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Among Clutch Variation in Reproductive Output and Egg Size in the Wall Lizard (*Podarcis muralis*) from a Lowland Population of Northern Spain

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ABSTRACT.—Among clutch variation in reproductive output and egg size of the wall lizard (*Podarcis muralis*) are reported. Females under semi-natural conditions laid eggs from late April to early July. The smallest reproductive female in our sample was 51.2 mm SVL, and all females larger than this size produced at least one clutch per season. Of the 53 females, 13 laid three clutches, 27 laid two clutches, and 13 laid one clutch. Females that laid only one clutch were smaller than those laying two or three clutches. Oviposition frequency was 16.8–54.7 (mean = 30.4 ± 1.4) d between first and second clutches, and 18.6–32.1 (mean = 25.2 ± 1.2) d between second and third clutches. Clutch size was 3–11 (mean = 5.0 ± 0.2) for first clutch and 2–6 for second (mean = 3.9 ± 0.2) and third (mean = 4.0 ± 0.3) clutches, and was positively correlated with female SVL. Although there was a trade-off between egg mass and the total number of eggs produced per season, eggs from first clutches were larger than eggs from subsequent clutches. In all three clutches, an increase in egg mass was accommodated by a decrease in egg length. There were both among clutch and among individual variation in clutch size and among clutch variation in egg mass, but no individual dependence of egg mass was found.

The wall lizard, *Podarcis muralis*, is one of most conspicuous lizard species in many localities of central and southern Europe (Arnold and Burton, 1978). However, except for few reports (Barbault and Mou, 1986, 1988; Mou and Barbault, 1988; Edsman, 1990), data on among clutch variation in reproductive output and egg size are limited. The data without detailed descriptions of each clutch may be less informative, because reproductive output may differ considerably among clutches in many multiple-clutched lizards, including *P. muralis* (Barbault and Mou, 1986, 1988; Edsman, 1990; Belakovic et al., 1996). In addition, measurements of reproductive outputs need to be carried over a time span appropriate to account for different sources of energy for reproduction (Doughty and Shine, 1998).

In animals lacking post-hatching parental cares, egg size is determined by offspring number (Smith and Fretwell, 1974). As a general principle, later clutches might contain larger eggs, as offspring born later in the active season could have lower opportunities for growth (Ferguson and Snell, 1986). However, in iteroparous lizards the interaction between egg size and clutch order can be complex. For instance, Sinner and Doughty (1996) presented evidence of seasonal changes in optimal offspring size of side-blotched lizards, and Ferguson and Snell (1986) reported changes in the balance between

egg size and number from first to second clutches in the lizard *Sceloporus undulatus garmani*.

Previous studies of squamate reptiles have showed that many reproductive traits exhibit phenotypic plasticity, and resource availability may explain much of the variance in life history traits (Ballinger, 1983; Ford and Seigel, 1989; Seigel and Ford, 1991). In lacertid lizards the first clutch is mainly constructed from stored reserves, but later clutches depend on current energy intake (Braña et al., 1991). In nature, lizards are subjected to conflicting energy demands, such as those for reproduction, escaping predators, and foraging and basking activities. Thus, the relationships among clutch size, clutch number, egg size, and annual fecundity can be much more complicated than expected. However, under semi-natural conditions, the substantial availability of food, the absence of predators, and the suitable thermal environments allow the study of these relationships without complications arising from the conflicting energetic demands in nature.

Data presented here were gathered from reproductive *P. muralis* females that were captured from the field and then kept under semi-natural conditions in the laboratory (see below for details). Our aims are to determine (1) among clutch variation in clutch size and egg size and mass, (2) the relationships among clutch size, egg mass, and female SVL, and (3) the possible

trade-off between egg mass and annual fecundity (the total number of eggs produced per season).

MATERIALS AND METHODS

This study was conducted in Oviedo, Asturias (northern Spain), from mid-March to early July 1996. This period covered the whole breeding season of *P. muralis* (Braña et al., 1992).

