

SEASONAL VARIATION IN REPRODUCTIVE EFFORT AND ITS EFFECT ON OFFSPRING SIZE IN THE LIZARD *SCELOPORUS UNDULATUS*

MICHAEL J. ANGILLETTA, JR.^{1,2}, MICHAEL W. SEARS^{1,3}, AND R. SCOTT WINTERS¹

¹*Department of Biology, University of Pennsylvania, Philadelphia, PA 19104-6018, USA*

ABSTRACT: Fence lizards, *Sceloporus undulatus*, reproduce multiple times per year. Survival of reproducing females drops dramatically between clutches from first to final clutch of the year. Also, offspring from later clutches emerge with less time available for growth and storage prior to hibernation. Considering these two facts, life history theory predicts that (1) females should exhibit greater reproductive effort (RE) in the second clutch of the active season than in the first, and (2) that the increase in RE should be mediated by a greater allocation of energy per offspring. To test these hypotheses, we compared reproductive traits (RE, clutch size, and egg mass) of lizards from a New Jersey population laying their first and second clutches. Two different estimates of RE (relative clutch mass, and clutch mass adjusted for condition) were significantly lower for the second clutch than for the first clutch. The difference in RE was manifested primarily as a decrease in clutch size. Clutch size was correlated with female body size and condition, but average egg mass was not correlated with either variable. Egg mass varied twice as much among clutches as it did within clutches. In fact, the variation in average egg mass observed among clutches was almost as great as that which exists among populations of *S. undulatus*. Variation in egg mass within and among clutches has consequences for offspring quality because egg mass was positively correlated with snout-vent length, body mass, and condition of hatchlings. Our data do not support the predictions of existing theories regarding the optimal allocation of RE among offspring.

Key words: Clutch size; Egg mass; Reproductive effort; *Sceloporus undulatus*

THE allocation of available energy to reproduction has been a major focus of life history theory since its inception (Stearns, 1992). Traits such as offspring size, offspring number, and reproductive effort (RE) have been considered in both theoretical and empirical contexts. Theory predicts that the relationship between age and RE should evolve such that reproductive value is maximized at each age (Pianka and Parker, 1975; Taylor et al., 1974). Actual magnitudes of RE should depend on the age-specific survival and fecundity schedules of the organism (Hirshfield and Tinkle, 1975). Greater RE will increase current reproductive value, but may reduce residual reproductive value (Reznick, 1985). Individuals with greater RE may suffer increased mortality because of predation during reproductive activities, energetic stress from increased energy ex-

penditure and reduced feeding, or smaller body size caused by reduced growth (Brown and Weatherhead, 1997; Nilsson and Svensson, 1996; Shine, 1980). Future fecundity is reduced by the depletion of energy stores, decreased resource intake during reproduction, or smaller body size due to reduced growth (Landwer, 1994; Schwarzkopf, 1993; Weeks, 1996). Factors such as age, size, and resource availability should all affect an individual's reproductive effort (Gadgil and Bossert, 1970; Ricklefs, 1977).

Because of the numerous mechanisms by which RE can affect fitness, it is difficult to determine the optimal age-specific RE in practice, and few generalizations can be made (Hirshfield and Tinkle, 1975). Thus, it is hardly surprising that a number of interesting questions regarding the allocation of energy to reproduction still await answers. These questions include but are not limited to the following. First, by what mechanisms does natural selection act on the level of RE (for recent debate, see Niewiarowski and Dunham, 1994, 1998; Shine and Schwarzkopf,

² PRESENT ADDRESS: Department of Life Sciences, Indiana State University, Terre Haute, IN 47809, USA.

³ PRESENT ADDRESS: Biological Resources Research Center, Department of Biology, University of Nevada, Reno, NV 89557, USA.

1992; Shine et al., 1996)? Second, what factors (e.g., environmental, maternal) determine the allocation of energy to reproduction (Madsen and Shine, 1996)? Finally, are differences in RE expressed through changes in offspring number, offspring size, or both?

Analysis of natural variation in reproductive traits can provide tentative answers to the questions posed above, and such an exercise is particularly worthwhile in cases where a priori hypotheses are formulated. For example, perennial lizards that produce multiple clutches per year usually experience dramatically different mortality risks between episodes of reproduction. Female fence lizards, *Sceloporus undulatus*, are more likely to survive between successive clutches within a season than they are to survive between the last clutch of one season and the first clutch of the following season (Jones and Ballinger, 1987; Tinkle and Dunham, 1986). Not surprisingly, this pattern is observed in other phrynosomatid lizards (e.g., Jones and Ballinger, 1987; Tinkle and Dunham, 1983; Tinkle et al., 1993) because of the greater duration between reproductive episodes separated by winter ($\approx 7-9$ mo) than that between reproductive episodes that occur within a season (< 2 mo) and the thermal and energetic stresses of hibernation. Several theories predict that natural selection will favor greater RE immediately prior to episodes of high mortality and less RE immediately following episodes of high mortality (Gadgil and Bossert, 1970; Hirshfield and Tinkle, 1975; Law, 1979; Michod, 1979). Therefore, RE by fence lizards should be relatively great at the end of the active season and relatively low at the beginning of the active season. A specific prediction that follows from this notion is that females should expend more RE in the last clutch of the season than in the first clutch of the season.

