



The American Society of Naturalists

Behavioral Modification as a Means of Reducing the Cost of Reproduction

Author(s): Edmund D. Brodie III

Source: *The American Naturalist*, Vol. 134, No. 2 (Aug., 1989), pp. 225-238

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <http://www.jstor.org/stable/2462100>

Accessed: 09/04/2009 14:58

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=ucpress>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press and The American Society of Naturalists are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

BEHAVIORAL MODIFICATION AS A MEANS OF REDUCING THE COST OF REPRODUCTION

EDMUND D. BRODIE III

Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637

Submitted March 3, 1988; Accepted September 14, 1988

One of the basic tenets of life-history theory is that trade-offs exist between major components of fitness. In particular, many models assume that costs are associated with reproduction, whereby an increase in current fecundity or parental investment results in a reduction in reproductive value (Williams 1966; Gadgil and Bossert 1970; Schaffer 1974; Law 1979; Michod 1979; Charlesworth 1980). Costs of reproduction could be manifested through two major mechanisms (Shine 1980): (1) the survival of females may be adversely affected by the behavioral and physiological changes associated with reproduction; and (2) the allocation of energy to current reproduction instead of to growth and maintenance may reduce reproductive value. Empirical evidence from a number of taxa indicates that such trade-offs exist and could be important in determining life-history patterns (review in Reznick 1985).

An increased risk of predation or parasitism may accompany mating in many organisms (Walker 1964; Cade 1975, 1979; Aleksasuk 1977; Bell 1979; Ryan et al. 1981, 1982), but the burden of carrying a clutch is thought to be the most important factor affecting female survival during reproduction, especially in reptiles (Shine 1980). Relative clutch mass (RCM), usually expressed as the ratio of clutch mass to the body mass of the female, is used as a measure of the physical burden experienced by a female during pregnancy and is often considered a life-history trait (Vitt and Congdon 1978; Shine 1980; Vitt 1981; Vitt and Price 1982; Cuellar 1984; Seigel and Fitch 1984; Seigel et al. 1986, 1987). Recent feeding (Garland and Arnold 1983; Huey et al. 1984; Ford and Shuttlesworth 1986) and pregnancy (Shine 1980; Bauwens and Thoen 1981; Garland 1985; Seigel et al. 1987) are known to reduce the locomotor capabilities of many reptiles, presumably because of the increased mass associated with these conditions. It is further assumed that such reduced locomotion has a detrimental effect on survival. If high RCM decreases the probability of survival to the next reproductive event, selection should favor an RCM that strikes a balance between current fecundity and survival probability. This hypothesis is supported by observations of lizard species: those that depend mainly on speed to avoid predators have lower RCM's than those that rely primarily on crypsis (Vitt and Congdon 1978; Vitt 1981; Vitt

and Price 1982; Magnusson et al. 1985; Anan'eva and Shammakov 1986). Furthermore, terrestrial snakes have higher RCM's than aquatic ones, apparently because aquatic locomotion is more adversely affected by an increase in mass than is terrestrial locomotion (Shine 1988).

Whether selection constrains RCM depends on (1) the effect of RCM on locomotor performance and (2) the importance of locomotion to survival (Vitt and Congdon 1978; Shine 1980; Vitt and Price 1982; Seigel et al. 1987). Decreased dependence on locomotion should alleviate pressure to reduce RCM, thereby providing the potential for increased reproductive output. Changes in antipredator behavior and activity patterns during pregnancy could reduce the reliance on speed and endurance. Even though evidence of such changes exists (Bauwens and Thoen 1981), most previous treatments do not consider behavioral modification an important factor in the evolution of RCM (Vitt and Congdon 1978; Shine 1980; Vitt 1981; Vitt and Price 1982; Seigel and Fitch 1984; Seigel et al. 1986; but see Seigel et al. 1987).

In this study, I examine changes in individual locomotor performance and antipredator behavior associated with gestation by comparing behavior during and following pregnancy in female Northwest garter snakes, *Thamnophis ordinoides* (Colubridae). I assess the significance of observed behavior shifts with respect to current theories on the evolution of RCM, and I propose that behavioral modification during pregnancy may function to reduce the costs of reproduction.

METHODS

Between late June and early July 1986, 47 pregnant *Thamnophis ordinoides* females were collected from three localities in the Pacific Northwest: 20 from Alsea River (Lincoln Co.), Oregon; 11 from McGribble (Curry Co.), Oregon; and 16 from East Sooke, Vancouver Island, British Columbia. Females were brought into the lab, housed in plastic shoeboxes (35 cm × 17 cm × 9 cm), kept at 20°–30°C at a natural (northern California) photoperiod, and maintained on a diet of earthworms. After parturition in August, all females and offspring were weighed, measured, and scored for a number of behaviors.