Fifty-three adult females and 10 adult males were collected from various localities near Oviedo, on 13–25 April 1996. The lizards were then brought to the University of Oviedo, where they were marked individually by toe-clipping for future identification. All females were palpated for judging reproductive conditions. Males and females with various sized yolked follicles were housed in a $2.2 \times 1.6 \times 0.5$ m (length \times width \times height) plastic enclosure. The enclosure was built in a greenhouse at the top of a building. To mimic natural conditions, we placed bricks, debris, blocks of wood, grasses, moist soil, and water dishes into the enclosure. Supplementary heating was provided by a 300 W light bulb suspended approximately 400 mm above the enclosure floor.

Females bearing oviductal eggs were assigned randomly to terraria (400×500 mm) placed in a room. At no time were more than five lizards housed in a single terrarium. Each terrarium contained 2–3 small water dishes and rocks. A 100×150 mm rock-covered wood box filled with moist soil served as the egg laying site. Heating was provided by a 100 W light bulb suspended 150 mm above the terrarium floor.

The greenhouse and room were illuminated with a natural photoperiod, but the lights were switched on at 0800 on a 12 light:12 dark cycle. Lizards in both places were exposed to a natural light cycle and some direct sunlight, and could regulate their body temperatures within their voluntary range during the photophase (Braña et al., 1991; Braña, 1993) and cool to air temperature when the lights were switched off. We fed lizards with mealworms (larvae of *Tenebrio molitor*), crickets, and water with mixed vitamins and minerals. Lizards in the enclosure completed an oviposition cycle similar to the cycle described for neighboring populations in the field (Braña, 1984; Braña et al., 1992).

Terraria were checked at least five times every day for the presence of eggs, and more frequently when there was an evidence of egg laying so that the eggs were usually collected within a few minutes after laying. Postpartum females and their eggs were removed from the terraria for weighing and measuring, and females were then moved to the enclosure. Body measurements of postpartum females included snout-vent length (SVL), tail length (TL), and body

mass. Eggs were weighed to the nearest 0.001 g, and egg length and width were measured to the nearest 0.05 mm.

The enclosure was checked daily. Females bearing oviductal eggs were noosed and then brought to the indoor terraria. Females usually laid and buried eggs in moist soil substrates, but they occasionally laid eggs on the dry floor of the terrarium. Except for the records of clutch size, we excluded from analyses the eggs that were laid outside the soil substrate, because they were usually abnormally lighter and could not be further incubated due to the loss of water.

We calculated RCM (relative clutch mass) using two methods: RCM1 was calculated by dividing clutch mass by the female postpartum mass (Shine, 1992), and RCM2 by dividing clutch mass by total female (clutch plus body) mass (Vitt and Price, 1982; Seigel and Fitch, 1984). Because the values of RCM are highly dependent on the tail mass, for tail-mutilated lizards, we considered their body mass as the sum of the tailless lizard mass plus the recently autotomized tail mass.

All data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances (F-max test), and transformed when necessary to achieve the conditions for using parametric tests. We used one-way ANOVA to determine whether there were differences in the size (SVL) of females, in the time interval among clutches, and in the characteristics of the clutches. We used ANCOVA with SVL as the covariate to test for differences among clutches in reproductive traits significantly related with female's size. We used two-way ANOVA to search for among individual variation in clutch size and egg mass. Partial correlation analyses were used to examine relationships between the selected pairs of variables while holding other variables constant. We used the Mann-Whitney U-test for differences in egg width among clutches, because normality assumptions were not met. Values are presented as mean \pm 1 SE.

RESULTS

The smallest reproductive female in our sample was 51.2 mm SVL, and all females larger than this size reproduced at least one clutch at some point of the breeding season. Females laid eggs from 22 April to 7 July. First clutch deposition occurred between 22 April and 2 June, second clutch deposition between 17 May and 5 July, and third clutch deposition between 6 June and 5 July. Table 1 summarizes data on female reproductive characteristics.

Clutch Frequency.—Clutch frequency, defined as the number of clutches produced per season, varied from 1 to 3 clutches. Of the 53 reproductive females, 13 laid only one clutch, 27 laid two

TABLE 1. Female size and mass, egg size and mass, clutch size and mass, and relative clutch mass at different points of the breeding season in the wall lizard *Podarcis muralis* from a lowland population of northern Spain.

