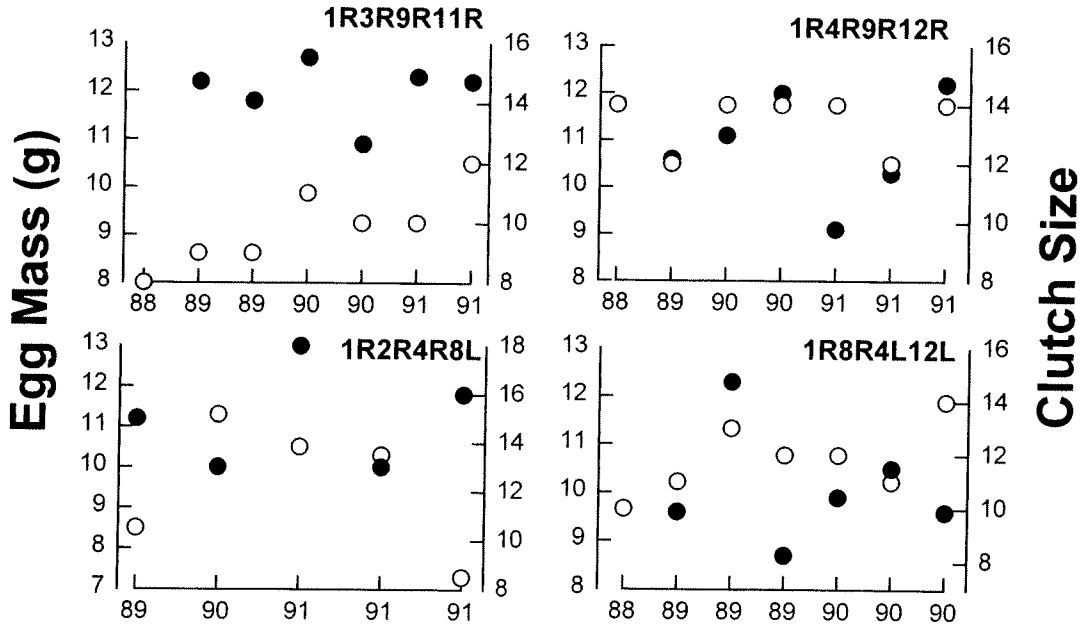


Fig. 2. Variation in clutch size (○) and egg mass (●) over multiple nestings of four female terrapins. All nests are presented in their actual sequence. The numbers on the x-axis are the year in which that nest was observed. Individuals with large numbers of observed nestings were selected because they illustrate best how egg size and clutch size can vary independently within a female. There were several other females that had the same number of observed nestings that showed similar patterns in clutch and egg size. Egg mass in this figure was determined in the field as clutch mass divided by clutch size.

mined when a female has sufficient resources to ensure that those follicles will meet the minimum energetic requirement to produce successful offspring. Further increases in egg size may result if a female enters a high productivity environment during follicular maturation. Food availability has been shown to affect egg size in *Plethodon cinereus* (Fraser, 1980) and clutch size in snakes (Ford and Seigel, 1989; Seigel and Ford, 1991). In addition, thermal differences among microhabitats chosen by terrapins can result in differences in temperature-dependent physiology resulting in differences in NAE, possibly affecting energy available for reproduction (Dunham et al., 1989). For example, temperature affects ovum size in the pupfish, *Cyprinodon n. nevadensis* (Shrode and Gerking, 1977), and both food availability and temperature can simultaneously effect egg size in the frog, *Bombina orientalis* (Kaplan, 1987).