For a given amount of RE there will be a trade-off between offspring size and offspring number (Stearns, 1992), and the distribution of energy among offspring may be an additional factor determining the optimal RE (Winkler and Wallin, 1987). Packaging of RE should be influ-

enced by the timing of reproduction. Offspring from the second clutch of the season emerge about 4 wk later than those from the first clutch, leaving less time for growth and storage prior to hibernation. The difference in activity time may reduce survival during hibernation, delay maturity, or reduce size at maturity. Females can compensate for the timing of later clutches by increasing the amount of energy allocated to each egg at the expense of clutch size. Therefore, we predict that females should increase RE between the first and last clutch of the season by producing larger eggs.

We tested the hypotheses that females expend greater RE and produce larger eggs in the second clutch of the season by examining the natural covariation between the time of reproduction and reproductive traits of individuals. Specifically, we compared average egg mass, clutch size, and RE between clutches in the lizard *Sceloporus undulatus*. Furthermore, we incubated eggs from these clutches to assess the effects of seasonal variation in egg size on offspring quality. We present our results with one caveat. Certain patterns may be obscured when correlations between life history traits are sought among individuals that vary significantly in available energy (Heulett et al., 1995; Stearns, 1989). For example, variation in reproductive traits of females may reflect differences in the size and condition of females collected early and late in the year, rather than an adaptive strategy of energy allocation. Before seasonal variation in reproductive traits can be considered an adaptive strategy, one must control for variation in energy availability among individuals (e.g., Gregory and Skebo, 1998). We use body size and condition of females to partition variation in reproductive traits into that which can be attributed to energy availability and that which may be explained by hypotheses of adaptive energy allocation.

MATERIALS AND METHODS

Measurement of Reproductive Traits

We measured reproductive traits of females from a population in Burlington

County, New Jersey, laying their first and second clutches of the active season. By periodically assessing the reproductive condition of females in this population, we were able to identify reproductive episodes as either the first clutch of the year (CL1) or the second and final clutch of the year (CL2). Females laying CL2 were collected in June of 1997 and those laying CL1 were collected in May of 1998. Gravid females were transported to The University of Pennsylvania, where they were maintained until oviposition. When a female entered the laboratory, we measured body mass to the nearest 0.01 g and snout-vent length (SVL) to the nearest 1 mm. Each female was placed in a plastic terraria (28 × 18 × 8 cm) with a substrate of moistened sand and sphagnum moss. Terraria were kept in an incubator with a light cycle of 14L:10D and a constant temperature of 30 C. This temperature maximizes embryonic survival in the laboratory (Angilletta et al., 2000). Vitamin-dusted crickets were offered daily.

We inspected terraria for eggs several times each day. We removed freshly laid eggs from terraria and weighed them individually to the nearest 0.01 mg. If any eggs appeared dehydrated, that female and her clutch were excluded from all analyses. Females were weighed to the nearest 0.01 g. Clutch mass was calculated as the sum of the masses of individual eggs. Because time between collection and oviposition varied, female mass prior to oviposition was estimated as the sum of clutch mass and female mass after oviposition.

Does Reproductive Effort Vary Seasonally?

In theory, RE is the proportion of available energy that is allocated to reproduction over a biologically meaningful time period (Hirshfield and Tinkle, 1975). Unfortunately, this definition is difficult for empiricists to apply in most cases. We used two estimates of RE: (1) relative clutch mass (clutch mass/body mass of nongravid female) and (2) clutch mass adjusted for total body lipid. Relative clutch mass (RCM) is correlated with RE when the en-

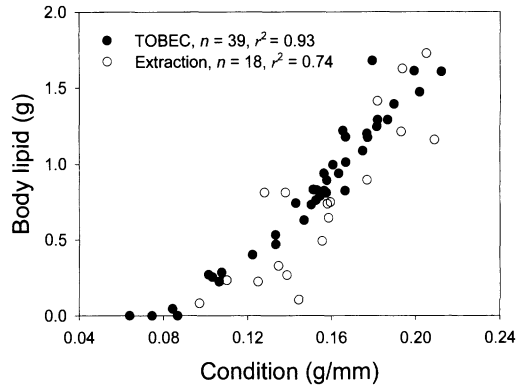


FIG. 1.—Relationship between female condition and total body lipid in *Sceloporus undulatus*. Total body lipid was estimated by total body electrical conductivity and petroleum-ether extraction (Angilletta, 1999).

ergy available for allocation to reproduction is related directly to and organisms' body size, and RCM is often used as estimate of RE (Dunham et al., 1986). Because RCM is a ratio, direct statistical analysis of this variable is inappropriate (Dunham et al., 1986; Packard and Boardman, 1987). Therefore, we used ANCOVA to compare RCM between CL1 and CL2 by assigning clutch mass as the dependent variable and female body mass after oviposition as the covariate. Our second estimate of RE, clutch mass adjusted for total body lipid, is correlated with RE when the energy available for reproduction is related directly to the lipid mass of a female during egg production. Total body lipid was estimated by an index of condition (body mass prior to oviposition/SVL). Condition is a convenient, non-invasive estimator of total body lipid because it is highly correlated with the mass of non-polar lipid in adult females (Fig. 1). Therefore, the residual of clutch mass regressed onto condition should provide a relative measure of the proportion of available energy that is invested in eggs. We used ANCOVA to compare clutch mass with condition as a covariate. SVL was not used as a covariate because it was not correlated with either estimate of RE.

To assess the means by which females altered RE between clutches (i.e., change in clutch size or change in average egg

TABLE 1.—Summary of female and reproductive traits for *Sceloporus undulatus* in first ($n = 12$) and second ($n = 16$) clutches of the year. Masses and SVL are reported in g and mm, respectively. Asterisks denote traits that differed significantly between clutch 1 and clutch 2.