	First clutch			Second clutch			Third clutch		
	N	Mean \pm SE	Range	N	Mean \pm SE	Range	N	Mean \pm SE	Range
Female size and mass									
Mass (g)	53	3.7 \pm 0.1	2.2–5.5	40	3.7 \pm 0.1	2.6–4.8	13	3.7 \pm 0.2	2.7–4.8
SVL (mm)	53	59.6 \pm 0.4	51.2–68.2	40	60.9 \pm 0.4	55.7–68.8	13	60.9 \pm 0.7	56.1–65.0
TL (mm)	53	77.3 \pm 2.7	14.6–103.5	40	48.7 \pm 5.4	4.0–100.9	13	60.1 \pm 7.0	13.1–99.8
Egg size and mass									
Length (mm)	44	11.6 \pm 0.1	10.0–13.4	36	11.2 \pm 0.1	10.4–12.6	13	11.2 \pm 0.2	9.9–12.2
Width (mm)	44	7.0 \pm 0.1	6.2–7.7	36	6.8 \pm 0.1	6.1–7.7	13	6.6 \pm 0.1	6.1–7.3
Wet mass (g)	44	0.34 \pm 0.01	0.25–0.45	36	0.30 \pm 0.01	0.23–0.43	13	0.29 \pm 0.01	0.22–0.35
Clutch size and mass									
Clutch size	53	5.0 \pm 0.2	3–11	40	3.9 \pm 0.2	2–6	13	4.0 \pm 0.3	2–6
Clutch mass (g)	44	1.74 \pm 0.08	0.92–3.59	36	1.17 \pm 0.05	0.64–1.76	13	1.15 \pm 0.09	0.66–1.65
Relative clutch mass									
RCM1	44	0.47 \pm 0.02	0.27–0.77	36	0.30 \pm 0.01	0.14–0.44	13	0.30 \pm 0.02	0.16–0.40
RCM2	44	0.31 \pm 0.01	0.21–0.43	36	0.23 \pm 0.01	0.12–0.30	13	0.23 \pm 0.01	0.14–0.28

clutches, and 13 laid three clutches. There were significant differences in mean SVL among females that laid different numbers of clutches ($F_{2,50} = 6.69$, $P < 0.01$): females (57.1 ± 0.7 mm) that laid only one clutch were smaller than those having laid two (60.6 ± 0.6 mm) or three clutches (60.1 ± 0.9 mm) (Tukey's test, both $P < 0.05$), whereas females producing two and three clutches did not differ in SVL (Tukey's test, $P > 0.05$).

The time interval between two successive

clutches varied from 16.8 to 54.7 d (30.4 ± 1.4 , $N = 40$) between first and second clutches, and from 18.6 to 32.1 d (25.2 ± 1.2 , $N = 13$) between second and third clutches ($F_{1,51} = 4.09$, $P < 0.05$).

Clutch Size.—Clutch size (log-transformed) was positively correlated with female SVL in first ($r^2 = 0.52$, $F_{1,51} = 55.34$, $P < 0.0001$) and second ($r^2 = 0.12$, $F_{1,38} = 5.48$, $P < 0.05$) clutches, but no such a significant relationship was found in the third clutch ($r^2 = 0.23$, $F_{1,11} = 3.21$, $P > 0.05$) (Fig. 1). An ANCOVA was employed to test for differences of clutch size–SVL relationship among clutches. This analysis revealed homogeneity of slopes ($F_{2,100} = 1.91$, $P > 0.05$) but significant difference in intercepts ($F_{2,102} = 22.12$, $P < 0.0001$). Clutch size of first clutch was larger than that of second and third clutches (Tukey's test, in both cases, $P < 0.05$), whereas the subsequent clutches did not differ in clutch size (Tukey's test, $P > 0.05$). When setting female SVL at 60.2 mm, the adjusted mean clutch size of first, second, and third clutches was 4.9, 3.6, and 3.7, respectively. A two-way ANOVA on the females laying three clutches showed both among clutch ($F_{2,20} = 5.58$, $P < 0.05$) and among individual ($F_{10,20} = 5.56$, $P < 0.01$) differences in clutch size.

