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Allocation of Reproductive Investment in the Redbelly Snake Storeria occipitomaculata

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ABSTRACT.—Reproductive traits of a population of the redbelly snake *Storeria occipitomaculata* were studied for 2 consecutive years and assessed for congruence with optimal egg size models. Litter size and total litter mass were correlated with female size but mean offspring size was not, indicating that larger females invested more in total reproduction but partitioned it into more rather than larger offspring. After adjusting for female size differences, yearly variation was observed in offspring mass, but not in total litter mass or litter size, suggesting that factors determining total investment and investment per offspring may be different. Within-litter variance in offspring size was generally small, but in some cases was substantial. Whether this variation was due to a physiological inability to produce uniform litters or selection for variation in offspring size is unknown. Finally, we discuss why an observed positive correlation between total litter mass and offspring size need not be viewed as evidence against the optimal egg size concept if the fractional clutch problem is considered.

INTRODUCTION

A central concept among studies of offspring size is the existence of an optimal egg size or level of parental investment (=investment per offspring; Trivers, 1972) for females within a given population, and studies on a wide variety of organisms have addressed how the total investment in a reproductive bout is partitioned among individual offspring in a litter or clutch (*e.g.,* Wilbur, 1977; Kaplan and Salthe, 1979; Nussbaum, 1981; Berven, 1982; Ferguson *et al.,* 1982). Much of this work was derived from, or was in response to, the optimal parental investment model of Smith and Fretwell (1974), which is based on a curvilinear relationship between offspring fitness and investment per offspring, and extensions of this model by Brockelman (1975) and Wilbur (1977). Some authors have proposed that this model should also address variation in parental investment among years or environments, and whether or not such plasticity is a product of selection (Berven, 1982; Kaplan, 1980; Kaplan and Cooper, 1984). In addition, it has been suggested that within-litter variation in parental investment may increase long-term fitness (Capinera, 1979; Crump, 1981, 1984; Kaplan and Cooper, 1984). However, McGinley *et al.* (1987) convincingly argued that selection would only rarely favor such variation.

Because life history traits often are intercorrelated, a multivariate approach in which a number of different traits for a population are studied simultaneously is most appropriate (Stearns, 1977; Reznick, 1985). Multiyear studies are preferable because environmental fluctuations often significantly affect short-term expression of reproductive characters (Tinkle, 1979; Stearns, 1977; Dunham, 1982; Seigel and Fitch, 1985). In addition, because controversy exists over whether variation itself may be the product of selection (Capinera, 1979; Kaplan, 1980; Kaplan and Cooper, 1984; McGinley *et al.,* 1987), the traits should be examined on a number of different levels, including within litters, among litters, and among populations whenever possible. By simultaneously analyzing offspring size, litter

size (number of offspring), litter mass, and relative clutch mass (RCM—the ratio of litter mass to female mass), the nutrient allocation between offspring size and number can be addressed.

In order to study patterns of resource allocation, we examined the reproductive traits of the redbelly snake *Storeria occipitomaculata* over 2 years for a population in New York. We recorded total litter mass, litter size, offspring mass and RCM and tested for yearly variation and correlations between each of the reproductive parameters and female size. To study variation in parental investment, we also examined variation in offspring size within and among litters.

METHODS

We collected 42 gravid female *Storeria occipitomaculata* on or near the E. N. Huyck Preserve, Albany Co., New York, by turning surface debris during mid- to late July in 1979 (29 females) and 1980 (13 females). Snakes were housed individually in screen-topped 1-gallon glass aquaria at 24 C with water and offered invertebrates once weekly. None of the females accepted food during their captivity. In no case were females captive for more than 40 days prior to parturition, and feeding habits during this period are unlikely to affect offspring size and certainly not litter size.

Females and their offspring were weighed and measured within 14 h of birth. Snout-vent lengths (SVL) were measured to the nearest 1.0 mm and wet mass recorded to 0.01 g. Females were palpated and later dissected to check for the presence of unreleased embryos. All specimens were subsequently deposited in the University of Texas at Arlington Collection of Vertebrates (R13092–R13573).

Total litter mass (TLM) was calculated as the sum of the masses of released and unreleased offspring for each female. RCM was calculated as the ratio of TLM to postpartum female mass. The residuals of a regression of TLM on female mass were used for RCM in subsequent analyses to avoid the statistical problems associated with the analysis of ratios (Packard and Boardman, 1987).