Trait	Clutch 1		Clutch 2	
	Mean (95% CI)	CV	Mean (95% CI)	CV
Female				
Condition	0.17 (± 0.02)	16.7	0.17 (± 0.01)	11.1
SVL	71.9 (± 1.9)	4.1	75.0 (± 3.1)	7.7
Post-laying mass	9.0 (± 0.8)	14.1	9.7 (± 1.0)	18.6
Reproductive				
Number of eggs**	9.1 (± 1.0)	16.5	8.4 (± 1.0)	22.5
Average egg mass	0.43 (± 0.03)	10.7	0.39 (± 0.02)	12.2
Clutch mass**	3.87 (± 0.44)	17.9	3.29 (± 0.40)	22.7
RCM**	0.43 (± 0.03)	7.7	0.34 (± 0.04)	16.3

mass), we used ANCOVA to compare clutch size and average egg mass of females laying their first clutch to those of females laying their second clutch. In both analyses, female SVL was used as a covariate. Also, we used multiple linear regression to calculate partial correlations between female characters (SVL and condition) and reproductive traits (clutch size and average egg mass). Statistical analyses were performed with STATISTICA for Windows (release 5.0 B; Statsoft, 1996). All descriptive statistics are given as mean \pm 95% confidence interval.

Does Egg Mass Affect Offspring Quality?

A total of 129 eggs from 17 females was incubated to determine relationships between egg mass and size and condition of hatchlings. We assigned four eggs to each incubation container by a stratified random design to ensure that no eggs from the same clutch were incubated in the same container. The containers were made of opaque plastic and held approximately 500 g of fine sand. Water content of the medium was established at 1 g per 100 g of sand, yielding a water potential of -400 kPa (Angilletta et al., 2000). We maintained water content gravimetrically by replacing evaporated water every other day. Because a gradient in temperature of 0.5 C was known to exist within our incubator, we shuffled the position of incubation containers within the incubator after each replacement of evaporated water. After approximately 40 days of incubation, eggs

were checked daily to determine the day of pipping. Incubation period was calculated as the number of days from oviposition until pipping. Within 24 h of full emergence from the egg, hatchlings were weighed to the nearest 0.01 mg, and SVL and tail length (TL) were measured to the nearest 1 mm. Effects of maternal identity on incubation period, body mass, SVL, and TL were evaluated with MANCOVA, in which initial egg mass was used as a covariate. The relationships between egg mass and hatchling phenotypes were evaluated by Pearson product-moment correlation. To determine the influence of egg mass on hatchling condition, the semi-partial correlation between egg mass and hatchling mass was computed using the residuals of hatchling mass regressed onto SVL.

RESULTS

Seasonal Variation in Reproductive Effort

We obtained reproductive data for 28 females (Table 1). Laying date of CL1 was earlier for females in better condition ($t = -2.84$, $df = 10$, $P = 0.02$, $r^2 = 0.45$), but laying date of CL2 was not correlated with condition ($t = -0.14$, $df = 14$, $P = 0.88$, $r^2 = 0.00$). Both measures of RE differed significantly between CL1 and CL2, but the direction of change was opposite of that predicted; RE, estimated as either RCM ($MS = 3.69$, $F_{1,25} = 10.06$, $P = 0.004$) or clutch mass adjusted for female condition ($MS = 2.59$, $F_{1,25} = 7.41$, $P = 0.01$), decreased from CL1 to CL2 (Table 1).

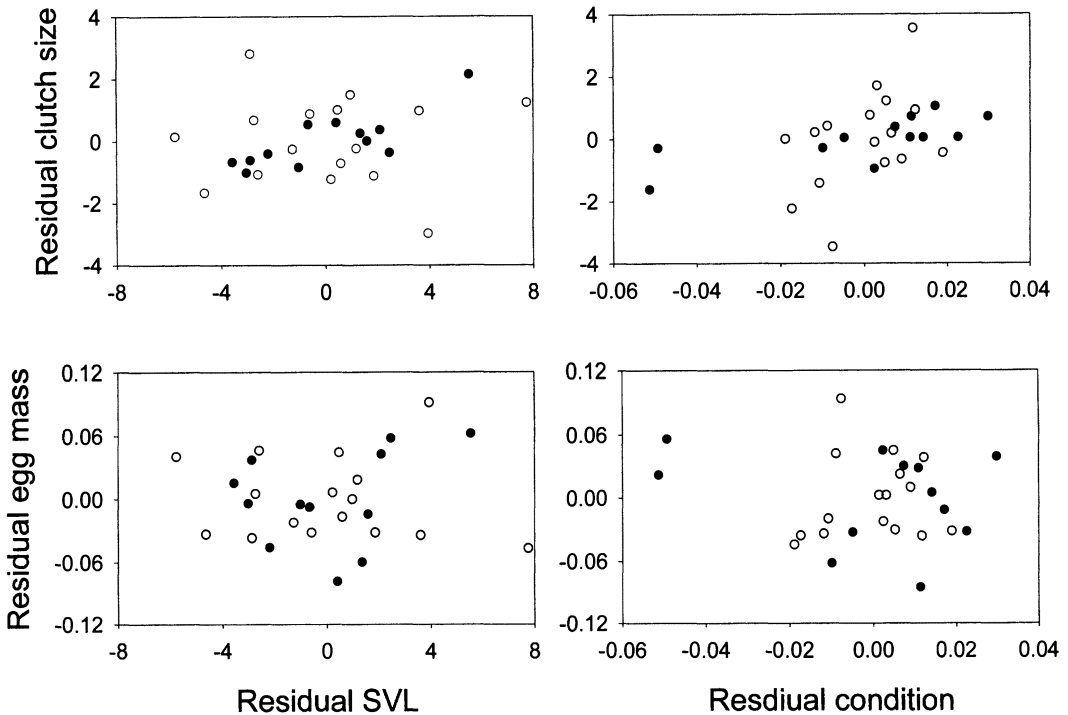


FIG. 2.—Partial correlations between female traits and reproductive traits in *Sceloporus undulatus*. Solid and open circles are data for clutch 1 and clutch 2, respectively. Residual clutch size was significantly correlated with residual SVL ($r^2 = 0.64$) and residual condition ($r^2 = 0.51$) in clutch 1, but not in clutch 2. Residual egg mass was not correlated with residual SVL or residual condition in either clutch.