We followed van Damme et al. (1992) to estimate female condition using the residuals derived from the regression of log (female postpartum mass) on log (female SVL). We employed a partial correlation analysis to test for relationships between clutch size (log transformed) and female condition when holding female SVL constant. The analysis showed that clutch size was not correlated with female condition in the first two clutches (in both cases, P

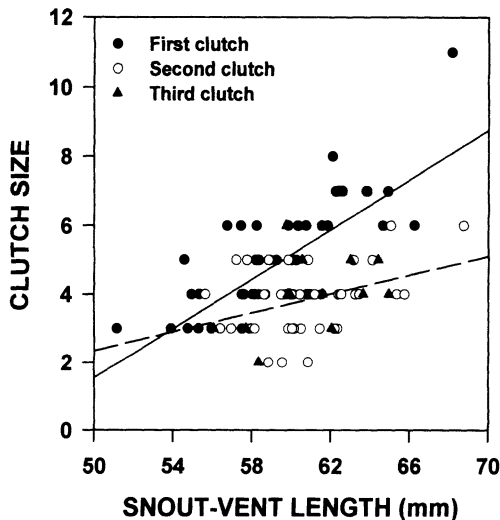


FIG. 1. The relationships between clutch size and female SVL. The solid line represents first clutch ($CS = -16.48 + 0.36 \text{ SVL}$, $r^2 = 0.53$, $F_{1,51} = 56.73$, $P < 0.0001$), and the dash line denotes second clutch ($CS = -4.55 + 0.14 \text{ SVL}$, $r^2 = 0.15$, $F_{1,36} = 6.66$, $P < 0.05$).

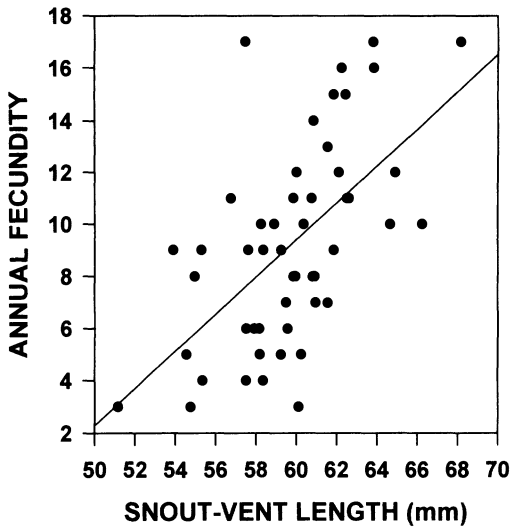


FIG. 2. The relationship between annual fecundity (AF) and female SVL. $AF = -33.28 + 0.71 SVL$, $r^2 = 0.35$, $F_{1,48} = 25.67$, $P < 0.0001$.

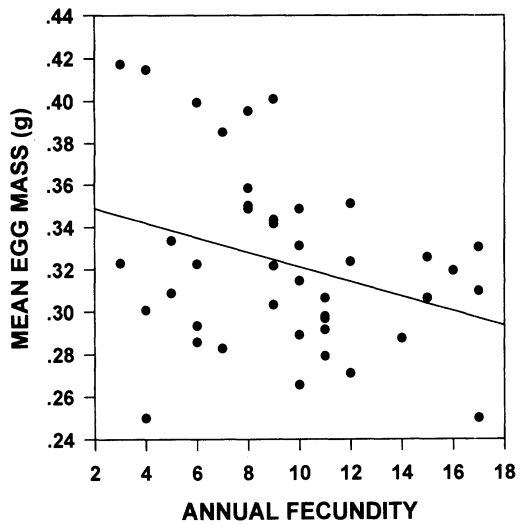


FIG. 3. The relationship between mean egg mass (MEM) and annual fecundity (RP). $MEM = 0.3557 - 0.0034 AF$, $r^2 = 0.10$, $F_{1,40} = 4.46$, $P < 0.05$.

> 0.05) but was negatively correlated with female condition in third clutch ($r = -0.74$, $t = 3.46$, $df = 11$, $P < 0.05$).