Behavioral Measurements

Locomotor performance and antipredator behaviors (described below) of all females were scored at 30°C over 4 consecutive days: on the sprint track on days 1 and 2 and on the circular track on days 3 and 4. Each individual was scored during pregnancy and again after parturition. Behaviors during pregnancy were measured during the same 4-day period for all snakes. The average time from the onset of these tests to parturition was 25 days (± 1.1 days SE; range, 14–40). Postpartum behaviors were measured on the third through sixth days after parturition for each female.

Sprint speed.—Sprint speed was measured with electronic timers on a 2-m linear racetrack lined with Astroturf (cf. Garland 1985). Snakes were stimulated to crawl by tapping them on the tail with a forefinger. Each snake was raced twice

per trial, and the fastest 0.5-m velocity was taken as the maximum sprint speed. Trials were conducted twice a day (with a minimum of 4 h between trials) on two consecutive days for a total of four trials. The mean sprint speed for the four trials was then used for further analysis.

Distance crawled.—A circular racetrack 294 cm in circumference and lined with Astroturf was used to measure the distance crawled once a day on two consecutive days for a total of two trials. Snakes were again stimulated to crawl by tapping the tail. Trials were terminated when a snake refused to continue after 10 successive taps. At this point, the distance crawled was recorded.

Display.—When garter snakes cease flight on the circular track, they perform antipredator displays (described in Arnold and Bennett 1984). These displays are scored on a 0–6 scale that Arnold and Bennett interpreted as measuring increasing offensiveness. The individuals of *Thamnophis ordinoides* in my sample virtually never performed any of the displays interpreted as offensive (4–6 on this scale). For this study, it seemed more logical to interpret this scale as one of decreasing defensiveness (0, most defensive; 3, least defensive).

Reversals.—During flight on the circular track, snakes performed a behavior termed a reversal, in which the snake suddenly turns 180°, such that its tail occupies the position previously held by its head. This is usually accompanied by a rapid wagging of the tail and slow crawling in the opposite direction from its original course. The number of reversals performed during flight was recorded for each trial.

Behavioral profiles.—The profile of each behavior was calculated as the postpartum score minus the score during pregnancy. Profiles were calculated for each female and used as a measure of the change in an individual's behavior from pregnancy to after parturition.

Reproductive Parameters

Mass and snout-vent length were recorded for each of the females and their litters within 24 h after parturition. The litter size (number of offspring) was also recorded at this time.

Relative clutch mass.—Relative clutch mass (RCM) was measured as the ratio of litter mass to female body mass (postpartum). This estimate of RCM, commonly used in previous studies (Seigel et al. 1986), is the value reported in table 1. The residuals from a regression of litter mass on female body mass (both corrected for population differences; see below) were substituted for RCM in all analyses to avoid the statistical problems associated with the analysis of ratios (Sokal and Rohlf 1981; Packard and Boardman 1987).

Effective relative clutch mass.—Effective relative clutch mass (ERCM) was measured as the ratio of the mass a female lost between the pregnant-behavior tests and parturition to the postpartum mass of the female. Residuals from the analogous regression were used in all statistical analyses. Because the burden carried during pregnancy includes more than just the offspring (e.g., water and membranes), ERCM is a more direct estimate of the burden experienced by the female at the time of her first behavior tests than is RCM measured postpartum.

TABLE 1
PARAMETER MEANS OF THE VARIABLES CALCULATED FOR ALL FEMALES AND FOR
EACH OF THE POPULATIONS

VARIABLE	POPULATION			
	All (<i>N</i> = 47)	Alsea (<i>N</i> = 20)	McGribble (<i>N</i> = 11)	Sooke (<i>N</i> = 16)
RCM	0.31 ± 0.02	0.37 ± 0.02	0.27 ± 0.02	0.28 ± 0.03
ERCM	0.63 ± 0.02	0.68 ± 0.04	0.59 ± 0.04	0.61 ± 0.04
Litter size	6.1 ± 0.3	6.8 ± 0.4	5.2 ± 0.9	5.8 ± 0.5
Stage of pregnancy (–day)	–25.2 ± 1.1	–25.1 ± 1.6	–32.1 ± 1.7	–20.6 ± 1.0
Snout-vent length (mm)	433.7 ± 5.7	440.5 ± 7.6	414.2 ± 16	438.7 ± 7.5
Pregnant speed (cm/s)	40.9 ± 1.4	43.1 ± 2.1	44.7 ± 2.0	35.5 ± 2.2
Pregnant distance (cm)	1253 ± 76	989 ± 79	1106 ± 155	1685 ± 107
Pregnant display	2.5 ± 0.1	2.23 ± 0.2	2.21 ± 0.4	2.92 ± 0.1
Pregnant reversals	0.9 ± 0.2	1.3 ± 0.3	0.8 ± 0.2	0.4 ± 0.1
Speed profile (cm/s)	40.8 ± 2.0	46.6 ± 3.0	36.8 ± 3.9	36.4 ± 3.1
Distance profile (cm)	739 ± 109	948 ± 176	398 ± 263	726 ± 123
Display profile	–0.8 ± 0.2	–1.0 ± 0.3	–1.3 ± 0.5	–0.25 ± 0.2
Reversal profile	–0.4 ± 0.1	–0.5 ± 0.2	–0.4 ± 0.2	–0.3 ± 0.1

NOTE.—Values are means ± one standard error; negative values of profiles indicate an increase in the behavior score after parturition. RCM, Relative clutch mass; ERCM, effective relative clutch mass.

