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ANNUAL VARIATION OF LITTER SIZE AND OFFSPRING SIZE IN A VIVIPAROUS SKINK

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ABSTRACT: This study examines variation in reproductive characteristics over 2 yr in the viviparous Australian skink *Eulamprus tympanum*. Litter size ($\bar{x} = 2.8$) was positively related to female body size in both years of this study, and there was no variation in the form of this relationship between years. However, offspring size, and the relationship of offspring size to female body size varied from 1989 to 1990. In most other species of lizard that have been examined, offspring size either does not change from year to year or changes concurrently with changes in clutch (litter) size. Here I suggest that because litter size is small, and additional offspring apparently cannot be produced without substantial growth by the female ($\approx 11\%$ of body length), the response to exogenous variables affecting reproductive investment may be mostly in terms of offspring size.

Key words: Skinks; *Eulamprus tympanum*; Reproductive characteristics; Clutch size; Offspring size; Annual variation

LIFE-HISTORY tactics were defined by Stearns (1976:4) as a "series of co-adapted traits designed, by natural selection, to solve particular ecological problems." Comparisons of life-histories of reptiles among species and among higher taxonomic levels have suggested that, in addition to local adaptation, plasticity of response to environmental variation, physiological constraints, and phylogenetic constraints all play important roles in determining aspects of the life-history (Dunham et al., 1988). Documentation of annual variation in reproductive characteristics within populations of reptiles has helped to elucidate some of the constraints influencing life-history tactics at a micro-evolutionary level. Many groups of lizards show variation in clutch size and/or frequency in response to food availability (e.g., various oviparous Phrynosomidae: Ballinger, 1977; Ferguson et al., 1980, 1990; Jones et al., 1987; Laurie, 1990; Tinkle and Ballinger, 1972; Vinegar, 1975). In some of these species, variation in offspring size occurs concomitantly with variation in litter size (e.g., Ferguson et al., 1990; Laurie, 1990). In species in which clutch frequency is fixed at 1/yr, as in most snakes and some lizards, variation in clutch size and/or offspring

size occurs in response to environmental variation (Seigel and Fitch, 1985; Vinegar, 1975). In species with fixed clutch sizes, such as anoline (Polychridae) and gekkonid lizards, reproductive variation in response to resource variation occurs only in clutch frequency (Andrews and Rand, 1974; Guyer, 1988; Vitt, 1986). There have been few studies of annual variation in reproductive characteristics of viviparous reptiles, but they are apparently constrained to a single reproductive episode per season, or less (Ballinger, 1983). As in many oviparous species, studies of viviparous squamate reptiles have demonstrated annual variations in litter size (Reznick and Sexton, 1986; Seigel and Fitch, 1985; Zweifel and Lowe, 1966). A few studies of viviparous squamates have also found variations in offspring size either in addition to variation in clutch size (Andren and Nilsson, 1983) or independent of it (Bauwens and Verheyen, 1987; Brodie and Ducey, 1989). This paper documents annual variation in reproductive characteristics of the viviparous skink *E. tympanum*. To determine where most variability occurs among years, I examine relationships between female body size, litter size, and mean mass of individual offspring. I then discuss how environmental variation in food availability and weather may have influenced these variables.

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METHODS

I conducted this study from January 1989–March 1991 in Kanangra Boyd National Park (33°52' S, 150°3' E, elevation = 1220 m), in the Blue Mountains 110 km southwest of Sydney, in New South Wales, Australia. Southern water skinks (*Eulamprus tympanum*) used in this study were collected between late January and mid-February in 1989 and 1990, late in the reproductive season. I collected skinks by noosing from open, moist eucalypt woodland in one of five locations within the Park. These locations were all ≤ 5 km from one another, and I assume that reproductive characteristics among areas were similar. Snout–vent length (SVL), tail length (to the nearest 1 mm), and mass (to the nearest 0.1 g) were recorded at the time of capture. I collected a total of 93 females (48 in 1989 and 45 in 1990). I brought these females to the laboratory at the University of Sydney, where they were housed individually in glass terraria, and where they were provided with water and incandescent lights for basking. They were fed commercially-prepared cat food twice a week. No female was in the laboratory for more than 21 days before giving birth, and it is unlikely that the feeding regime influenced offspring or litter size. As all females were kept under the same conditions for at least 2 wk, variability in measures of maternal size and offspring size is unlikely to have been influenced by hydration status of the females. Terraria were checked daily for the presence of neonates. Date of birth and mass (to the nearest 0.1 g) of the female after parturition, number of offspring, and the mass and SVL of each neonate were recorded as soon as neonates were seen.

I used these data to determine relative clutch mass (RCM: the ratio of litter mass to the mass of female post-parturition), effective relative clutch mass (ERCM: the ratio of mass lost due to parturition, including offspring, membranes and liquid, to the mass of the female post-parturition; Brodie, 1989), and litter size/body size relationships. I used ANCOVA to compare size-dependent variables between years.

