

GENETIC BASIS OF ACTIVITY METABOLISM.
I. INHERITANCE OF SPEED, STAMINA, AND ANTIPREDATOR
DISPLAYS IN THE GARTER SNAKE
THAMNOPHIS SIRTALIS

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Abstract.—Recent conceptual advances in physiological ecology emphasize the potential selective importance of whole-animal performance. Empirical studies of locomotor performance in reptiles have revealed surprising amounts of individual variation in speed and stamina. The present study is the first in a series examining the genetic basis of variation in locomotor performance, activity metabolism, and associated behaviors in garter snakes. Maximal sprint crawling speed, treadmill endurance, and antipredator displays (Arnold and Bennett, 1984; exhibited as snakes reached exhaustion on the treadmill) were measured for approximately six offspring (presumed to be full siblings) from each of 46 wild-caught gravid garter snakes (*Thamnophis sirtalis*). Each character was measured on two days; all were individually repeatable. Correlations of these characters with body mass, snout–vent length, age at testing, litter size, dam mass, and dam snout–vent length were removed by computing residuals from multiple-regression equations. These residuals were used in subsequent genetic analyses. Approximate coefficients of variation of residuals were 17% for speed, 48% for endurance, and 31% for antipredator displays. Broad-sense heritabilities were significant for all characters: speed $h^2 = 0.58$; stamina $h^2 = 0.70$; antipredator display $h^2 = 0.42$. All three residual characters showed positive and statistically significant phenotypic correlations ($r = 0.19$ – 0.36). Genetic correlations (estimated and tested by restricted maximum likelihood) among residuals were positive and highly significant between speed and endurance (0.58), but nonsignificant between speed and antipredator display (0.43), and between endurance and antipredator display (0.26). All environmental correlations were nonsignificant. These data suggest that, contrary to expectations based on previous physiological studies, there may be no necessary evolutionary trade-off between speed and stamina in these animals. This tentative conclusion will have important implications for future theoretical studies of the evolution of locomotor performance and associated antipredator behaviors.

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All animal activities, including foraging, finding and courting mates, and escaping from predators, depend on “activity metabolism,” the physiology of active animals. The potential selective importance of variation in activity metabolism is thus apparent (reviews and references in Garland, 1988; Hertz et al., 1988). Broadly defined, activity metabolism includes characters at multiple levels of biological organization: whole-animal performance, physiology, morphology, and biochemistry. However, organismal performance capacities are the component of activity metabolism affected directly by natural selection (Huey and Stevenson, 1979; Arnold, 1983; Bartholomew, 1986). Therefore, direct measures of locomotor performance have received consid-

erable attention in recent years (e.g., Bennett, 1980; Garland, 1984, 1985, 1988; Huey et al., 1984; Hertz et al., 1988).

One surprising finding of these studies has been the large range of variation in speed and stamina among individual animals (Bennett, 1980, 1988). Even after statistical removal of the confounding effects of body size, individual lizards taken from a single population often vary 2–4 fold in sprint speed and by an order of magnitude in endurance running times on a motorized treadmill (Bennett, 1980; Garland, 1984, 1985, 1988; Garland and Else, 1987). These individual differences are repeatable on a day-to-day basis, for up to eight weeks in captivity (Bennett, 1980; Garland and Arnold, 1983; Garland, 1985; Garland and Else, 1987), and even over one year in the field (Huey and Dunham, 1987).

Most evolutionary biologists would not

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be surprised if there were a genetic component to this extensive individual variation in locomotor performance. On the other hand, such physiologically and biochemically based characters often show considerable acclimatization to environmental conditions on a day-to-day basis or over other short-term time scales (Prosser, 1986). Locomotor performance, in particular, is known to be influenced strongly by training effects in humans, other mammals, amphibians, and fishes (although training effects may be of less importance in natural populations of lizards [Garland et al., 1987]). Such environmental effects would inflate phenotypic variances, leading to lower heritabilities ($h^2 = \text{additive genetic variance} / [\text{additive genetic variance} + \text{dominance variance} + \text{environmental variance}]$; Falconer, 1981). Moreover, physiological characters may vary ontogenetically. The foregoing points suggest that such plastic physiological characters as locomotor performance might generally exhibit relatively low heritabilities. Similar arguments can be made for many behavioral traits.