Thus, ERCM is a more pertinent variable with which to examine the quantitative relationship between physical burden and changes in locomotor performance and behavior.

Stage of pregnancy.—Pregnant behaviors were scored at a different point during gestation for each female. The number of days between the pregnant-behavior test and parturition was recorded and termed the stage of pregnancy. In order to clarify interpretation, this variable is expressed as a negative number so that larger values correspond to later stages in gestation.

Statistical Techniques

All reproductive and behavioral variables were tested for normality using the Shapiro-Wilk statistic (SAS 1985). Because none of the variables showed significant departure from normality, no transformations were performed. Significance was taken at $P < 0.05$, but all probabilities less than 0.10 are reported and discussed. All statistical analyses were performed using SAS Version 6 for Personal Computers.

Population differences in a number of parameters were detected (using population-class ANOVA's, $P < 0.05$). To avoid confounding interpopulation trends with relationships between the parameters in the regression and correlation analyses, all variables were adjusted to remove differences between populations. This was accomplished by substituting residuals from population-class ANOVA's for the original variables in all regression and correlation analyses.

TABLE 2
DIFFERENCES BETWEEN BEHAVIOR DURING AND AFTER PREGNANCY FOR ALL FEMALES
AND FOR EACH POPULATION

VARIABLE	POPULATION							
	ALL (N = 47)		ALSEA (N = 20)		MCGRIBBLE (N = 11)		SOOKE (N = 16)	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Speed profile	20.52	0.0001	15.65	0.0001	9.35	0.0001	11.71	0.0001
Distance profile	6.79	0.0001	5.39	0.0001	1.51	NS	5.89	0.0001
Display profile	-4.50	0.0001	-3.56	0.002	-2.88	0.016	-1.26	NS
Reversal profile	-3.75	0.0005	-2.35	0.030	-1.88	0.089	-2.33	0.034

NOTE.—Results of paired *t*-tests. Negative values of the *t* statistic indicate a decrease in the behavior after parturition.

RESULTS

The means and standard errors of each of the variables for the total sample of 47 females and for each of the populations separately are reported in table 1.

Repeatability of Behavior

Repeatable individual variation was detected for all of the behaviors examined. Repeatabilities based on intraclass correlations (Falconer 1981) ranged from 0.36 to 0.51 for the behaviors scored during pregnancy and from 0.55 to 0.86 for the behaviors scored postpartum. Comparisons of mean behaviors during pregnancy and after parturition revealed that individual differences were consistent over this period ($R = 0.47 - 0.68$). All repeatabilities were significant at $P < 0.01$.

Differences between Pregnant and Postpartum Behavior

To test whether behaviors differed before and after parturition, a paired *t*-test was performed using individual behavioral profiles. Because of population differences in behaviors, this analysis was conducted both for all 47 females together and for each population (table 2). In the analysis of all females, the change in each behavior from pregnancy to after parturition was significant. Locomotor performance (sprint speed and distance crawled) increased significantly postpartum. The index of antipredator display decreased following parturition, indicating less-defensive behavior during pregnancy. The number of reversals was greater during pregnancy than after parturition. Although the significance of these results differed when populations were analyzed separately, the direction of change was always the same (table 2).

Effect of Size on Behavior

To determine if the behaviors were related to the size of an individual, regressions of each behavior on female snout-vent length were performed. No signifi-

TABLE 3
EFFECT OF STAGE OF PREGNANCY ON BEHAVIOR

Pregnant Behavior	<i>F</i>	<i>r</i> ²	Behavioral Profile	<i>F</i>	<i>r</i> ²
Speed (pregnant)	2.31	0.049	Speed profile	6.89 ^a	0.133
Distance (pregnant)	0.015	0.0003	Distance profile	10.96 ^b	0.203
Display (pregnant)	0.009	0.0002	Display profile	10.47 ^b	0.192
Reversals (pregnant)	0.152	0.003	Reversal profile	2.53	0.054

NOTE.—Results of linear regressions of pregnant behaviors and behavioral profiles on point of pregnancy (*df* = 1,44). All variables are adjusted for population differences (see the text). The slopes of all significant regressions are positive, indicating an increase in the profiles with progressing gestation.

^a *P* = 0.012.

^b *P* = 0.002.

cant effect of size (*P* < 0.10) was noted for any of the pregnant behaviors or for any of the behavioral profiles.