TABLE 1.—Body size, litter size, and offspring size of female southern water skinks kept in captivity until parturition, in 1989 ($n = 48$) and 1990 ($n = 45$).

Variable	Mean \pm SD	
	1989	1990
Maternal SVL (mm)	90.5 \pm 3.0	91.4 \pm 3.4
Maternal mass before birth (g)	12.5 \pm 2.0	13.0 \pm 1.7
Maternal mass after birth (g)	9.5 \pm 1.4	9.6 \pm 1.2
Mean offspring number	2.8 \pm 1.1	2.7 \pm 0.9
Mean litter mass (g)	2.1 \pm 0.8	2.2 \pm 0.7
Mean individual offspring mass (g)	0.75 \pm 0.1	0.83 \pm 0.1*
Mean RCM	0.222 \pm 0.1	0.233 \pm 0.1
Mean effective RCM	0.354 \pm 0.2	0.359 \pm 0.1

* Years significantly different, $t = 5.6$, $df = 91$, $P < 0.001$.

Variances among treatments were not significantly different (F_{\max} tests, $P > 0.05$; Sokal and Rohlf, 1981). Differences among variables were considered to be significant if $P < 0.05$, and I discuss differences with values of P between 0.1 and 0.05.

RESULTS

Means and standard deviations of various reproductive parameters for 93 females collected in 2 yr are shown in Table 1. There was a significant positive correlation between SVL of the mother and number of offspring, and there was no significant difference between years in either slope or elevation of this relationship (ANCOVA, $F_{1,86 \text{ slopes}} = 0.141$, $P > 0.05$, $F_{1,85 \text{ elevations}} = 0.733$, $P > 0.05$; overall relationship: $y = 0.10x - 6.6$; $r^2 = 0.11$, $P < 0.002$; Fig. 1 top). On average, litter size increased by one neonate for every 9.7 mm SVL. Similarly, there was a significant positive correlation between SVL of the mother and mass of the litter, and there was no significant difference between years in either slope or elevation of this relationship (ANCOVA, $F_{1,86 \text{ slopes}} = 2.0$, $P > 0.05$, $F_{1,86 \text{ elevations}} = 0.111$, $P > 0.05$; overall relationship was $y = 0.10x - 7.3$; $r^2 = 0.18$, $P < 0.002$; Fig. 1 bottom).

There was no significant correlation between SVL of the mother and RCM in either year of the study. When both years were combined, this correlation was pos-

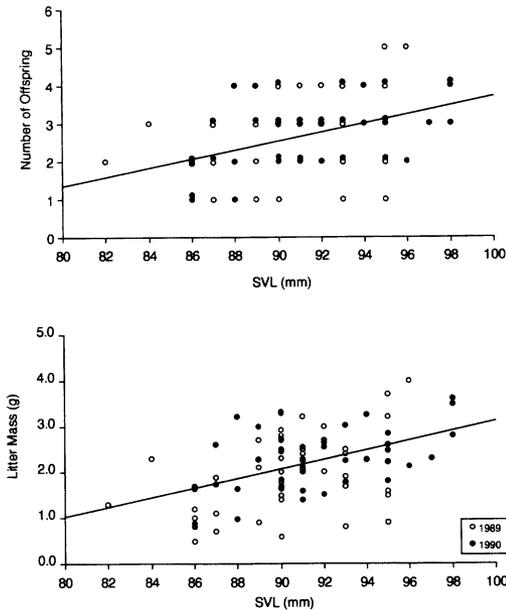


FIG. 1.—The relationship of (top) litter size (number of offspring) to maternal body size (SVL) and (bottom) litter mass (g) to maternal body size (SVL) in *E. tympanum* in 1989 and 1990, combined.

itive and marginally significant, but as SVL explained only 4% of the variation in RCM, this correlation may not be biologically important (1989 relationship: $y = 0.006x - 0.36$, 1990 relationship: $y = 0.004x - 0.15$; overall relationship: $y = 0.005x - 0.26$; $r^2 = 0.04$, $P = 0.07$; Fig. 2). There was a significant difference between years in the slope of the relationship between SVL and individual offspring mass (ANCOVA, $F_{1,86}^{\text{slopes}} = 4.5$, $P < 0.05$; Fig. 3 top). This relationship was significant in 1989 ($y = 0.017x - 0.75$; $r^2 = 0.15$, $P < 0.01$), but was not significant in 1990 ($y = 0.001x - 0.67$; $r^2 = 0.01$, $P > 0.05$), the year in which offspring were larger. The slope of the relationship between number and mass of offspring was not significantly different in 1989 and 1990, but the elevations were significantly different (ANCOVA, $F_{1,86}^{\text{slopes}} = 1.4$, $P > 0.05$, $F_{1,86}^{\text{elevations}} = 12.9$, $P < 0.001$). Examining each year separately showed that this relationship was significant and negative in 1990 ($y = 0.034x - 0.92$; $r^2 = 0.13$, $P < 0.02$; Fig. 3 bottom) but not significant in 1989 ($y = 0.006x - 0.77$; $r^2 = 0.003$, $P > 0.05$; Fig. 3 bottom).