The genetic bases of locomotor performance and activity metabolism are poorly known. Various physiological and morphological characters that affect locomotion appear to have a genetic basis in humans (Bouchard and Malina, 1983a, 1983b). Race performance is heritable in horses (Hintz, 1980; Langlois, 1980; Tolley et al., 1983) and greyhounds (Ryan, 1975), although the indirect nature of some such performance measures (e.g., lifetime earnings) confounds extrapolation to more natural situations. Van Berkum and Tsuji (1987) have published the only study addressing the quantitative-genetic basis of variation in locomotor performance in a natural (nonhuman) population of vertebrates. These authors report highly significant among-family variance in sprint speed in *Sceloporus* lizards, with broad-sense heritabilities estimated as approximately 0.4–0.6. The inheritance of stamina has apparently not been studied in wild vertebrates (but see DiMichele and Powers [1982]).

The first goal of this study was, therefore, to estimate heritabilities of both speed and stamina in the common garter snake, *Thamnophis sirtalis*. Heritabilities, how-

ever, are not the only quantitative-genetic parameters affecting the evolutionary response to natural selection. Genetic correlations (or covariances) are also of crucial importance (Lande, 1979; Cheverud, 1984). When two or more characters are under directional selection, negative genetic correlations can slow the rate of adaptive phenotypic evolution by a significant amount (review in Arnold [1988]). Genetic and phenotypic correlations often differ in magnitude and even in sign (Falconer, 1981), and the former can only be estimated from information on sets of relatives or from selection experiments.

Comparative studies suggest a necessary phenotypic trade-off between speed and stamina. Among lacertid lizards (Huey et al., 1984), fast species often have limited stamina and vice versa. Similarly, the fastest species of mammals may have limited stamina (e.g., cheetahs [Howell, 1944; Garland, 1983]). Moreover, individual humans are rarely if ever both excellent sprinters and excellent marathoners (Heinrich, 1985).

Physiological and morphological considerations also suggest a necessary trade-off between speed and stamina. For example, vertebrate skeletal muscle consists of different fiber types, which possess different contractile properties and biochemical profiles (Guthe, 1981; Komi, 1984; Gleeson and Harrison, 1986). Most notably, "fast-twitch" fibers contract rapidly (rapid contraction should enhance speed) but also fatigue relatively rapidly, whereas "slow-twitch" fibers contract less rapidly and are more fatigue-resistant. Among humans, variation in fiber-type percentages is considerable, and world-class sprinters tend to have higher percentages of fast-twitch fibers, whereas marathoners tend to have high percentages of slow-twitch fibers (Komi, 1984). Analogous trade-offs are seen among species of anuran amphibians (Putnam and Bennett, 1983 [and references therein]). Thus, one might predict that individual garter snakes with high percentages of fast-twitch fibers would be fast but have low stamina, whereas those with more slow-twitch fibers could attain lower maximal speeds but would have higher stamina. Given that fiber-type distribution appears to have some genetic basis in humans (Bouchard and Malina, 1983a,

1983*b*; Komi, 1984), one might predict a negative genetic correlation between speed and stamina.

A negative genetic correlation between speed and stamina would suggest a necessary evolutionary trade-off or constraint on their joint evolution (Cheverud, 1984; Reznick, 1985; Burger, 1986; Arnold, 1988). Specifically, selection for increased speed would result in a correlated response to selection involving a decrease in stamina and vice versa. Thus, I also estimated the genetic correlation between speed and stamina, hypothesizing that it would be negative.

While testing stamina on a motorized treadmill, I discovered that *T. sirtalis* individuals near exhaustion exhibit antipredator displays similar to those described by Arnold and Bennett (1984) for *T. radix*. Because these behaviors range from passive, defensive displays (coiling in a ball with head hidden) to aggressive, offensive displays that appear to require considerable physical exertion (striking and biting), one might expect correlations between defensive displays and stamina. In particular, I hypothesized that individual snakes exhibiting relatively offensive antipredator displays might also tend to have high stamina. I therefore scored these behaviors during endurance trials and analyzed their inheritance as well.