The difference in RE between clutches was achieved by alteration of both clutch size and egg mass. Females produced 1.3 fewer eggs in CL2 than in CL1 based on adjusted means from ANCOVA (MS = 10.28, $F_{1,25} = 4.89$, $P = 0.04$). Average egg mass of CL1 (0.43 g) was greater than that of CL2 (0.39 g), though the difference was only marginally significant (MS = 0.01, $F_{1,25} = 4.22$, $P = 0.050$). Clutch size was positively correlated with SVL and female condition (Fig. 2). Variation in clutch size exceeded variation in egg mass (Table 1), yet considerable variation in egg mass was observed. Egg mass was more variable among clutches (CV = 10.7 and 12.2 for CL1 and CL2, respectively) than it was within clutches (CV = 5.3 ± 1.5 and 5.8 ± 1.6 for CL1 and CL2, respectively). Average egg mass was not correlated with either SVL or female condition (Fig. 2). A negative correlation between clutch size and egg mass was not evident, even after

both variables were adjusted for effects of female condition (partial correlation: $t = -0.76$, $P = 0.46$, $r^2 = 0.38$).

Effects of Egg Mass on Offspring Quality

Of the 129 eggs, 119 hatched successfully after 49.6 ± 0.3 days of incubation. We excluded 16 of these hatchlings from analyses of hatchling traits because they had highly kinked tails. The observation that all hatchlings with kinked tails were produced by four females and that eggs from the same clutch were incubated separately indicates a genetic basis for the tail defects. MANOVA revealed a significant effect of clutch on hatchling phenotypes (Wilk's $\lambda = 0.07$, $F_{51,298} = 8.36$, $P < 0.001$). For the remaining 103 hatchlings, mean SVL, TL, and body mass were 29.5 ± 0.2 mm, 29.4 ± 0.3 mm, and 0.54 ± 0.01 g, respectively. Larger eggs produced hatchlings of greater size, mass, and condition (Fig. 3). Egg mass affected body mass of

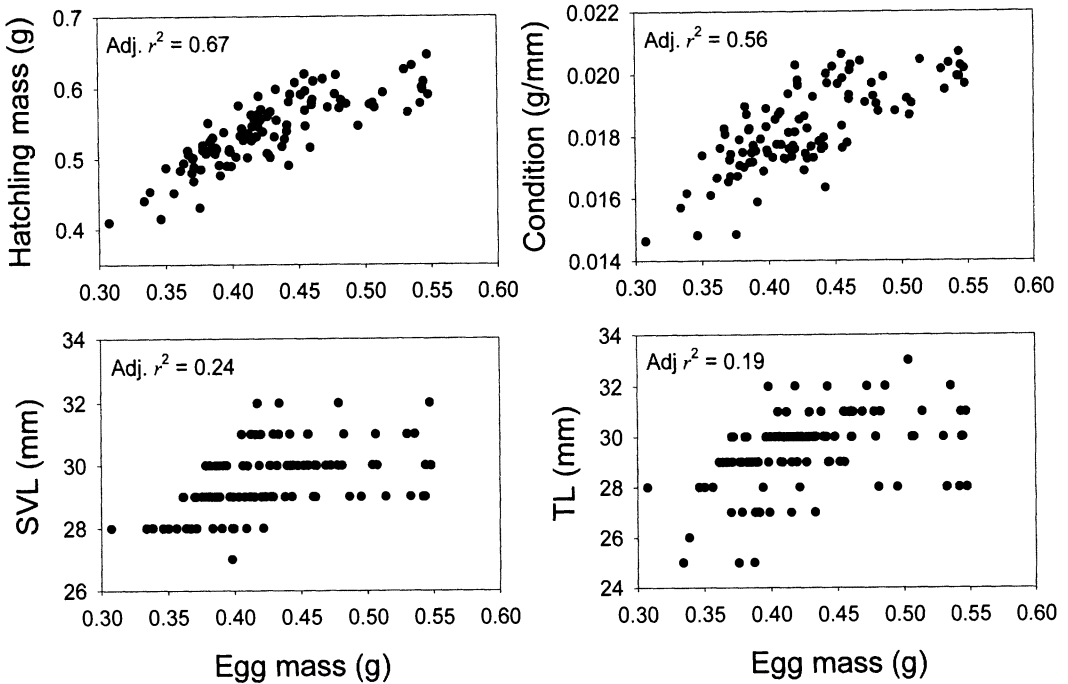


FIG. 3.—Relationship between egg mass and hatchling traits in *Sceloporus undulatus*. Snout-vent length (SVL), tail length (TL), body mass, and condition were all positively related to egg mass at oviposition ($n = 103$, all $P < 0.05$).

hatchlings more than SVL, and this accounts for the positive relationship between egg mass and condition of hatchlings.