Egg Dimension and Mass.—Mean egg width was significantly larger in first clutch than in second and third clutches (Mann-Whitney U-test; in both cases, $P < 0.01$), whereas second and third clutches did not differ in mean egg width (Mann-Whitney U test; $P > 0.05$). A partial correlation analysis was employed to examine relationships among egg length, egg width, and clutch size. When holding egg width constant, egg length was negatively correlated with clutch size (log-transformed) in all three clutches (First clutch, $r = -0.64$, $t = 5.34$, $df = 42$; Second clutch, $r = -0.46$, $t = 2.97$, $df = 34$; third clutch, $r = -0.69$, $t = 2.99$, $df = 11$; in all cases, $P < 0.05$). The analysis also showed that, only in the first clutch, egg length was positively correlated with egg width ($r = 0.47$, $t = 3.36$, $df = 42$, $P < 0.01$) and egg width was positively correlated with clutch size ($r = 0.44$, $t = 3.14$, $df = 42$, $P < 0.01$).

Because no linear relationships between egg mass and female SVL were found in all three clutches (in all cases, $P > 0.05$), use of ANCOVA was precluded to compare data. An ANOVA showed that there were significant differences in egg mass among clutches ($F_{2,90} = 10.70$, $P < 0.001$). Mean egg mass of first clutch was greater than that of second and third clutches (Tukey's test, in both cases, $P < 0.01$), whereas mean egg mass of the subsequent two clutches was almost the same (Tukey's test, $P > 0.05$). A two-way ANOVA on the females laying three clutches confirmed the existence of between clutch dif-

ferences in egg mass ($F_{2,20} = 4.53$, $P < 0.05$) and also showed that there was no individual dependence of egg mass ($F_{10,20} = 1.99$, $P > 0.05$). A partial correlation analysis showed that there was no significant egg mass—clutch size trade-off within single clutches when holding female SVL constant (in all cases, $P > 0.05$).

Relative Clutch Mass.—Among clutch differences in RCM could not be tested using an ANCOVA with clutch mass as dependent variable and female postpartum mass as the covariate, as suggested by Ford and Seigel (1989), because no linear relationship existed between the two variables. An ANOVA showed significant differences in RCM (arcsine-transformed) among clutches (RCM1, $F_{2,90} = 35.60$; RCM2, $F_{2,90} = 37.26$; in both cases, $P < 0.0001$). RCM of the first clutch were greater than those of subsequent clutches (Tukey's test for RCM1 and RCM2, both $P < 0.001$), whereas RCM of the later two clutches were almost the same (Tukey's test for RCM1 and RCM2, both $P > 0.05$) (Table 1).

Annual Fecundity.—Annual fecundity, defined as the total number of eggs produced per season, varied from 3 to 17 eggs (9.2 ± 0.6 , $N = 50$), and its log transformed values was correlated with SVL of the females ($r^2 = 0.36$, $F_{1,48} = 26.56$, $P < 0.0001$) (Fig. 2). When employing a partial correlation analysis to hold female SVL constant, we found mean egg mass was negatively correlated with annual fecundity ($r = -0.33$, $t = 2.16$, $df = 40$, $P < 0.05$) (Fig. 3). The analysis also confirmed that annual fecundity was positively correlated with female SVL ($r = 0.66$, $t = 5.43$, $df = 40$, $P < 0.0001$) and egg mass

was independent of female SVL ($r = 0.15$, $t = 0.93$, $P > 0.05$). When employing a partial correlation analysis to hold female SVL constant, we found that clutch masses of the subsequent two clutches were independent of clutch masses of the first clutch (in both cases, $P > 0.05$).

DISCUSSION

The smallest reproductive female in our study was 51.2 mm SVL, which is within the range of the values reported for the smallest females in other populations (USA—45 mm, Kwiat and Gist, 1987; Italy—49 mm, Edsman, 1990; France—54 mm, Barbault and Mou, 1988; Balkan—55 mm, Belakovic et al., 1996). The observed differences in the minimum size of reproductive females among populations presumably reflect responses of lizards to environmental variations and/or sampling bias, as different samples taken from the same population studied here exhibited a similar size range (Braña, 1984; Braña et al., 1991, 1992).