Finally, the exact allocation processes that determine the number of follicles that will mature in the next clutch is unknown. Mammalian follicle stimulating hormone (FSH) can induce follicular growth in snakes (Aldridge, 1982) and can increase clutch size in lizards (Sinervo and Licht, 1991). Additionally, clutch size can be adjusted through atresia of "committed" follicles

in the snake, *Tantilla coronata* (Aldridge and Semlitsch, 1992). However, we still do not understand the mechanism by which the number of follicles that will mature for a reproductive bout is determined. Females that do not have sufficient resources at the time of the year when reproductive commitments are made may forego reproduction that year, as has been observed in the turtle, *Chrysemys picta* (Tinkle et al., 1981). Despite considerable data on reproductive output (RO) of turtles (reviewed in Wilbur and Morin, 1988; Elgar and Heaphy, 1989; Iverson 1992), little is known of their reproductive physiology.

Three sets of information are necessary if we are to understand the physiological factors that contribute to variation in RO. First, patterns of variation in RO must be described to document the occurrence of potential trade-offs and environmental variation; i.e., descriptive and correlative studies as we have done here. Second, the timing of particular reproductive events must be documented to determine how and when proximate factors might influence reproductive decisions and allocation strategies reflected in reproductive output. Third, experimental studies should manipulate ecological factors during various stages of the reproductive

cycle to determine how proximate environmental variation affects allocation. Resource availability, microclimatological variation, and variation in the physiological state of the organism may function as factors that cause natural variation in reproductive output. This paradigm should identify some of the mechanisms and environmental factors that contribute to variation in clutch and egg size.

There are several variables missing from our data set that are likely to be contribute to variation in reproductive output in terrapins. Female age was not included in our analyses because determining the age of terrapins is difficult once they reach maturity (8–13 yr). Within-female variation suggests that age may not be important for clutch and egg size in terrapins. However, it may remain important for total annual reproductive output. Second, the geography of the study site enables females to nest undetected; thus total annual reproductive output can be determined for only those females that were observed nesting three times in a single season. Our sample size of triple nesting females is small ( $n = 7$ ), and we cannot determine the relationship between age and clutch frequency. Additionally, we were unable to detect any relationship between egg or clutch size and interclutch intervals as suggested by Parker and Begon (1986). The lack of age-specific reproductive data illustrate the need for long-term life-history studies and the need to establish accurate assessments of lifetime reproductive success.

Our study demonstrates that within-female variation in reproductive traits can be an important source of variation overlooked by short-term or cross-sectional studies of populations. Much of our current understanding of life histories, particularly reproductive traits, is prejudiced toward the reporting of data that are consistent with the predictions of a particular model. Complex data sets are difficult to analyze and interpret, yet they reveal the complexity of trade-offs in life-history evolution (Stearns, 1989). We have presented one example where trade-offs are not apparent and reproductive output is a complex phenomenon that does not conform to current models. Clearly, investigating the interaction between proximate environmental factors and the physiologically based mechanisms related to reproduction is necessary to developing an understanding of variation in reproductive output and how it contributes to life-history evolution.

#### ACKNOWLEDGMENTS

We are grateful to the N. Dodge family and the L. McCormick-Goodhart family for letting

us conduct this study on their property. M. Robbins, K. Kelley, V. Baccadori, J. Sanderson, C. Sheridan, J. Finnerty, N. Yorinks, B. Cresko, D. Colbert, S. Herzog, A. Zirkle, M. Modisette, S. Stoszek, and K. Wojciechowski are thanked for their many hours of patiently waiting for turtles to nest. P. Petraitis patiently assisted us with the path analyses. We thank J. Barron, J. Bernardo, J. Congdon, K. Kelley, D. Miles, and S. Reilly for helpful comments on this manuscript. This study was funded by Shell Foundation Award to the University of Pennsylvania, Sigma Xi, Patuxent River Appreciation Days Grant, the W. Deshler family, Calvert County Optimist Club, and Maryland Department of Natural Resources Contract # F218-90-008 and # S183-89-008 to WMR. The contents of this document do not in any way reflect the views, opinions, or policies of the Maryland Department of Natural Resources. All fieldwork was conducted under collecting permits issued to WMR by the Maryland Department of Natural Resources, Tidewater Administration. Animal use was conducted according to IACUC proposal #B-890014 issued to WMR through the Office of Research Administration at the University of Pennsylvania.