DISCUSSION

Seasonal Variation in Reproductive Effort

We predicted that the RE of female lizards would be greater in CL2 than in CL1. This prediction was based on the fact that the risk of mortality during the interval between CL2 and the next reproductive episode (i.e., CL1 of the subsequent year) is much greater than that between CL1 and the next reproductive episode (i.e., CL2). The difference in probabilities of survival to the next reproductive event should favor greater RE in CL2 relative to CL1 (Hirshfield and Tinkle, 1975; Law, 1979; Michod, 1979). The traditional means of assessing a difference in RE would be to compare RCM of CL1 and CL2. Available data on seasonal variation in RCM provide little support for our hypothesis. In Nebraska, *Sceloporus undulatus* had a signif-

icantly lower RCM for CL2 than for CL1 (Jones and Ballinger, 1987). No significant difference in RCM was found for the lesser earless lizard, *Holbrookia maculata* (Droge et al., 1982; Jones and Ballinger, 1987). In *Sceloporus woodi*, clutch mass (wet or dry) did not vary between early and late season clutches (DeMarco, 1989).

The use of RCM as an index of RE has been criticized sharply. Because RCM is a ratio, data on RCM are prone to violate the assumption of normality required for parametric statistics (Dunham et al., 1986; Packard and Boardman, 1987). This problem can be avoided by use of ANCOVA to analyze variation in clutch mass adjusted for total body mass, rather than direct comparison of RCM by ANOVA. Another potential problem is that RCM may not reflect actual caloric investment in reproduction. This is true if the energy content of an egg is not related directly to its size, but for squamates there is good agreement between estimates of RE based on egg masses and those based on calories (Bal-

linger and Clark, 1973; Vitt, 1978). These two problems aside, there is little reason to believe that RCM is an accurate estimator of the proportion of available energy that is allocated to reproduction (Hirshfield and Tinkle, 1975; Tinkle and Hadley, 1975). The implicit assumption in the use of RCM as an estimator of RE is that all of the body mass may potentially be used for reproduction or that body mass is correlated with the amount of energy available for reproduction. The former is certainly not true and the latter is rarely, if ever, established by investigators prior to using RCM as an index of RE (including this study). Clearly, there is a rift between the use of the term RE by theoreticians and the application of the term by empiricists. Relative clutch mass may not be a suitable estimate of RE, and one cannot expect necessarily that trends in RCM will match predictions of theory regarding RE.

We tried to construct a more accurate index of RE to compare with seasonal variation in RCM of *S. undulatus*. Clutch mass reflects the energy invested in a particular episode of reproduction (Vitt, 1978). Condition correlates strongly with available energy in the form of lipid (Fig. 1). Assuming that only the energy stored as lipid can be used to produce a clutch, clutch mass adjusted for condition should be a qualitative index of the proportion of available energy that is invested in reproduction. Interestingly, we observed the same pattern of RE using this index as we did when RCM was used. Both RCM and clutch mass adjusted for female condition were significantly lower in the second clutch than in the first. Not only do our two estimates of RE agree with one another, the seasonal pattern of RE that we observed is the same as that reported for *Sceloporus undulatus* in Nebraska (Jones and Ballinger, 1987).

What might explain the lack of support for the predictions of life history theory regarding RE? One possibility is that neither of our estimates of RE are accurate. Although it is generally agreed that RE is the proportion of available energy that is allocated to reproduction (Congdon et al., 1982; Gadgil and Bossert, 1970; Hirshfield

and Tinkle, 1975), not all investigators agree on what should be considered "available energy." Hirshfield and Tinkle (1975) cautioned that "available energy" should be defined as energy assimilated by an organism over a meaningful biological time period. For a female lizard, a meaningful biological time period over which to sum available energy is that time that elapses between the production of consecutive clutches (inter-clutch interval). Defining "available energy" is more difficult. If available energy is defined as that energy that remains after metabolism is subtracted from the energy budget (Congdon et al., 1982), then our estimate of RE should reflect actual RE. However, many theorists define "available energy" as the total amount of energy assimilated by an organism during a given period, which includes that used in metabolism (Gadgil and Bossert, 1970; Law, 1979; Michod, 1979). According to this interpretation of "available energy", our estimates of RE underestimate actual RE and the magnitude of underestimation increases with increasing inter-clutch interval. Importantly, the inter-clutch interval that preceded CL1 was longer than the one that preceded CL2; CL2 was produced in June, about one month after laying the previous clutch, whereas nine months without reproduction preceded the production of CL2. Consequently, the same energetic investment in eggs in CL2 as in CL1 would represent a much larger RE because of the smaller quantity of available energy during that interval. Therefore, our inability to find support for the prediction of life history theory may be the result of a poor consensus on the use of the term RE and practical considerations that make it difficult to estimate RE as defined by theorists.

Seasonal changes in clutch size have been studied extensively in lizards, but no generalizations can be made from the wealth of data. Consider seasonal variation in clutch size that has been documented in *S. undulatus*. In four populations (Kansas, Nebraska, South Carolina, and New Jersey), females laid fewer eggs in CL2 than in CL1 (Ferguson et al., 1980; Jones and Ballinger, 1987; Tinkle and Ballinger,

1972; this study). However, no difference in clutch size between seasons was found in populations of *S. undulatus* in Texas and Colorado (Tinkle and Ballinger, 1972). Moreover, seasonal patterns of clutch size can vary annually. *Sceloporus woodi* produced smaller clutches in late season during 1985, but not during 1984 and 1986 (DeMarco, 1989). In *Urosaurus ornatus*, females produced fewer eggs in CL2 than in CL1 during 1973, but not during 1974 (Ballinger, 1977).