As the pattern reported for other multiple-clutched lizards (Hahn and Tinkle, 1965; Derickson, 1976; Ballinger, 1977; Guillelte and Bearce, 1986; Anderson and Karasov, 1988), the initial clutch of *P. muralis* is larger than subsequent clutches, presumably due to the energy reserves in the fat bodies. It is noteworthy, however, that *P. muralis* also lay larger eggs in the initial clutches. Laying larger eggs in the initial clutch might result in increased fitness in *P. muralis*, as larger eggs would produce larger young that should exhibit faster growth, better condition in the autumn, and improved survival during winter (van Damme et al., 1992). Therefore, advantages of larger eggs could be translated to survival and size advantages at first reproduction. One seemingly important fact, namely the time available for growth and stores repletion until the winter dormancy, would select for larger egg size in later clutches (see Ferguson and Snell, 1986). In our study, on the contrary, first clutches had larger eggs, likely because total energy investment was largely reduced in later clutches, so that any increase in egg size would represent a reduction of fecundity. In addition, as developmental time exhibits a strong thermal dependence in *P. muralis* (van Damme et al., 1992), and environmental temperature increases dramatically from the date of first clutch laying (early spring) to that of the last clutch (mid-summer), hatching interval would be closer than egg-laying interval.

The previous conclusion that female condition has an influence on clutch size (van Damme et al., 1992) is not supported by the data presented in this study. Female condition is, if any, less important in modifying clutch size. Actually, variation in clutch size can be explained by mul-

tle factors, so the relationship between female condition and clutch size can be more complex than expected. A female in a poor condition prior to vitellogenesis can be expected to have low reproductive investment and a poor post-laying status as well. However, a female in a very good condition prior to vitellogenesis may also have a bad post-laying condition because of investing a relatively larger amount of resources in reproduction.

Our data indicates that female size is a major determinant of the reproductive investment: larger (and presumably older) females had more clutches in the reproductive season and laid more eggs in each clutch, so that they had larger total egg number (annual fecundity) and total egg mass. This is a frequent pattern of variation of reproductive investment in iteroparous species with indeterminate growth at rates decreasing with age (Reiss, 1989). As revealed by their tiny weight increment, larger females did not significantly grow nor accumulate energy stores during the reproductive period, but diverted most of their energy intake to egg production, an expected result for the trade-offs of energy allocation in female lizards (Anderson and Karasov, 1988; Schwarzkopf, 1994). High expenditure in current reproduction could reduce "residual reproductive value" by decreasing survival, growth, or the amount of energy available for future reproduction (Schwarzkopf, 1994). Therefore, our results conform to the prediction that, because reproductive value declines after the onset of sexual maturity, maximization of fitness should be achieved by diverting a successively higher fraction of the available energy to reproduction (Pianka and Feener's argument, in Smith and Fretwell, 1974).

Under the assumptions that the amount of energy available is limited and egg size is not invariant, clutch size should be inversely correlated with egg size in each particular clutch, because of energy and space constraints (Smith and Fretwell, 1974; Roff, 1992; Doughty and Shine, 1997). In this study, however, the egg size-clutch size trade-off within single clutches could not be predicted, as in all three clutches egg size was independent of clutch size when female SVL was held constant. The negative relationship we have found among individuals between annual fecundity and mean egg mass indicates a trade-off for the whole reproductive season, which means that, when female SVL was held constant, more eggs laid per season correspond to smaller eggs. Overall, clutch size is far more variable than egg size, both among females and between successive clutches of the same female, confirming the more frequent pattern demonstrated by lacertid lizards exhibiting

steep slopes in the regression of clutch size on female size (but see Castilla et al., 1992).

Egg dimension (or shape) is, in various degrees, determined by clutch size, abdominal shape and volume, uterine anatomy, and pelvic passage (Smith and Fretwell, 1974; Iverson and Ewert, 1991). We do not have data to test individually the influences of these factors; however, in *P. muralis*, more rounded eggs are clearly accommodated by larger clutch size and/or egg size. Our conclusion can be supported by the results that egg length was inversely correlated with clutch size in all three clutches and, only in the initial clutch of which the mean egg size was larger, egg length was positively correlated with egg width. The influence of clutch size and egg size on egg shape has also been reported for other lacertid lizards (Castilla et al., 1992).