Effect of Stage of Pregnancy on Behavior

Because the time elapsed between the measurement of pregnant behavior and the measurement of postpartum behavior differed among females, it was possible to examine whether stage of pregnancy affected the behaviors. Regression of ERCM on number of days before parturition showed no significant relationship (*F* = 0.22, *P* = 0.65), indicating that relationships between the stage of pregnancy and behaviors should not reflect indirect effects of the burden of RCM.

Both the sprint-speed and distance profiles had a significant positive regression on the stage of pregnancy. The later in pregnancy the behaviors were measured, the greater the difference between pregnant and postpartum behavior. The opposite relationship was observed for the profile of defensive display: the positive slope of the regression, coupled with the negative values of the profile, indicates that the difference in behavior was smaller late in gestation. The profile of the number of reversals was unrelated to the stage of pregnancy, as were all of the behaviors measured during pregnancy (table 3).

Relationships between Relative Clutch Mass and Behavior

Pearson product-moment correlations were performed to examine the bivariate relationships between the reproductive parameters and the behaviors (table 4). None of the pregnant behaviors showed a significant relationship with any reproductive parameters. This result was unchanged even when the correlations were partialled with respect to stage of pregnancy and snout-vent length.

To control for the effect of the stage of pregnancy, residuals of regressions on this variable were substituted for the behavior profiles in the correlation analysis (table 4). Only the number-of-reversals profile showed a marginal correlation (0.10

TABLE 4
CORRELATIONS BETWEEN REPRODUCTIVE PARAMETERS AND BEHAVIOR

	VARIABLE			
	Speed	Distance	Display	Reversals
Behavior during pregnancy				
RCM	-0.031	-0.044	-0.037	-0.205
ERCM	-0.133	-0.028	-0.024	-0.085
Litter size	-0.032	0.026	-0.131	-0.196
Behavioral profile				
RCM	0.195	0.039	-0.127	0.258 ^a
ERCM	0.240 ^b	0.276 ^c	-0.108	0.073
Litter size	0.066	0.036	0.055	0.192

NOTE.—Correlation coefficients from correlation analyses comparing relative clutch mass (RCM), effective relative clutch mass (ERCM), and litter size with behaviors ($N = 45$ in all cases). All variables are adjusted for population differences, and the behavioral profiles are partialled with respect to the stage of pregnancy (see the text).

^a $P = 0.088$.

^b $P = 0.100$.

^c $P = 0.070$.

$> P > 0.05$) with RCM as measured postpartum. However, the sprint-speed and distance-crawled profiles were both marginally correlated with the ERCM (the correlation between RCM and ERCM was $r = 0.75$, $P < 0.0001$).

Canonical correlations (partialled to remove the effects of the stage of pregnancy) were performed to examine the relationship between the set of reproductive parameters (RCM, litter size, and snout-vent length) and both the set of pregnant behaviors and the set of behavioral profiles. No significant canonical correlations were observed between either pair of variable sets (Wilks' lambda $F < 0.61$, $P < 0.66$ for the first canonical correlations for each analysis). These analyses were repeated, substituting ERCM for RCM without qualitatively changing the results.

DISCUSSION

Changes in hormone levels and the physical stress associated with pregnancy and parturition probably continue to affect locomotion and antipredator behavior for a short time after parturition. For this reason, postpartum behavior as measured in this study (i.e., 3–6 days after parturition) should not be equated with behavior of nonpregnant females. Nonetheless, differences between scores during and after pregnancy were observed and are probably indicative of the existence and direction of changes in behavior due to pregnancy.

Effects of Pregnancy on Behavior

Sprint speed and distance crawled increased by an average of 49% and 37% (respectively) after parturition. The magnitude of this difference was quantitatively related to the stage of pregnancy: the later in gestation females were measured, the greater the reduction in performance. Because the stage of preg-

nancy was unrelated to the mass lost between the behavior tests administered during pregnancy and those administered postpartum, the reduction in speed and distance crawled is probably associated with some changing aspect of the pregnant females' physiology. Pregnant snakes are known to have faster heart rates and greater oxygen consumption than nonpregnant individuals (Birchard et al. 1984). Female reptiles also experience altered hormonal levels during gestation (Chan et al. 1973; Highfill and Mead 1975; Jones and Guillette 1982; Xavier 1982). Unfortunately, the schedules of these and other physiological changes during pregnancy are not well known for snakes, making it difficult to identify potential factors involved in decreased locomotor performance.