Variation in Egg Mass

It is important to establish that egg masses measured from oviposited eggs are comparable to those measured from autopsies of females, a method used commonly for determining reproductive traits of lizards. Egg masses determined by autopsies may be underestimates of actual egg masses at oviposition because eggs that are still in the oviduct may not be fully shelled. Egg masses derived from oviposited eggs, such as those reported here, may be overestimates of actual egg masses because squamate eggs can absorb water rapidly from a substrate. We endeavored to weigh eggs as close to oviposition as possible, but we do not know whether eggs gained or lost mass prior to weighing. Fortunately, we can compare our values of average egg mass of females from New Jersey with those observed by other investigators. Niewiarowski and Roosenburg (1993) reported average egg masses of females in New Jersey to be 0.36 g and 0.45 g based on autopsy of gravid females and oviposition in the laboratory, respectively. Our values (0.39 g and 0.43 g for CL1 and CL2, respectively) are within the same range. Other lines of evidence suggest that the variation in egg mass that we observed was not an artifact of our methodology. First, egg mass was positively correlated with SVL, TL, body mass, and condition of hatchlings, indicating that variation in egg mass was, in part, due to differences in energy content of eggs. Second, average egg mass and average hatchling mass from our laboratory study are consistent with those measured by other investigators using autopsies (Fig. 4). It is unlikely that water gain

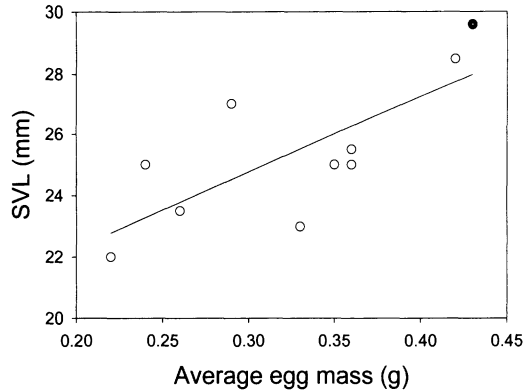


FIG. 4.—A positive correlation between average egg mass and hatchling size in *Sceloporus undulatus* ($n = 10$; $t = 3.20$, $r^2 = 0.56$, $P = 0.01$). Open circles are published values for nine populations (Parker, 1994; tabulated by Tinkle and Dunham, 1986). If only range of hatching sizes was provided, we plotted the midpoint of the range for that population. The filled circle is the datum for our population of *S. undulatus* in New Jersey.

or loss prior to weighing influenced hatchling traits because SVL, TL, and body mass of hatchlings produced in our laboratory were very similar to those of newly-emerged hatchlings collected in New Jersey during 1998 (SVL = 30.8 ± 0.4 mm, TL = 28.6 ± 0.6 mm, body mass = 0.55 ± 0.02 ; $n = 39$; Angilletta, unpublished). For these reasons, we feel that our values of egg mass are reasonably accurate and that the variation in egg mass observed within and among clutches reflects variation in the allocation of energy by females.

We predicted that average egg mass would be greater for CL2 than for CL1. This prediction is based on two assumptions: (1) hatchling quality depends on egg mass, and (2) hatchling quality is an important determinant of hatchling survival. We considered hatchlings that were larger, heavier, and in better condition (i.e., heavier for a given SVL) to be those of higher quality. Based on these criteria, hatchlings from larger eggs are higher in quality than those from smaller eggs (Fig. 3). Does variation in hatchling quality translate to variation in offspring fitness? Some experimental evidence suggests that body size at hatching is an important determinant of hatchling survival in *S. occidentalis* (Siner-

vo, 1993). It is reasonable to expect that hatchlings from larger eggs would enjoy better survival than those from smaller eggs. Yet, we did not observe any difference in average egg mass between CL1 and CL2. This result is consistent with observations of body sizes of yearlings in New Jersey. In spring, two size-classes of yearlings are distinguished readily (Angilletta, personal observation). Both our laboratory and field observations indicate that females do not adjust the allocation of RE to offspring to compensate for the later hatching date of offspring in CL2.

Our observations of reproductive traits in *S. undulatus* were not consistent with the prediction of optimal egg size theory. Classical models demonstrate that females maximize their fitness by producing eggs of a single size (McGinley et al., 1987; Smith and Fretwell, 1974); egg size should not vary within or among clutches. Rather, it is expected that variation in RE among females would be influenced primarily by differences in clutch size. Indeed, average egg mass was far less variable than clutch size (Table 1). However, average egg mass varied considerably among clutches, and the magnitude of this variation was approximately twice that observed in egg mass within clutches ($CV = 5.3 \pm 1.5$ and 5.8 ± 1.6 for CL1 and CL2, respectively). Variation in egg mass within and among clutches was similar to that observed in other reptiles and amphibians (Crump, 1984; Roosenburg and Dunham, 1997; Rowe, 1994).

Why does egg mass vary so much among females? Several hypotheses have been offered to explain variation in the size of eggs. Some of these hypotheses claim that variation in egg size is adaptive. For example, McGinley et al. (1987) demonstrated that spatial variation in environmental conditions can select for production of a range of egg sizes if females are able to assess the specific conditions that their offspring will experience. Also, Temme (1986) noted that differences in genetic quality of offspring can favor variation in seed size within and among females, and this idea applies equally well to eggs as it does seeds. It is not possible for us to tease

apart environmental and genetic factors that favor variable egg size in lizards, but these hypotheses should be given careful scrutiny.