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LITERATURE CITED

- ANDERSON, R. A., AND W. H. KARASOV. 1988. Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. *Ecol. Monogr.* 58:79–110.
- ARNOLD, E. N., AND J. A. BURTON. 1978. A Field Guide to the Reptiles and Amphibians of Britain and Europe. Collins, London.
- BALLINGER, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology* 58:628–635.
- . 1983. Life-history variations. In R. B. Huey, E. R. Pianka, and T. W. Tinkle (eds.), *Lizard Ecology. Studies of a Model Organism*, pp. 241–260. Harvard Univ. Press, Cambridge, Massachusetts.
- BARBAULT, R., AND Y. P. MOU. 1986. A population analysis of the common wall lizard *Podarcis muralis* in Southwestern France. In Z. Roček (ed.), *Studies in Herpetology*, pp. 513–518. Charles Univ., Prague.
- , AND ———. 1988. Population dynamics of the common wall lizard, *Podarcis muralis*, in southwestern France. *Herpetologica* 44:38–47.
- BELAKOVIC, D., I. ALEKSIC, J. CRNOBRNJA-ISAILOVIC, G. DZUKIC, AND M. L. KALEZIC. 1996. Female reproductive traits in the common wall lizard (*Podarcis muralis*) from the Skadar Lake region, Montenegro. *Rev. Esp. Herp.* 10:91–96.
- BRAÑA, F. 1984. Biogeografía, biología y estructura de nichos de la taxocenosis de saurios de Asturias. Ph.D. Thesis, Universidad de Oviedo.
- . 1993. Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos* 66:216–222.
- , A. BEA, AND M. J. ARRAYAGO. 1991. Egg retention in lacertid lizards: relationships with reproductive ecology and the evolution of viviparity. *Herpetologica* 47:218–226.
- , F. GONZÁLEZ, AND A. BARAHONA. 1992. Relationship between ovarian and fat body weights during vitellogenesis for three species of lacertid lizards. *J. Herpetol.* 26:515–518.
- CASTILLA, A. M., L. J. BARBADILLO, AND D. BAUWENS. 1992. Annual variation in reproductive traits in the lizard *Acanthodactylus erythrusus*. *Can. J. Zool.* 70:395–402.
- DERICKSON, W. K. 1976. Ecological and physiological aspects of reproductive strategies in two lizards. *Ecology* 57:445–458.
- DOUGHTY, P., AND R. SHINE. 1997. Detecting life history trade-offs: measuring energy stores in "capital" breeders reveals costs of reproduction. *Oecologia* 110:508–513.
- , AND ———. 1998. Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). *Ecology* 79:1073–1083.
- EDSMAN, L. 1990. Territoriality and competition in wall lizards. Ph.D. Thesis, Univ. Stockholm.
- FERGUSON, G. W., AND H. L. SNELL. 1986. Endogenous control of seasonal change of egg, hatchling, and clutch size of the lizard *Sceloporus undulatus garmani*. *Herpetologica* 42:185–191.
- FORD, N. B., AND R. A. SEIGEL. 1989. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. *Ecology* 70:1768–1774.
- GUILLETTE, L. J., AND D. A. BEARCE. 1986. The reproductive and fat body cycles of the lizard, *Sceloporus grammicus disparilis*. *Trans. Kansas Acad. Sci.* 89:31–39.
- HAHN, W. E., AND D. W. TINKLE. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. *J. Exp. Zool.* 158:79–86.
- IVERSON, J. B., AND M. A. EWERT. 1991. Physical characteristics of reptilian eggs and a comparison with avian eggs. In D. C. Deeming, and M. W. J. Ferguson (eds.), *Egg Incubation, Its Effect on Embryonic Development in Birds and Reptiles*, pp. 87–100. Cambridge Univ. Press, Cambridge.
- KWIAT, G. A., AND D. H. GIST. 1987. Annual reproductive cycle of an introduced population of European wall lizard (*Podarcis muralis*) in Ohio. *J. Herpetol.* 21:205–209.
- MOU, Y. P., AND R. BARBAULT. 1988. Determination of clutch frequency and clutch size in free-living iteroparous lizards; application of laparotomy. *Amphibia-Reptilia* 9:197–200.
- REISS, M. J. 1989. The Allometry of Growth and Reproduction. Cambridge Univ. Press, Cambridge.
- ROFF, D. A. 1992. The Evolution of Life Histories. Chapman & Hall, New York.
- SCHWARZKOPF, L. 1994. Measuring trade-offs: A review of studies of costs of reproduction in lizard. In L. J. Vitt, and E. R. Pianka (eds.), *Lizard Ecology: Historical and Experimental Perspectives*, pp. 7–29. Princeton Univ. Press, Princeton, New Jersey.
- SEIGEL, R. A., AND H. S. FITCH. 1984. Ecological pat-