Reduced speed and endurance have been linked to recent feeding (Garland and Arnold 1983; Huey et al. 1984; Ford and Shuttlesworth 1986) and pregnancy (Shine 1980; Bauwens and Thoen 1981; Garland 1985; Seigel et al. 1987) in many reptiles. The burden of the extra mass carried during these times is thought to be the cause of this trend. Much theory concerning the evolution of life-history traits in reptiles is based on the assumption that an increase in relative clutch mass (RCM) is associated with a decrease in locomotor ability (Vitt and Congdon 1978; Shine 1980; Vitt and Price 1982; Seigel and Fitch 1984; Seigel et al. 1986; Shine 1988). I was unable to detect any quantitative relationship between reduced locomotor performance and either RCM or litter size. Marginally significant positive correlations with effective relative clutch mass (ERCM) were observed, indicating that changes in mass may be partially responsible for the reduction in speed and distance crawled, although this association is certainly not a strong one. The discrepancy between the effects of RCM and ERCM suggests that RCM measured postpartum is not an accurate estimate of the mass increase experienced by a female during all stages of gestation.

The antipredator displays of females were less defensive during pregnancy than after parturition, but this difference was less pronounced in individuals measured late in pregnancy. The decrease in the display profile with progressing gestation supports the ideas that the display may be hormonally controlled and that the postpartum measurement was conducted so soon after parturition that hormones had not yet returned to nonpregnant levels. If these ideas are valid, the profile of antipredator display actually measures the change in display between early and late gestation because the postpartum display may still be mediated by late-pregnancy hormone levels. Pregnancy-induced and postpartum aggressions in mice are known to begin only a few days before parturition and to last throughout the lactation period. Attempts to link this behavior with various hormones have failed (Svare et al. 1980, 1982; Mann and Svare 1982), although progesterone has been shown to augment the onset of aggression during pregnancy (Mann et al. 1984). Other behaviors apparent only at parturition or oviposition in lizards are also thought to be hormonally controlled (Tokarz and Jones 1979; Jones and Guillette 1982).

The tendency of females to perform more reversals during pregnancy is interpreted as an increased tendency toward crypsis. Pough (1976, 1988) described sudden terminations of flight for the water snake *Nerodia sipedon*, suggesting that this behavior functions as a modification of crypsis. The vertebrate eye tends to

follow the path of a moving object even after the movement has ceased (Walls 1963). Abrupt termination of flight may then result in a predator's losing track of the quarry, providing the prey an opportunity to adopt crypsis as a defensive mechanism even after initial detection. In *T. ordinoides* in the field, an individual generally performs this behavior when its head is near a cover object or a mammal run; after reversing, it slowly crawls into this refuge. A shift in predator-avoidance tactic from flight to crypsis during pregnancy has also been noted in the lizard *Lacerta vivipara* (see Bauwens and Thoen 1981). Other species of lizards (see Rand 1964; Herz et al. 1982; Crowley and Pietruszka 1983) and snakes (Arnold and Bennett 1984) are known to become more aggressive at low temperatures, presumably to compensate for reduced locomotor ability (Herz et al. 1982; Crowley and Pietruszka 1983).

When the analyses were repeated using pregnant-behavior rather than individual-behavior profiles, no relationship between any of the behaviors and the reproductive parameters was observed. These results contradict those of other studies arguing that RCM negatively affects pregnant locomotor performance (Shine 1980; Seigel et al. 1987). This discrepancy could result from differences in experimental design and sample sizes. Using a ratio of pregnant-female speed to average male speed in the same trial as an estimate of the reduction in locomotor ability due to pregnancy, Shine (1980) found that the decrease in performance was negatively associated with RCM in skinks. Differences in activity metabolism between the sexes have been documented for lizards (Garland and Else 1987), casting doubt on the appropriateness of such a comparison. Seigel et al. (1987) observed negative correlations between locomotor performance (speed, distance, and time crawled) and RCM and litter size for *Thamnophis marcianus*, ranging from $r = -0.66$ to $r = -0.96$. Comparing the same variables, the largest correlation found in this study was $r = -0.04$ (for RCM with distance; table 4). Seigel et al. advised caution in interpreting their results because they are based on only 5 and 10 individuals in their two experimental groups. Such caution is supported by demonstrations that Pearson product-moment correlations based on small samples are unreliable estimates of the true population value (Simpson 1986). Contradictions in the results of these two studies are probably also due to differences in the females tested. Snakes examined by Seigel et al. were on controlled diets and were all in the penultimate week of gestation, whereas the subjects used in the current study reflect a wide range of reproductive and physical conditions. The latter sample better represents natural conditions but may be less likely to detect correlations between reproductive parameters and performance than that used by Seigel et al.

The results of this study corroborate other findings that pregnancy adversely affects speed and endurance in reptiles (Shine 1980; Bauwens and Thoen 1981; Garland 1985; Seigel et al. 1987), but they also indicate that RCM may not be as important a factor in the reduction of locomotor performance as was previously thought. Gestation causes a decrease in speed and endurance independent of the burden associated with carrying the clutch. In addition to its effect on locomotion, pregnancy is associated with changes in antipredator tactics and probably foraging behavior (1987 field data on stomach contents show food items in 1 of 123

pregnant *T. ordinoides* females compared with 47 of 188 males and nonpregnant females). Information on basking, foraging, and movement patterns in other reptiles indicates that females tend to be less active during pregnancy (Shine 1980; Bauwens and Thoen 1981), which suggests that behavioral modifications reducing the dependence on locomotion may be widespread.