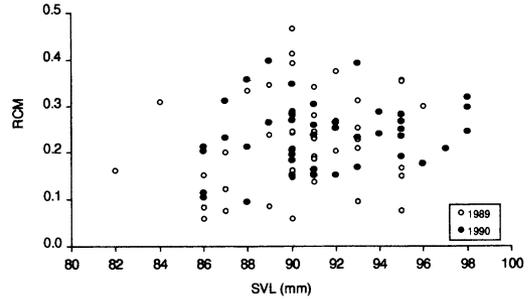


FIG. 2.—The relationship between maternal body size (SVL in mm) and Relative Clutch Mass (RCM) in southern water skinks in 2 yr combined (1989 and 1990).

Correcting for maternal SVL (using residuals of the regression of SVL versus clutch size on the x-axis, and offspring size on the y-axis as recommended by Ford and Seigel, 1989) did not change this result; the relationship between litter size and offspring size (corrected for maternal SVL) was still negative and significant in 1990 ($r^2 = 0.16$, $P < 0.01$) and not significant in 1989 ($r^2 = 0.03$, $P > 0.05$).

DISCUSSION

As in most squamate reptiles that have been studied (reviewed by Seigel and Ford, 1987), there was a positive relationship between body size and litter size (number and mass) in *E. tympanum*. The slope of these relationships in *E. tympanum* did not vary between years. Most theoretical treatments of offspring size versus number suggest that litter or clutch size should be more variable than offspring size (e.g., Brockelman, 1975; Smith and Fretwell, 1974; Winkler and Wallin, 1987), and empirical observations, particularly in birds, tend to support this (e.g., Brockelman, 1975). However, there was no significant annual variation in litter size in the 2 yr of this study. In contrast, there was significant annual variation in offspring size: in 1989, offspring were significantly smaller than in 1990. Variation in offspring size, with no concomitant variation in litter or clutch size, has rarely been observed in reptiles (Ford and Seigel, 1989), and I am aware of only two examples of this phenomenon. Offspring size varied from year

to year in *Lacerta vivipara* in response to food availability, with no variation in litter size (adjusted for female size) (Bauwens and Verheyen, 1987). Also, there was significant variation in offspring size in the viviparous snake *Storeria occipitomaculata*, and litter size remained constant (Brodie and Ducey, 1989). Other studies have revealed annual variation in litter size as well as offspring size. European adders (*Vipera berus*) produced smaller offspring in response to lowered food availability, and these smaller offspring occurred in smaller litters (Andren and Nilson, 1983). Also, in *Uta stansburiana*, *Sceloporus undulatus*, *S. graciosus*, and *S. woodi*, offspring size is smaller, and litter size larger, in early clutches compared to late clutches, and this has been linked to monthly variations in food availability (DeMarco, 1989; Derickson, 1976; Nussbaum, 1981).

In addition to offspring size variation per se, the relationship between offspring size and female size varied from year to year in *E. tymanum* (Fig. 1). In 1989, when offspring were small, offspring size increased with female SVL. In 1990, when offspring were larger, there was no relationship between maternal size and offspring size. If large offspring have higher fitness, each female may "attempt" to produce the largest possible offspring. Therefore, if larger females have more available resources (e.g., more stored energy), they may be able to produce relatively larger offspring than small females in "bad years" (Stewart, 1979). Presumably, in 1990 there was sufficient energy available for all females to produce large offspring, or, alternatively, only those females with sufficient stored resources to produce large offspring reproduced in 1990. This distinction may be important, because in a trapped population near the area where females for this study were collected, fewer females (17% of mature females) reproduced in 1990 than reproduced in 1989 (58% of mature females) (Schwarzkopf, 1991).