An analysis of covariance between years—treating female size as a covariate—was used to examine the relationship of female size with litter size (LS) and mean offspring mass (MOM), as well as to inspect yearly variation in these measures. Within-litter variation in individual offspring mass and snout-vent length was assessed via ranges and coefficients of variation.

Female mass was natural log-transformed and litter size was square-root transformed to approach normality and reduce heteroscedasticity (Sokal and Rohlf, 1981). Some statistical analyses were performed using MIDAS on Michigan Terminal System (Fox and Guire, 1976).

RESULTS

Offspring were born 7–27 August in 1979 and 31 July–20 August in 1980. Means and standard errors for all parameters are reported in Table 1.

Females were significantly larger in SVL in 1979 than in 1980 (t = 2.43, df = 39, P < 0.05), although there was considerable overlap (range for 1979: 16.9–26.1 cm; 1980: 18.1–23.3 cm). There was no significant difference in female mass between the 2 years.

Larger females produced both more total litter mass and greater numbers of offspring (Table 2 and Fig. 1). Litter size and total litter mass were positively correlated (r = 0.948, P < 0.001). Neither litter size nor total litter mass differed between years when adjusted for female size (Table 2). An ANOVA revealed no differences in RCM between years (F = 0.044, df = 1, 39, P > 0.05).

TABLE 1.—Summary of female parent and litter measurements for *S. occipitomaculata.* FM = female postpartum mass (g); FSVL = female snout-vent length (mm); TLM = total litter mass (g); RCM = relative clutch mass (TLM/FM); LS = litter size; and MOM = mean offspring mass (g)

	1979			1980			Totals		
	n	$\bar{x}$	s_x	n	$\bar{x}$	s_x	n	$\bar{x}$	s_x
FM	29	4.50	0.228	12	4.13	0.169	41	4.39	0.169
FSVL	29	213.0	3.6	12	200.7	4.0	41	209.4	2.89
TLM	29	2.58	0.202	13	2.52	0.174	42	2.56	0.148
RCM	29	0.58	0.038	12	0.62	0.038	41	0.59	0.029
LS	29	9.0	0.67	13	9.7	0.6	42	9.2	0.5
MOM	29	0.28	0.007	13	0.26	0.007	42	0.28	0.006

Mean offspring mass was not significantly correlated with female size or litter size (Table 2 and Fig. 2) but was positively correlated with total litter mass. When adjusted for either total litter mass or female mass, mean offspring mass was significantly greater in 1979 than in 1980.

We calculated within-litter coefficients of variation (CV) and within-litter ranges for both individual offspring mass and SVL in 1979, and for mass alone in 1980. The overall mean CV for individual offspring mass was 9% and the CVs were not significantly different between years (Mann-Whitney U = 198). The overall mean for within-litter range in offspring mass was 0.084 g and the ranges were not significantly different between years (Mann-Whitney U = 197). The distributions of both range and CV were significantly skewed to the right (Fig. 3). Neither of these measures was significantly correlated with litter size or total litter mass. Offspring SVLs at birth in 1979 ranged from 42–75 mm (mean = 64.8), and showed low within-litter variation similar to that seen for mass (mean CV = 5%).

TABLE 2.—Results from one-way analyses of covariance for each combination of dependent variable and covariate over both years of collection. The P-values for the partial correlations of the dependent variable and each covariate, and for the difference between the adjusted means for each year, are shown. *See* text for the transformations used in the analyses. NS = P > 0.05; * = P < 0.05; ** = P < 0.01. Abbreviations as in TABLE 1