Behavioral Shifts and Costs of Reproduction

The proposed mechanism by which RCM constitutes a cost of reproduction operates through viability selection: the reduction in locomotor abilities related to carrying a large RCM presumably increases the risk of predation (Vitt and Congdon 1978; Shine 1980; Vitt and Price 1982; Seigel et al. 1987; Shine 1988). Thus, selection that reduces RCM does not act on RCM directly, but rather on the increased probability of predation associated with it. The results of this study suggest that pregnancy itself, and not merely RCM, adversely affects speed and endurance, implying that a decrease in RCM could only partially improve locomotor performance and therefore the probability of survival. A mechanism that relieves the dependence of pregnant females on locomotion has the potential to decrease predation risk more than a reduction in RCM. Shifts toward less-mobile antipredator tactics and foraging modes by females during pregnancy might compensate for poor locomotor ability without the cost of reduced reproductive output that accompanies a smaller RCM. Thus, behavioral modification might allow females to maintain a high level of current fecundity without compromising future reproduction.

The only two studies that have examined the effects of pregnancy on both locomotion and antipredator behavior have found evidence to support this hypothesis. Females shift their antipredator strategies from flight toward crypsis and/or defensiveness during pregnancy (Bauwens and Thoen 1981; this study). Furthermore, in a population of *Lacerta vivipara* that exhibited this type of behavioral shift (Bauwens and Thoen 1981), gravid females did not experience greater mortality during the reproductive season than did males or non-gravid females. The RCM in this population of lizards was also much larger than expected, given the species' normal speed-dependent modes of foraging and predator avoidance, suggesting that the behavioral modification does indeed alleviate selection against reduced locomotor performance.

Although shifts in antipredator strategies and activity patterns may relieve dependence on locomotion, most available information suggests that RCM is being constrained by selection. Small RCM is known to be interspecifically correlated in lizards with mobile escape and foraging modes (Vitt and Congdon 1978; Vitt and Price 1982; Magnusson et al. 1985; Anan'eva and Shammakov 1986) and in snakes with viviparity (Seigel and Fitch 1984; Seigel et al. 1986; for contradictory evidence, see Dunham et al. 1988) and aquatic locomotion (Shine 1988). Behavioral shifts may not be feasible for many species, particularly those that are specialized feeders or have specific habitat requirements (e.g., the iguanid lizard *Platynotus semitaeniatus*; Vitt 1981). Moreover, some types of constraints may not be affected by changes in behavioral modes. In viviparous species, the adverse effects of gestation on survival are manifested over a longer period than in oviparous species, probably intensifying the costs of reproduction for live-bearers

(Seigel and Fitch 1984). Because of the mode of locomotion, carrying a clutch affects the performance of aquatic snakes more severely than that of terrestrial species (Jayne 1985; Shine 1988). Changes in antipredator and foraging modes may not reduce their dependence on locomotion enough to overcome these additional constraints. Nonetheless, exceptions to the relationships between RCM and ecological variables have been observed (see, e.g., Bauwens and Thoen 1981) and may be explained by behavioral modification during gestation.

The data necessary to fully evaluate the potential for selection on RCM and the possibility that behavioral shifts could alleviate such selection are not yet available. While a few studies have shown that pregnant female reptiles experience reduced speed and endurance (Shine 1980; Bauwens and Thoen 1981; Garland 1985; Seigel et al. 1987; this study) and abnormally high mortality (Shine 1980; Andren 1982; Madsen 1987), no evidence has been presented that locomotor performance and probability of survival are quantitatively related (as noted in Seigel et al. 1987). Information on activity patterns and antipredator strategies of reptiles suggests that many species modify their behavior during gestation (Shine 1980; Bauwens and Thoen 1981; this study) and other periods of reduced locomotor ability (Herz et al. 1982; Crowley and Pietruszka 1983), but whether such changes can compensate for the potential decrease in survival probability associated with poor locomotor ability remains untested. Furthermore, for RCM and behavioral shifts to respond to selection, they must exhibit heritable variation, which has not yet been established. Until such information is available, we cannot fully judge the importance of decreased survival as a cost of reproduction in reptiles.

SUMMARY

Because relative clutch mass (RCM) adversely affects locomotor performance, and therefore presumably the survival rate of pregnant females, it is assumed to be constrained by natural selection. I propose that changes in antipredator tactics during pregnancy can reduce females' dependence on locomotion, thereby alleviating selection acting on RCM. Such a behavioral shift would be a more likely response to selection against poor locomotor ability because reductions in RCM have obvious disadvantages (i.e., decreasing fecundity) and can only partially improve speed and endurance.