Alternatively, variation in egg size can arise from morphological or physiological constraints. Congdon and Gibbons (1987) proposed that egg size varies among females when pelvic size places a physical constraint on egg size. The pelvic constraint model is supported when a strong correlation between female body size and egg mass is found (e.g., Michaud and Echternacht, 1995). We doubt that pelvic constraint on egg size is a major source of variation in egg mass in *S. undulatus* because average egg mass was not correlated with female SVL. Though, it is possible that pelvic size is only weakly related to SVL, in which case direct measures of pelvic diameter would be required to test this hypothesis adequately. Roosenburg and Dunham (1997) argued that growth of eggs may occur after clutch size is determined if a female experiences an increased rate of energy gain during maturation of follicles. Based on their argument, females that experience better resource environments would produce larger eggs. We do not have data on environmental conditions to test this hypothesis directly. However, females in better condition did not produce larger eggs, indicating that Roosenburg and Dunham's argument is not a plausible explanation in this case.

It is worth considering the possibility that egg size is not subject to natural selection in some populations of *S. undulatus*. We have shown that greater egg mass results in larger body size and better condition at hatching. Often, it is assumed that larger hatchling size confers greater survival, but this assumption may be unfounded (Congdon et al., 1999). Body size at hatching may not affect survival at all or it may only affect survival in some years. In the New Jersey population of *S. undulatus*, Niewiarowski (1992) was unable to detect a difference in winter survival between hatchling size classes during winters of 1986–1987 to 1991–1992. However, extraordinarily low survival of hatchlings was observed in this population during the

winter of 1997–1998 (B. W. Grant, personal communication), presumably because of extremely warm conditions created by El Niño. If the relatively high mortality of 1997–1998 was related to the energetic stress during hibernation, larger hatchlings should have exhibited greater winter survival. The strength of selection on hatchling body size could be quantified through experimental manipulation of offspring size (Sinervo, 1996). Furthermore, supplemental feeding studies can be used to assess whether females would alter egg size if given more energy for reproduction. Our understanding of reproductive allocation would be enhanced by a concerted effort to examine relative costs and benefits of reproductive strategies to both parent and offspring.

Acknowledgments.—Animals were collected with permission from the NJDEP Division of Fish, Game, and Wildlife. All work was performed in accordance with the regulations and recommendations of the Institutional Animal Care and Use Committee of the University of Pennsylvania. Financial support was provided by a Sigma Xi Grant-in-Aid of Research. We thank P. Niewiarowski for providing comments on an earlier version of this manuscript.

LITERATURE CITED

- ANGILLETTA, M. J., JR. 1999. Estimating body composition of lizards from total-body electrical conductivity and total-body water. *Copeia* 1999:587–595.
- ANGILLETTA, M. J., JR., R. S. WINTERS, AND A. E. DUNHAM. 2000. Thermal effects on the energetics of lizard embryos: implications for hatchling phenotypes. *Ecology* 81:2957–2968.
- BALLINGER, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology* 58:628–635.
- BALLINGER, R. E., AND D. R. CLARK, JR. 1973. Energy content of lizard eggs and the measurement of reproductive effort. *Journal of Herpetology* 7: 129–132.
- BROWN, G. P., AND P. J. WEATHERHEAD. 1997. Effects of reproduction on survival and growth of female northern water snakes, *Nerodia sipedon*. *Canadian Journal of Zoology* 75:424–432.
- CONGDON, J. D., A. E. DUNHAM, AND D. W. TINKLE. 1982. Energy budgets and life histories of reptiles. Pp. 233–271. *In* C. Gans and F. H. Pough (Eds.), *Biology of the Reptilia*, Vol. 16B. Academic Press, New York, New York, U.S.A.
- 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 U.S.A.* 84:4143–4147.
- CONGDON, J. W., R. W. 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* (Berlin) 121:224–235.
- CRUMP, M. L. 1984. Intraclutch egg size variability in *Hyla crucifer* (Anura: Hylidae). *Copeia* 1984: 302–308.
- DEMARCO, V. G. 1989. Annual variation in the seasonal shift in egg size and clutch size in *Sceloporus woodi*. *Oecologia* (Berlin) 80:525–532.
- DROGE, D. L., S. M. JONES, AND R. E. BALLINGER. 1982. Reproduction of *Holbrookia maculata* in western Nebraska. *Copeia* 1982:356–362.
- DUNHAM, A. E., P. J. MORIN, AND H. M. WILBUR. 1986. Methods for the study of reptile populations. Pp. 331–385. *In* R. B. Huey (Ed.), *Biology of the Reptilia*, Vol. 16B. Alan R. Liss, New York, New York, U.S.A.
- FERGUSON, G. W., C. H. BOHLEN, AND H. P. WOOLLEY. 1980. *Sceloporus undulatus*: comparative life history and regulation of a Kansas population. *Ecology* 61:313–322.
- GADGIL, M., AND W. H. BOSSERT. 1970. Life historical consequences of natural selection. *American Naturalist*. 104:1–24.
- GREGORY, P. T., AND K. M. SKEBO. 1998. Trade-offs between reproductive traits and the influence of food intake during pregnancy in the garter snake, *Thamnophis elegans*. *American Naturalist* 151:477–486.
- HEULETT, S. T., S. C. WEEKS, AND G. K. MEFFE. 1995. Lipid dynamics and growth relative to resource level in juvenile eastern mosquitofish (*Gambusia holbrooki*: Poeciliidae). *Copeia* 1995:97–104.
- HIRSHFIELD, M. F., AND D. W. TINKLE. 1975. Natural selection and the evolution of reproductive effort. *Proceedings of the National Academy of Sciences U.S.A.* 72:2227–2231.
- JONES, S. M., AND R. E. BALLINGER. 1987. Comparative life histories of *Holbrookia maculata* and *Sceloporus undulatus* in western Nebraska. *Ecology* 68:1828–1838.
- LANDWER, A. J. 1994. Manipulation of egg production reveals costs of reproduction in the tree lizard (*Urosaurus ornatus*). *Oecologia* (Berlin) 100:243–249.
- LAW, R. 1979. Optimal life histories under age-specific predation. *American Naturalist* 114:399–417.
- MADSEN, T., AND R. SHINE. 1996. Determinants of reproductive output in female water pythons (*Liasis fuscus*: Pythonidae). *Herpetologica* 52:146–159.
- MCGINLEY, M. A., D. H. TEMME, AND M. A. GEBER. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *American Naturalist* 130:370–398.
- MICHAUD, E. J., AND A. C. ECHTERNACHT. 1995. Geographic variation in the life history of the lizard *Anolis carolinensis* and support for the pelvic constraint model. *Journal of Herpetology* 29:86–97.
- MICHOD, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. *American Naturalist* 113:531–550.
- NIEWIAROWSKI, P. H. 1992. Ecological and Evolu-