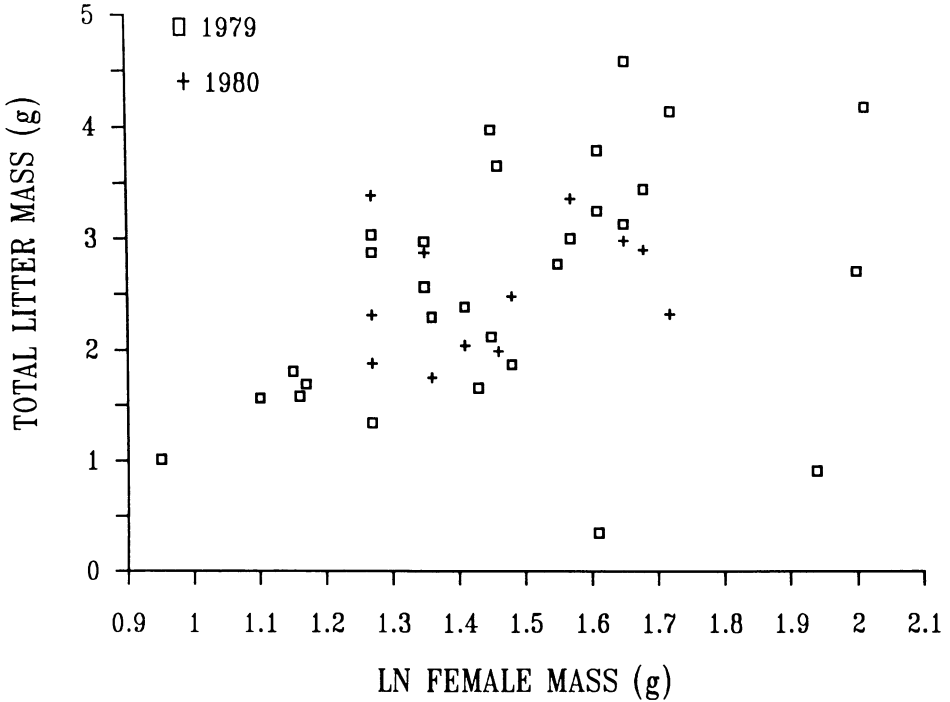| Dependent variable	Covariate	Pooled within years			Between years adjusted means		
		Partial correlation	P		1979	1980	P
LS	FSVL	0.390	*		8.36[a]	10.41	NS
	FM	0.291	NS		8.55	9.91	NS
TLM	FSVL	0.481	**		2.48	2.76	NS
	FM	0.404	**		2.55	2.60	NS
MOM	FSVL	0.266	NS		0.282	0.263	NS
	FM	0.303	NS		0.283	0.260	*
	TLM	0.384	*		0.284	0.257	*
	LS	0.178	NS		0.285	0.255	*

[a] Adjusted means for litter size were back-transformed

FIG. 1.—Scatter plot of log-transformed female mass vs. total litter mass for 41 *S. occipitomaculata*. Squares = 1979; crosses = 1980

DISCUSSION

Total investment in reproduction, litter size and offspring size presumably is dependent on phylogeny, condition of the mother, and prevailing ecological conditions. In reptiles, larger females generally have more total resources available for reproduction than smaller females (Shine, 1980), but how this difference in available resources is allocated to individual offspring is the subject of much research. In the current study, both total litter mass and litter size were positively correlated with female SVL, whereas mean offspring mass was not, indicating that larger females not only invested more total energy in reproduction than smaller ones, but also produced more offspring. Total litter mass was strongly correlated with litter size but only slightly correlated with offspring mass. In light of the fractional clutch problem (below), these results suggest that females invested additional resources in more rather than larger offspring.

