SNAKE LITTER SIZE = LIVE YOUNG + DEAD YOUNG + YOLKS

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(Accepted 21.6.91)

A common method of estimating litter size of viviparous snakes is to hold gravid females in captivity until they give birth. Captive-born litters often include dead young (either partly or fully developed), or undeveloped yolky eggs, or both. Because we do not know the extent to which captive conditions influence the occurrence of dead young or undeveloped eggs, it is not clear what constitutes a reasonable estimate of litter size: live young only or live young plus some subset of the remaining off-spring and eggs. Different authors have used slightly different criteria (e.g. Gregory, 1977; Larsen, 1986; Ford & Seigel, 1989; see review by Farr & Gregory, 1991), but undeveloped eggs seem to be rarely, if ever, counted as part of the litter.

In this note, we examine the degree to which estimates of litter size are influenced by the inclusion or exclusion of dead or undeveloped young, using data for the garter snake, *Thamnophis sirtalis*, from ten Canadian populations.

Gravid females were captured at various stages of gestation in various years from 1972 to 1988 and maintained in more or less standard conditions at 20 - 28°C, with *ad lib* access to water but usually no food, until they gave birth, whereupon measurements of litters and neonates were taken.

We classified each litter into one of three categories, following Farr & Gregory (1991):

Status 1   –   litters that consisted only of live young.

Status 2   –   litters that consisted entirely of fully developed young, of which some or all were dead.

Status 3   –   litters that contained one or more dead, incompletely developed young and/or undeveloped eggs.

In order to compare estimates of litter size among categories, we first had to consider that there were significant differences among locations in frequencies of the three litter categories and in the linear relationship between litter size and snout-vent length (SVL) of mother. Therefore, we calculated a separate regression of litter size on SVL of mother for each location, using Status 1 litters only. We then expressed sizes of Status 2 and 3 litters from each location as deviates from the corresponding Status 1 regression line. We did this three times, using (i) live young, (ii) live plus normal dead young, and (iii) all "progeny"

as measures of litter size. Because the variances around the various regression lines were all different, we re-expressed each value as a standard normal deviate by dividing it by the standard deviation of the residuals from the appropriate regression line. We then pooled the data from all locations and compared mean adjusted sizes of Status 1, 2, and 3 litters by ANOVA.

We also tested whether neonate SVL differed among litter categories. First, we compared the SVLs of live and dead babies in Status 2 and 3 litters by two-way ANOVA (individual litter by live versus dead young), using the General Linear Model. Second, we compared SVL of neonates (using both live and dead young) among litter categories, again as a two-way ANOVA (location by litter status) of mean SVL of neonates in a litter. Location was used as a factor in the ANOVA because neonate SVL differs significantly among locations (Gregory & Larsen, unpubl.).

To test for potential influences of captivity on incidence of Status 2 and 3 litters, we did a one-way ANOVA of days in captivity (all locations combined) with litter status as the factor.

All statistical analyses were done with PC-SAS Release 6.03 and conclusions were based on Type III sums of squares. All were considered significant at alpha = 0.05.

Of 162 captive-born litters, 83 were Status 1, 41 Status 2, 38 Status 3, but not all could be used in all analyses. Mean litter size differed significantly among the three categories, regardless of definition of litter size, but these differences became progressively smaller and less clear-cut as the definition of litter size was broadened (Table 1). Although Status 2 and 3 litters were smaller than Status 1 litters when only live young were considered, both turned out to be larger than Status 1 litters when all potential components of litters were summed.

	Litter Size		
	Live Young	Live Young + Fully developed Dead Young	All "Progeny", Including Undeveloped Young and Yolks
Status 1 (n=72)	0.000	0.000[A]	0.000[A]
Status 2 (n=27)	-3.300[A]	1.469	1.469[B]
Status 3 (n=31)	-2.338[A]	-0.510[A]	0.747[AB]
ANOVA (df = 2,127)	F = 9.20 P = 0.000	F = 5.24 P = 0.006	F = 3.55 P = 0.031

TABLE 1. Comparison of mean litter sizes of Status 1, 2, and 3 litters under different definitions of litter size. All values were calculated as standardized normal deviates from separate regression lines of litter size vs. female SVL for Status 1 litters of each population. Expressing values as deviates adjusts for differences in SVL of mothers. Standardizing values against a normal distribution eliminates heterogeneity of variance among populations, allowing them all to be pooled for final analysis. By definition, mean deviation of Status 1 litters is always zero. Symbols A and B indicate means with non-significant difference (Bonferroni test).

We compared SVLs of dead and live young within litters, using nine litters for which we had at least two measurements of each of live and dead young (most litters selected had more than two of each). There were significant differences in mean SVL among litters ($F_{8,118} = 113.37$, $P = 0.0001$), but not between live and dead neonates within litters ($F_{1,118} = 1.07$, $P = 0.0731$); the interaction factor was not significant ($F_{8,118} = 0.920$, $P = 0.545$).