Comparisons of the locomotor performance and antipredator behaviors of pregnant female garter snakes (*Thamnophis ordinoides*) before and after parturition indicate that locomotor ability declines and that antipredator tactics change during gestation. Females tend more toward cryptic behavior during pregnancy than after. These observations are consistent with behavioral shifts observed in lizards during periods of reduced locomotor ability.

ACKNOWLEDGMENTS

I would like to thank S. Altmann, S. J. Arnold, F. J. Janzen, K. Karoly, C. R. Peterson, N. L. Reagan, R. A. Seigel, R. Shine, and an anonymous reviewer for constructive comments on the manuscript. Reagan assisted with the collection of

animals and data. Arnold and A. F. Bennett graciously provided space and equipment used in this study. This work was supported by grants from Sigma Xi, the University of Chicago Hinds Fund, the National Science Foundation (BSR-8714955 to E.D.B. and BSR-8600066 to Bennett), and the National Institutes of Health (1 RO1 GM 35492-01 to Arnold).

LITERATURE CITED

- Aleksiuik, M. 1977. Sources of mortality in concentrated garter snake populations. *Can. Field-Nat.* 91:70-72.
- Anan'eva, N. B., and S. M. Shammakov. 1986. Ecologic strategies and relative clutch mass in some species of lizard fauna in the USSR. *Sov. J. Ecol. (Engl. Transl. Ekologiya)* 16:241-247.
- Andren, C. 1982. Effect of prey density on reproduction, foraging and other activities in the adder, *Vipera berus*. *Amphib. Reptilia* 3:81-96.
- Arnold, S. J., and A. F. Bennett. 1984. Behavioural variation in natural populations. III. Antipredator displays in the garter snake *Thamnophis radix*. *Anim. Behav.* 32:1108-1118.
- Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *J. Anim. Ecol.* 50:733-743.
- Bell, P. D. 1979. Acoustic attraction of herons by crickets. *J. N.Y. Entomol. Soc.* 87:126-127.
- Birchard, G. F., C. P. Black, G. W. Schuett, and V. Black. 1984. Influence of pregnancy on oxygen consumption, heart rate and hematology in the garter snake: implications for the "cost of reproduction" in live bearing reptiles. *Comp. Biochem. Physiol. A, Comp. Physiol.* 77: 519-523.
- Cade, W. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket songs. *Science (Wash., D.C.)* 190:1312-1313.
- . 1979. The evolution of alternative male strategies in field crickets. Pages 343-390 in M. Blum and N. Blum, eds. *Sexual selection and reproductive competition in insects*. Academic Press, New York.
- Chan, S. W. C., S. Ziegel, and I. P. Callard. 1973. Plasma progesterone in snakes. *Comp. Biochem. Physiol. A, Comp. Physiol.* 44:631-637.
- Charlesworth, B. 1980. *Evolution in age-structured populations*. Cambridge University Press, New York.
- Crowley, S. R., and R. D. Pietruszka. 1983. Aggressiveness and vocalization in the leopard lizard (*Gambelia wislizenii*): the influence of temperature. *Anim. Behav.* 31:1055-1060.
- Cuellar, O. 1984. Reproduction in a parthenogenetic lizard: with a discussion of optimal clutch size and a critique of the clutch weight/body weight ratio. *Am. Midl. Nat.* 111:242-258.
- Dunham, A. E., D. B. Miles, and D. N. Reznick. 1988. Life history patterns in squamate reptiles. Pages 441-552 in C. Gans and R. B. Huey, eds. *Biology of the Reptilia*. Vol. 16. Liss, New York.
- Falconer, D. S. 1981. *Introduction to quantitative genetics*. Longman, New York.
- Ford, N. B., and G. A. Shuttlesworth. 1986. Effects of variation in food intake on locomotory performance of juvenile garter snakes. *Copeia* 1986:999-1001.
- Gadgil, M., and W. Bossert. 1970. Life historical consequences of natural selection. *Am. Nat.* 104: 1-24.
- Garland, T., Jr. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool. (Lond.)*, Ser. A, 207:425-439.
- Garland, T., Jr., and S. J. Arnold. 1983. The effects of a full stomach on locomotory performance of juvenile garter snakes (*Thamnophis elegans*). *Copeia* 1983:1092-1096.
- Garland, T., Jr., and P. L. Else. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *Am. J. Physiol.* 252:R439-R449.
- Hertz, P. E., R. B. Huey, and E. Nevo. 1982. Fight versus flight: body temperature influences defensive responses of lizards. *Anim. Behav.* 30:676-679.
- Highfill, D. R., and R. A. Mead. 1975. Sources and levels of progesterone during pregnancy in the garter snake, *Thamnophis elegans*. *Gen. Comp. Endocrinol.* 27:389-400.