The Smith and Fretwell (1974) optimal offspring size model predicted a single optimal level of parental investment that would maximize the fitness for all females in a given population at a given time. The model did not address whether females would be able to sense and respond to yearly changes in the environment that affect optimal parental investment levels. Such plasticity has been suggested as a necessary modification to parental investment models because of numerous empirical observations of yearly variation in life history traits (Kaplan, 1980; Berven, 1982). We found significant variation between years in mean offspring mass suggesting that parental investment levels changed. The absence of
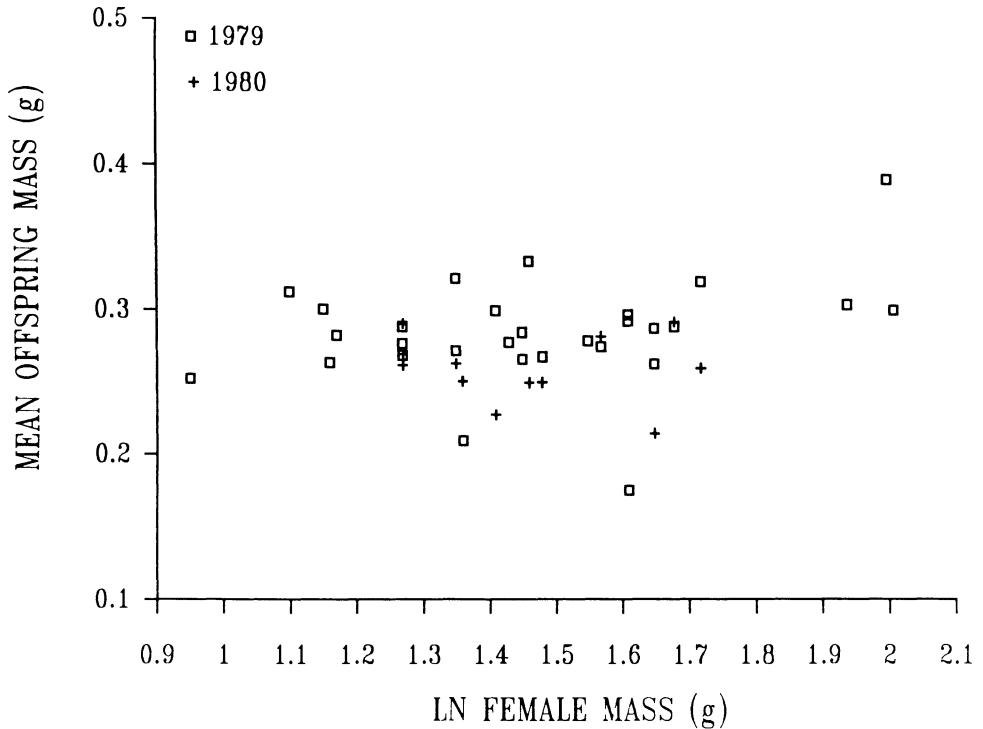
FIG. 2.—Scatter plot of log-transformed female mass vs. mean offspring mass for 41 *S. occipito-maculata* and their litters. Squares = 1979; crosses = 1980

any similar change in RCM, litter size or total litter mass suggests that the factors important in determining total investment by a female were different from those determining allocation per offspring, as is predicted by optimal offspring size models (Smith and Fretwell, 1974; Brockelman, 1975; Wilbur, 1977).

A further prediction of the Smith and Fretwell model (1974) was that the optimal offspring size for a population is dependent on the environment in which the offspring are placed and not on characteristics of the individual females. Congdon *et al.* (1983) and Congdon and Gibbons (1985) found a positive relationship between female size and egg size in some turtle populations. These authors hypothesized that female pelvic width constrained egg size in smaller females and that the optimal egg size concept was, therefore, inapplicable for turtles. Ford and Killebrew (1983) reported a positive correlation of female size and offspring size in *Thamnophis butleri* and Blanchard (1937) suggested a similar trend for *Storeria occipitomaculata* from Michigan. We found no correlation between mean offspring size and female size in our study, suggesting that investment per offspring is determined by factors other than characteristics of the female.