We restricted our comparison of SVLs of neonates from litters of different status to three locations for which there were at least three litters of each status. Neonate size differed significantly among these locations ($F_{2,39} = 15.06$, $P = 0.0001$), but not among status categories ($F_{2,39} = 1.58$, $P = 0.222$); the interaction was not significant ($F_{4,39} = 1.11$, $P = 0.3701$).

There were no significant differences in mean time spent in captivity by females producing litters of different status ($F_{2,112} = 0.79$, $P = 0.4551$).

Perforce, inclusion or exclusion of dead young or undeveloped eggs must change estimates of litter size. However, the important conclusions of this study are that this effect can be very significant in snakes and that variation among estimated litter sizes is maximally reduced by counting all potential progeny. This supports the recommendation of Farr & Gregory (1991) that a distinction be made between potential and actual litter size. At the very least, all potential components of litters should be reported in future studies, regardless of which of them are considered to be important. A case in point is that of Ford & Karges (1987), who obtained higher estimates of litter size in *Thamnophis marcianus* from live births than from counts of embryos. The factors that reduce the apparent potential size of some litters merit further study.

Preferably, estimates of actual litter size should include all normally developed dead young. We have no evidence that dead young are smaller or differ in any other obvious way from live young, in general. Stillbirths and deformed young occur in the wild (Larsen, 1986), but their incidence may be higher under captive conditions. A number of factors could have a negative influence, including death, on developing progeny in captivity (see Farr & Gregory, 1991, for review); chief among them is temperature (Fox, 1948; Burger *et al.*, 1987; Burger & Zappalorti, 1988; Burger, 1990), which we did not attempt to optimize in this study. Why some embryos in a litter die while others survive is not known. It is interesting to note that the adjusted sizes of Status 2 litters were significantly larger than those of Status 1 litters when both live and dead young were counted (Table 1). Perhaps there is a crowding effect *in utero* that does not manifest itself until late gestation, resulting in fully developed, but dead, young. Farr & Gregory (1991), however, found no significant differences in sizes of litters of *T. elegans* of different status when all potential litter components were counted.

It is not clear whether the undeveloped eggs seen in Status 3 litters were simply unfertilized vitellogenic follicles or fertilized eggs that ceased development at a very early stage. Clearly, some embryos do cease development in mid-gestation because some Status 3 litters were so classified on the basis of undeveloped young. Again, we have no field data on the occurrence of undeveloped eggs or young in litters. Whatever their significance, their inclusion as a component of potential litter size is important because such inclusion allows unambiguous

comparison between different populations and different studies. This is especially true if we want to compare data obtained from captive births with those from hand palpations in the field (cf. Farr & Gregory, 1991) or from dissections of females in early stages of pregnancy; in neither of these cases will it usually be possible to distinguish eventual live births, dead births, or undeveloped eggs.

REFERENCES

Burger, J. A. (1990). Effects of incubation temperatures on behavior of young black racers (*Coluber constrictor*) and kingsnakes (*Lampropeltis getulus*). *J. Herpet.* **24**, 158–163.

Burger, J. & Zappalorti, R. T. (1988). Effects of incubation temperature on sex ratios in pine snakes: Differential vulnerability of males and females. *Am. Nat.* **132**, 492–505.

Burger, J., Zappalorti, R. T., & Gochfield, M. (1987). Developmental effects of incubation temperature on hatchling pine snake, *Pituophis melanoleucus*. *Comp. Biochem. Physiol.* **87A**, 727–732.

Farr, D. R. & Gregory, P. T. (1991). Sources of variation in estimating litter characteristics of the garter snake, *Thamnophis elegans*. *J. Herpet.* **25**, 261–268

Ford, N. B. & Karges, J. P. (1987). Reproduction in the checkered garter snake, *Thamnophis marcianus*, from southern Texas and northeastern Mexico: Seasonality and evidence for multiple clutches. *Southwest. Nat.* **32**, 93–101.

Ford, N. B. & Seigel, R. A. (1989). Phenotypic plasticity in reproductive traits: Evidence from a viviparous snake. *Ecology* **70**, 1768–1774.

Fox, W. (1948). Effect of temperature on development of scutellation in the garter snake, *Thamnophis elegans atratus*. *Copeia* **1948**, 252–262.

Gregory, P. T. (1977). Life-history parameters of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in an extreme environment, the Interlake region of Manitoba. *Publ. Zool. No. 13, Natl. Mus. Natur. Sci. Canada.*

Larsen, K. W. (1986). *Ecology of the common garter snake, Thamnophis sirtalis, at the northern limit of its range.* M.Sc. Thesis, University of Victoria, Victoria.

BOOK REVIEWS

The Year of the Turtle. D. M. Carroll. (1991). 172 pp. Camden House Publishing, Charlotte, Vermont. $22.95(US), cloth. $17.95(US), paper.

It is popular among advertising agencies and writers of second-rate fiction to picture scientists as detached, emotionless beings peering over the edge of a clip board at "the phenomenon", clad in a white lab coat and thick glasses, armed with reams of stop-watches, pens and calculators. Yet what fool would endure years of university education, spend countless hours reading terse, factual articles, and then submit himself to