- Huey, R. B., A. F. Bennett, H. John-Alder, and K. A. Nagy. 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. *Anim. Behav.* 32:41–50.
- Jayne, B. C. 1985. Swimming in constricting (*Elaphe g. guttata*) and nonconstricting (*Nerodia fasciata pictiventris*) colubrid snakes. *Copeia* 1985:195–208.
- Jones, R. E., and L. J. Guillette, Jr. 1982. Hormonal control of oviposition and parturition in lizards. *Herpetologica* 38:80–93.
- Law, R. 1979. Optimal life histories under age-specific predation. *Am. Nat.* 114:399–417.
- Madsen, T. 1987. Cost of reproduction and female life-history tactics in a population of grass snakes, *Natrix natrix*, in southern Sweden. *Oikos* 49:129–132.
- Magnusson, W. E., L. J. de Paiva, R. M. da Rocha, C. R. Franke, L. A. Kasper, and A. P. Lima. 1985. The correlates of foraging mode in a community of Brazilian lizards. *Herpetologica* 41:324–332.
- Mann, M. A., and B. Svare. 1982. Factors influencing pregnancy-induced aggression in mice. *Behav. Neural Biol.* 36:242–258.
- Mann, M. A., C. Konen, and B. Svare. 1984. The role of progesterone in pregnancy-induced aggression in mice. *Horm. Behav.* 18:140–160.
- Michod, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. *Am. Nat.* 113:531–550.
- Packard, G. C., and T. J. Boardman. 1987. The misuse of ratios to scale physiological data that vary allometrically with body size. Pages 216–239 in M. E. Feder, A. F. Bennett, W. Burggren, and R. B. Huey, eds. *New directions in ecological physiology*. Cambridge University Press, New York.
- Pough, F. H. 1976. Multiple cryptic effects of cross-banded and ringed patterns of snakes. *Copeia* 1976:834–836.
- . 1988. Mimicry and related phenomena. Pages 153–234 in C. Gans and R. B. Huey, eds. *Biology of the Reptilia*. Vol. 16. Liss, New York.
- Rand, A. S. 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology* 45:863–864.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44:257–267.
- Ryan, M. J., M. D. Tuttle, and L. K. Taft. 1981. The costs and benefits of frog chorusing behavior. *Behav. Ecol. Sociobiol.* 8:273–278.
- Ryan, M. J., M. D. Tuttle, and A. S. Rand. 1982. Bat predation and sexual advertisement in a Neotropical anuran. *Am. Nat.* 119:136–139.
- SAS. 1985. SAS procedures guide for personal computers. Version 6 ed. SAS Institute, Cary, N.C.
- Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age structure. *Ecology* 55:291–303.
- Seigel, R. A., and H. S. Fitch. 1984. Ecological patterns of relative clutch mass in snakes. *Oecologia (Berl.)* 61:293–301.
- Seigel, R. A., H. S. Fitch, and N. B. Ford. 1986. Variation in relative clutch mass in snakes among and within species. *Herpetologica* 42:179–185.
- Seigel, R. A., M. M. Huggins, and N. B. Ford. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia (Berl.)* 73:481–485.
- Shine, R. 1980. "Costs" of reproduction in reptiles. *Oecologia (Berl.)* 46:92–100.
- . 1988. Constraints on reproductive investment: a comparison between aquatic and terrestrial snakes. *Evolution* 42:17–27.
- Simpson, M. J. A. 1986. What is the value of a correlation coefficient? *Anim. Behav.* 34:604–605.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Freeman, San Francisco.
- Svare, B., M. Mann, and O. Samuels. 1980. Mice: suckling stimulation but not lactation important for maternal aggression. *Behav. Neural Biol.* 29:453–462.
- Svare, B., M. Mann, J. Broida, and S. D. Michael. 1982. Maternal aggression exhibited by hypophysectomized parturient mice. *Horm. Behav.* 16:455–461.
- Tokarz, R. R., and R. E. Jones. 1979. A study of egg-related maternal behavior in *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* 13:283–288.
- Vitt, L. J. 1981. Lizard reproduction: habitat specificity and constraints on relative clutch mass. *Am. Nat.* 117:506–514.

- Vitt, L. J., and J. D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* 112:595–608.
- Vitt, L. J., and H. J. Price. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38:237–255.
- Walker, T. J. 1964. Experimental demonstration of a cat locating orthopteran prey by the prey's call. *Fla. Entomol.* 47:163–165.
- Walls, G. L. 1963. *The vertebrate eye and its adaptive radiation*. Hafner, New York.
- Williams, G. C. 1966. *Adaptation and natural selection*. Princeton University Press, Princeton, N.J.
- Xavier, F. 1982. Progesterone in the viviparous lizard *Lacerta vivipara*: ovarian biosynthesis, plasma levels, and binding to transcortin-type protein during the sexual cycle. *Herpetologica* 38: 62–70.