#### LITERATURE CITED

- ALDRIDGE, R. D. 1982. The ovarian cycle of the water snake, *Nerodia sipedon*, and effects of hypophysectomy and gonadotropin administration. *Herpetologica* 38:71–79.
- , AND R. D. SEMLITSCH. 1992. Female reproductive biology of the southeastern crowned snake (*Tantilla coronata*). *Amphibia-Reptilia* 13:209–218.
- BROCKELMAN, W. Y. 1975. Competition, fitness of offspring, and optimal clutch size. *Am. Nat.* 109:677–699.
- BURGER, J. 1977. Determinants of hatching success in the diamondback terrapin, *Malaclemys terrapin*. *Am. Midl. Nat.* 97:444–464.
- CAGLE, F. R. 1939. A system for marking turtles for future identification. *Copeia* 1939:170–173.
- CAPINERA, J. L. 1979. Qualitative variation in plants and insects: effect of propagule size on ecological plasticity. *Am. Nat.* 114:350–361.
- CONGDON, J. D. 1989. Proximate and evolutionary constraints on energy relations in reptiles. *Physiol. Zool.* 62:356–373.
- , AND J. W. GIBBONS. 1985. Egg components and reproductive characteristics of turtles: relationships to body size. *Herpetologica* 41:194–205.
- , AND ———. 1987. Morphological constraints on egg size: a challenge to optimal egg size theory? *Proc. Nat. Acad. Sci.* 84:4145–4147.
- , A. E. DUNHAM, AND D. W. TINKLE. 1982. Energy budgets and life histories of reptiles, p. 233–271. *In: Biology of the Reptilia*. Vol. 13. Physiology C. C. Gans and F. H. Pough (eds.). Academic Press, London.