- terns of relative clutch mass in snakes. *Oecologia* 61:293–301.
- , AND N. B. 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. 1992. Relative clutch mass and body shape in lizards and snakes: its reproductive investment constrained or optimized? *Evolution* 46:828–833.
- SINERVO, B., AND P. DAUGHTY. 1996. Interactive effects of offspring size and timing of reproduction on offspring reproduction: experimental, maternal, and quantitative genetic aspects. *Evolution* 50:1314–1327.
- SMITH, C. C., AND S. D. FRETWELL. 1974. The optimal balance between size and number of offspring. *Amer. Natur.* 108:499–506.
- VAN DAMME, R., D. BAUWENS, F. BRAÑA, AND R. F. VERHEYEN. 1992. Incubation temperature differentially affects hatching time, egg survival and hatching performance in the lizard *Podarcis muralis*. *Herpetologica* 48:220–228.
- VITT, L. J., AND H. J. PRICE. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38:237–255.

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Embryonic Survivorship of the Spotted Salamander (*Ambystoma maculatum*) in Roadside and Woodland Vernal Pools in Southeastern New Hampshire

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ABSTRACT.—Roadside wetlands are often contaminated by highway runoff; however, little is known about the impact of pollution on the organisms that use these wetlands. Most amphibians use wetlands as breeding habitats and are therefore vulnerable to aquatic pollutants. In 1995 and 1996, I conducted transplant experiments to compare the embryonic survivorship of *Ambystoma maculatum* in temporary woodland pools to that in roadside pools. Chemical parameters were monitored to identify differences between roadside and woodland pool environments. Failure time analysis was used to compare embryonic survival probabilities for transplant experiments in both years. The results indicate that deicing salts heavily contaminate roadside vernal pools. *Ambystoma maculatum* survivorship was significantly lower in roadside pools for four of five transplants in 1995 and all transplants in 1996. Deicing salts used for highway maintenance contaminated roadside vernal pools, and are a possible factor in the reduced embryonic survival observed in these pools.

Approximately one-half of the frog species and one-third of the salamander species in North America rely on ephemeral wetlands for embryonic and larval development (Pierce, 1985). Ephemeral (seasonal) wetlands include vernal pools, which dry annually, as well as semi-permanent ponds that dry more infrequently. In New Hampshire, *Rana sylvatica* (wood frog), *Ambystoma maculatum* (spotted salamander), *Ambystoma laterale* (blue spotted salamander), *Ambystoma jeffersonianum* (Jefferson's salamander) and hybrids of the latter two species depend on these unique wetlands for reproduction. Suitable breeding sites for these amphibians must dry often enough to exclude fish and must retain water long enough to allow amphibian larvae to complete development and metamorphose into terrestrial adults.

The impact of pollution on the chemical, physical, and biological properties of vernal pools is not well understood. The chemical composition of the water in vernal pools reflects the chemical content of upper soil horizons, leaf litter, runoff from surrounding areas, and even atmospheric conditions (Rowe and Dunson, 1993). The watersheds of these pools tend to be small; thus, precipitation and runoff entering these pools have little contact with soil buffering systems. There is often little water volume in the pool to dilute polluted inflow (Pough, 1976; Gascon and Planas, 1986), resulting in a greater effect of pollutants on the water in these wetlands than in lakes and streams. In addition, evaporation during late spring and summer may increase the concentration of ions in the water causing chemical and physical stress for