- tionary Sources of Geographic Variation in Individual Growth Rates of the Lizard *Sceloporus undulatus* (Iguanidae). Ph.D. Dissertation, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.
- 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.
- . 1998. Effects of mortality risk and growth on a model of reproductive effort: why the Shine and Schwarzkopf model is not general. *Evolution* 52:1236–1241.
- NIEMIAROWSKI, P. H., AND W. M. ROSENBERG. 1993. Reciprocal transplant reveals sources of geographic variation in growth rates of the eastern fence lizard, *Sceloporus undulatus*. *Ecology* 74:1992–2002.
- NILSSON, J.-A., AND E. SVENSSON. 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society of London B* 263:711–714.
- PACKARD, G. C., AND T. J. BOARDMAN. 1987. The misuse of ratios to scale physiological data that vary allometrically with body size. Pp. 216–236. *In* M. E. Feder, A. F. Bennett, W. W. Burggren, and R. H. Huey (Eds.), *New Directions in Ecological Physiology*. Cambridge University Press, Cambridge, U.K.
- PIANKA, E. R., AND W. S. PARKER. 1975. Age-specific reproductive tactics. *American Naturalist* 109:453–464.
- REZNICK, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44:257–267.
- RICKLEFS, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. *American Naturalist* 111:453–478.
- ROSENBERG, 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. W. 1994. Egg size and shape variation within and among Nebraskan painted turtles (*Chrysemys picta bellii*) populations: relationships to clutch and maternal body size. *Copeia* 1994:1034–1040.
- SCHWARZKOPF, L. 1993. Costs of reproduction in water skinks. *Ecology* 74:1970–1981.
- SHINE, R. 1980. “Costs” of reproduction in reptiles. *Oecologia* (Berlin) 46:92–100.
- SHINE, R., AND L. SCHWARZKOPF. 1992. The evolution of reproductive effort in lizards and snakes. *Evolution* 46: 62–75.
- SHINE, R., L. SCHWARZKOPF, AND M. J. CALEY. 1996. Energy, risk, and reptilian reproductive effort: a reply to Niewiarowski and Dunham. *Evolution* 50:2111–2114.
- SINERVO, B. 1993. The effect of offspring size on physiology and life history. *BioScience* 43:210–218.
- . 1996. Testing adaptation using phenotypic manipulations. Pp. 149–185. *In* M. W. Rose and G. V. Lauder (Eds.), *Adaptation*. Academic Press, New York, New York, U.S.A.
- SMITH, C. C., AND S. D. FRETWELL. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499–506.
- STATSOFT, INC. 1996. *STATISTICA for Windows* [Computer program manual]. Statsoft, Inc., Tulsa, Oklahoma, U.S.A.
- STEARNS, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- . 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford, U.K.
- TAYLOR, H. M., R. S. GOURLEY, C. E. LAWRENCE, AND R. S. KAPLAN. 1974. Natural selection of life history attributes: an analytical approach. *Theoretical Population Biology* 5:104–122.
- TEMME, D. H. 1986. Seed size variability: a consequence of variable genetic quality among offspring? *Evolution* 40:414–417.
- TINKLE, D. W., AND R. E. BALLINGER. 1972. *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. *Ecology* 53:570–584.
- TINKLE, D. W., AND A. E. DUNHAM. 1983. Demography of the tree lizard, *Urosaurus ornatus*, in central Arizona. *Copeia* 1983:585–598.
- . 1986. Comparative life histories of two syntopic sceloporine lizards. *Copeia* 1986:1–18.
- TINKLE, D. W., A. E. DUNHAM, AND J. D. CONGDON. 1993. Life history and demographic variation in the lizard *Sceloporus graciosus*: a long-term study. *Ecology* 74:2413–2429.
- TINKLE, D. W., AND N. F. HADLEY. 1975. Lizard reproductive effort: caloric estimates and comments on its evolution. *Ecology* 56:427–434.
- VITT, L. J. 1978. Caloric content of lizard and snake (Reptilia) eggs and bodies and the conversion of weight to caloric data. *Journal Herpetology* 12:65–72.
- WEEKS, S. C. 1996. The hidden cost of reproduction: reduced food intake caused by spatial constraints in the body cavity. *Oikos* 75:345–349.
- WINKLER, D. W., AND K. WALLIN. 1987. Offspring size and number: a life history model linking effort per offspring and total effort. *American Naturalist* 129:708–720.

Accepted: 30 September 2000
Associate Editor: Carl Anthony