- DUNHAM, A. E. 1993. Population response to environmental change: operative environments, physiologically structured models and populations dynamics, p. 95–119. *In: Biotic interactions and global change*. P. M. Kareiva, J. G. Kingsolver, and R. B. Huey. (eds.). Sinauer Assoc., Sunderland, MA.
- , P. J. MORIN, AND H. M. WILBUR. 1988. Methods for the study of reptile populations, p. 331–386. *In: Biology of the Reptilia*. Vol. 16. Ecology B. Defense and life history. C. Gans and R. Huey (eds.). Alan R. Liss, New York.
- , B. W. GRANT, AND K. L. OVERALL. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiol. Zool.* 62:335–355.
- ELGAR, M. A., AND L. J. HEAPHY. 1989. Covariation between clutch size, egg weight and egg shape: comparative evidence for chelonians. *J. Zool. Lond.* 219:137–152.
- FORD, N. E., AND R. A. SEIGEL. 1989. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. *Ecology* 70:1768–1774.
- FRASER, D. F. 1980. On the environmental control of oocyte maturation in a plethodontid salamander. *Oecologia* 46:302–307.
- GODFRAY, H. C. J., AND G. A. PARKER. 1991. Clutch size, fecundity, and parent-offspring conflict. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* 32:67–79.
- IVERSON, J. B. 1992. Correlates of reproductive output in turtles (order Testudines). *Herpetol. Monogr.* 5:25–42.
- KAPLAN, R. H. 1980. The implications of ovum size variability for offspring fitness and clutch size within several populations of salamanders (*Ambystoma*). *Evolution* 34:51–64.
- . 1987. Developmental plasticity and maternal effects of reproductive characteristics in the frog, *Bombina orientalis*. *Oecologia* 71:273–279.
- , AND W. S. COOPER. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the "adaptive coin flipping" principle. *Am. Nat.* 123:393–410.
- LI, C. C. 1975. Path analysis—a primer. The Boxwood Press, Pacific Grove, CA.
- LIGHT, P. 1983. Reptiles, p. 206–282. *In: Marshall's physiology of reproduction*. E. Lamming. (ed.). Academic Press, New York.
- MCGINLEY, M. A. 1989. The influence of a positive correlation between clutch size and offspring fitness on the optimal offspring size. *Evol. Ecol.* 3: 150–156.
- , AND E. L. CHARNOV. 1988. Multiple resources and the optimal balance between size and number of offspring. *Ibid.* 2:77–844.
- , D. H. TEMME, AND M. A. GEBER. 1987. Parental investment in variable environments: theoretical and empirical considerations. *Am. Nat.* 130:370–398.
- NIEMIAROWSKI, P. H., AND A. E. DUNHAM. 1994. The evolution of reproductive effort in squamate reptiles: costs, trade-offs, and assumptions reconsidered. *Evolution* 48:137–145.
- PARKER, G. A., AND M. BEGON. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am. Nat.* 128:573–592.
- ROOSENBERG, W. M. 1991. The diamondback terrapin: population dynamics, habitat requirements, and opportunities for conservation, p. 227–234. *In: New perspectives in the Chesapeake system: a research and management partnership*. Proceedings of a conference, 4–6 Dec. 1990, Baltimore, MD. J. A. Mihursky and A. Chaney (eds.). Chesapeake Research Consortium Publication No. 137, Solomons, MD.
- . 1994. Nesting habitat requirements of the diamondback terrapin: a geographic comparison. *Wetland Journal* 6:8–11.
- SEIGEL, R. A., AND N. E. FORD. 1991. Phenotypic plasticity in the reproductive characteristics of an oviparous snake *Elaphe guttata*: implications for life history studies. *Herpetologica* 47:301–307.
- SHINE, R., AND L. SCHWARTZKOPF. 1992. The evolution of reproductive effort in lizards and snakes. *Evolution* 46:62–75.
- SHRODE, J. B., AND S. D. GERKING. 1977. Effects of constant and fluctuating temperatures on reproductive performance of a desert pupfish, *Cyprinodon n. nevadensis*. *Physiol. Zool.* 50:1–10.
- SINERVO, B., AND P. LIGHT. 1991. Hormonal and physiological of clutch size, egg size, and egg shape in the side-blotched lizard (*Uta stansburiana*): constraints on the evolution of lizard life histories. *J. Exp. Zool.* 257:252–264.
- SMITH, C. C., AND S. D. FRETWELL. 1974. The optimal balance between size and number of offspring. *Am. Nat.* 108:499–506.
- STEARNS, S. C. 1989. Trade-offs in life-history evolution. *Funct. Ecol.* 3:259–268.
- TINKLE, D. W., J. D. CONGDON, AND P. C. ROSEN. 1981. Nesting frequency and success: implications for the demography of painted turtles. *Ecology* 62:1426–1432.
- TRIVERS, R. L. 1974. Parent-offspring conflict. *Am. Zool.* 14:249–264.
- WILBUR, H. M. 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. *Am. Nat.* 111:43–68.
- , AND P. J. MORIN. 1988. Life history evolution in turtles, p. 387–440. *In: Biology of the Reptilia*. Vol. 16. Ecology B. Defense and life history. C. Gans and R. Huey (eds.). Alan R. Liss, New York.
- WINKLER, D. W., AND K. WALLIN. 1987. Offspring size and number: a life history model linking effort per offspring and total effort. *Am. Nat.* 129:708–720.

(WMR) DEPARTMENT OF BIOLOGICAL SCIENCES, OHIO UNIVERSITY, ATHENS, OHIO 45701; AND (AED) DEPARTMENT OF BIOLOGY, UNIVERSITY OF PENNSYLVANIA, PHILADELPHIA, PENNSYLVANIA 19104. Send reprint requests to WMR. Submitted: 11 Jan. 1996. Accepted: 4 Dec. 1996. Section editor: J. R. Spotila.