Although the correlation between the total litter mass and mean offspring mass that we found was not predicted by the optimal egg size models as originally formulated, nor by the alternative models mentioned above, the discussions by Ricklefs (1968) and Nussbaum (1981) of the 'fractional clutch' problem in relation to optimal egg size models can be useful in interpreting our results. If a female's total investment in a clutch is not some whole
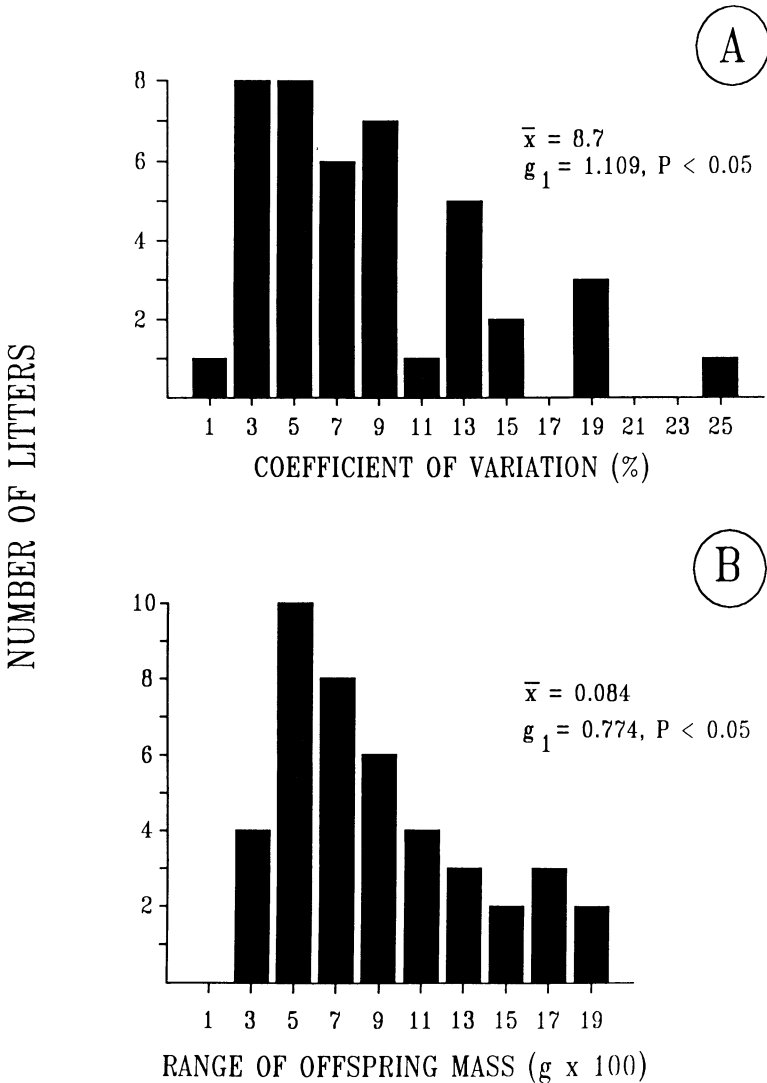
FIG. 3.—Frequency distribution histograms for (A) within-litter coefficient of variation and (B) within-litter range in offspring mass for 42 litters of *S. occipitomaculata*. The mean and third moment (g_1 = skewness) is reported for each distribution

number multiple of the optimal egg size, she may produce either the next highest whole number of slightly smaller than optimal eggs or the next lowest whole number of slightly larger than optimal eggs. It is apparent that this situation would show the greatest effect on egg size in the smallest clutches, where the fractional excess is spread among a few eggs, and that this effect would decrease in importance with increasing clutch size (Nussbaum, 1981). The effects would be negligible in fairly large clutches, and in these, the mean egg size should be nearest to the optimum for the population. If some females with small clutches

produced more but smaller than optimal eggs because of the fractional clutch problem, a positive correlation between total litter mass and offspring mass might be observed. If the fractional clutch problem is considered, we should not view such a correlation as evidence against the optimal egg size concept, even though the relationship is not predicted by current models.

Optimality models in general, and the optimal parental investment models in particular, have been challenged on the theoretical ground that selection may favor variation rather than a single value (Capinera, 1979; Kaplan and Cooper, 1984). Authors of some studies of parental investment have suggested that within-clutch variation in parental investment may lead to greater long-term fitness in variable environments (Capinera, 1979; Crump, 1981, 1984; Kaplan and Cooper, 1984). Predictions of actual levels of variation to be expected were not offered and empirical tests of these ideas have not been made. Crump (1984), however, proposed that platykurtotic distributions of egg size within clutches would be evidence for selection favoring within-clutch variation and tested for this in frogs. More recently, McGinley *et al.* (1987) argued that this line of reasoning has serious limitations and that natural selection would only rarely favor within-litter variation. Because our snakes had litters too small for meaningful measures of kurtosis, we investigated within-litter variation in offspring size via range and CV. Both measures of variation showed low nodes, a wide range of values, skewness to the right, and no correlation with litter size, indicating that most females produced fairly uniform litters, although some produced quite variable ones. Whether this magnitude of variation supports optimal offspring size or variable offspring size theories is unclear. Also, whether this variation in offspring size is a result of selection for non-zero variance or is simply the result of environmental and physiological noise cannot be determined from our data.

In general, the findings of this study are congruous with the predictions of optimal offspring size models (Smith and Fretwell, 1974; Brockelman, 1975; Wilbur, 1977) but are insufficient to test such models. Data presented here suggest several ways that the models should be modified, including consideration of yearly variation and the fractional clutch problem. Information on the survivorship curves of offspring and the physiological and genetic potential for producing uniform or variable litters is required to rigorously test the models. Additional theoretical studies on the selective value of variation vs. uniformity in parental investment are also needed to make more detailed empirical predictions.

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