In *E. tymanum*, reproductive frequency cannot be increased above one reproductive episode per season, because the gestation period is relatively long and the

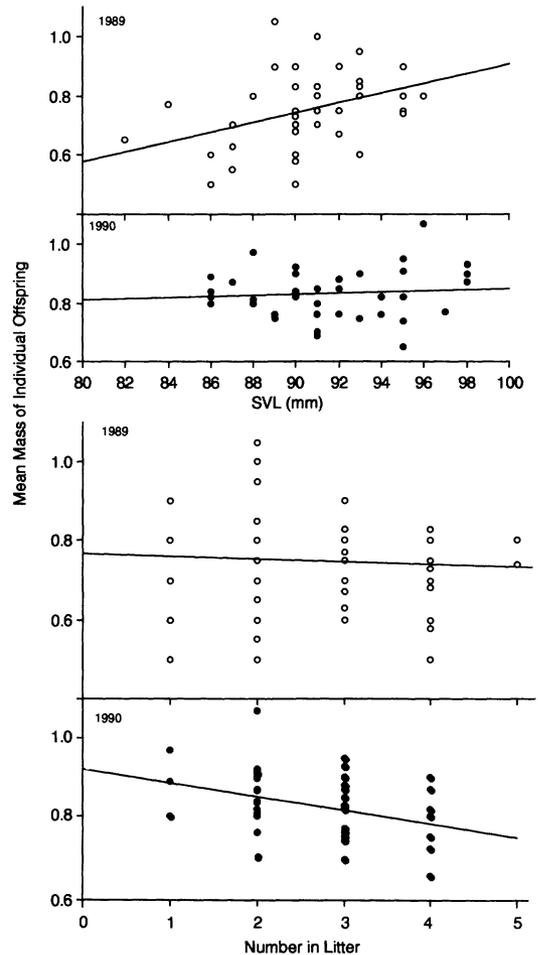


FIG. 3.—The relationship between (top) maternal body size (SVL in mm) and individual offspring mass (g), and (bottom) litter size (number of offspring) and individual offspring mass in southern water skinks, shown separately for 2 yr (1989 and 1990).

activity season is relatively short. In addition, the relationship between litter size and maternal size in *E. tymanum* was not very steep (slope = 0.1). This suggests that a large increment of growth (≈ 10 mm or 11% of the mean mature SVL) is required before females are able to produce an extra offspring. Perhaps because litter size is small, and strongly constrained by body size, the response to exogenous variables affecting reproductive investment is mostly in terms of offspring size rather than offspring number or frequency of litter production. This type of constraint may

also have been important in *Lacerta vivipara* in which a size increase of ≈ 4 mm (8% of the mean mature SVL) is required before females can increase clutch size by a single offspring (derived from data in Bauwens and Verheyen, 1987). In contrast, litter size increases by one embryo for every 3 mm of body length in mature females of *Sceloporus jarrovi* and *S. poinsetti* (4% of mean mature body size in *S. jarrovi* and 3% in *S. poinsetti*) (Ballinger, 1973). Similar "fractional offspring size" arguments have been made to explain changing offspring size in snakes producing small numbers of offspring (Brodie and Ducey, 1989; Nussbaum, 1981).

If there is a limited allocation of energy for reproduction, the amount of energy invested in individual offspring is determined by a trade-off between the allocation of resources between offspring size and offspring number, and we expect a negative relationship between these two variables (Brockelman, 1975; Smith and Fretwell, 1974). There was a weak negative relationship between offspring size and number in *E. tympanum* (corrected for maternal SVL as recommended by Ford and Seigel, 1989), and this relationship was significant in 1990, but not in 1989. In 1990, larger females produced more, relatively smaller offspring. In 1989, when offspring size was smaller, this relationship was not significant, suggesting that the trade-off did not occur; all energy appeared to be devoted to increasing offspring size. If there is variation between individuals in terms of the ability to acquire resources, and the variation in energy acquired is greater than the variation in the fraction of energy allocated to both number and size of offspring, then some individuals may be able to allocate energy both to increase size and increase numbers of offspring, while other individuals can do neither (van Noordwijk and de Jong, 1986). Therefore, variation in energy intake among females may obscure this relationship, although the trade-off between number and size of offspring still occurs. A negative relationship between size and number of offspring has been recorded in four of seven species of lizards (reviewed by Ford and Seigel, 1989).

There was no significant relationship between maternal size and RCM in either year of the study, although these data were marginally correlated when the data from 2 yr were combined. This suggests that the relative commitment of resources to reproduction does not change significantly with body size, and possibly with age, and also remains constant from year to year. Constant RCM with size and/or age has been observed in many lizards and snakes (e.g., Shine, 1980; reviewed by Pianka and Parker, 1975; Seigel and Ford, 1987). The constancy of RCM compared to all other reproductive variables (reproductive frequency, clutch size, and offspring size) prompted DeMarco (1989) to conclude that perhaps it was RCM, rather than other features of the life-history, that was optimized by selection. Studies of variation in RCM across species suggest that RCM may be optimized by selection on body size and shape related to a variety of characteristics of the biology of lizards and snakes, such as foraging mode and/or escape tactics (Vitt and Congdon, 1978; Vitt and Price, 1982). At least in the 2 yr of this study, it appears that in *E. tympanum*, it is offspring size, rather than litter size, litter frequency, or RCM, that responds to variations in resource availability.

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