The present study is the first in a series examining the quantitative genetics of activity metabolism in *T. sirtalis*. Subsequent papers will consider potential physiological, morphological, and biochemical correlates of locomotor performance, including maximal rate of oxygen consumption, hematocrit, relative heart mass, enzyme activities measured in vitro, and scale counts (cf. Garland, 1984; Garland and Else, 1987; Arnold and Bennett, 1988).

MATERIALS AND METHODS

Animal Collection and Maintenance.—Forty-six gravid garter snakes (*Thamnophis sirtalis*) were captured between 9 June and 4 July 1984 in the vicinity of Eagle Lake, Lassen Co., CA (State of California Department of Fish and Game Scientific Collecting Permit #0983 to S. J. Arnold). (Dietary ecology of snakes from this area is discussed in Kephart [1982] and Kephart

and Arnold [1982].) After transportation by car to the University of California, Irvine, on 5 July 1984, dams were housed individually in plastic shoeboxes, maintained in an environmental chamber on a 12-hr photophase (30°C days, 20°C nights). Water was always available. Dams were offered cooked fish mixed with chopped earthworms and a multivitamin-mineral supplement weekly. All appeared to remain in good health during the course of the experiments.

Cages were checked at least twice daily. As each dam gave birth, her offspring were weighed and checked for obvious deformities. From each litter, six nondeformed newborn snakes (or all individuals if litter size was less than 6) were chosen randomly and placed in individual transparent plastic containers (volume = 0.5 liters) with ground corn cob for substrate and water dishes. All newborn snakes were removed from the environmental chamber and housed at room temperature (approximately 20°C) until the day before performance trials began.

The presence of food in the stomach affects both locomotor performance and antipredator displays in garter snakes (Garland and Arnold, 1983; Ford and Shuttlesworth, 1986; Herzog and Bailey, 1987). On the other hand, withholding food (starvation) should also affect performance. Moreover, new born snakes vary greatly in their willingness to eat (Arnold, 1981*a*, 1981*b*, 1981*c*). In an attempt to reduce such effects in the present study, I chose to withhold food from all newborn snakes. However, not all individuals could be measured at the same age, so, as discussed below, I attempted to remove statistically the effects of age of testing (which is equivalent to days of fasting).

Testing Schedule.—Sets of six families of full sibs were tested on days 1 and 2 for maximal sprint crawling speed and on days 3 and 4 for treadmill endurance and antipredator displays. All measurements of organismal performance were conducted during the normal photophase in the environmental chamber at 30°C. This temperature approximates the mean body temperature of *T. sirtalis* when active in the field (Gibson and Falls, 1979; C. R. Peterson, pers. comm. [for Eagle Lake snakes]).

Maximal Sprint Crawling Speed.—Max-

imal sprint crawling speed was measured using standard techniques (Huey, 1982; Huey and Hertz, 1984; Huey et al., 1984; Garland, 1985; Huey and Dunham, 1987). Snakes were chased as fast as possible along the 2.0-m photocell-timed track described by Garland (1985), with artificial plastic grass carpet as substrate. Individuals were removed from their containers, placed in front of the first photocell, and induced to crawl at top speed by tapping the tail. Each was chased down the track twice in quick succession. After a rest of at least two hours, the sequence was repeated. Another four trials were conducted the following day.

For each of the eight trials, the fastest speed for any 0.5 m interval (representing at least three sets of photocells) was calculated. The single fastest speed recorded each day was noted. These fastest daily speeds were used to calculate repeatabilities.

Because maximal physiologically and/or morphologically determined performances were desired, the single fastest speed recorded on either day was used as the measure of maximal speed in subsequent analyses. (In the present study, timing errors for speed and stamina are negligible, relative to the range of individual variation.) Using maximal performances is analogous to human exercise physiologists' attempts to reduce the effects of differences in motivation (e.g., Heinrich, 1985) by using personal best performances in studies of the mechanistic determinants of individual differences. Previous studies of lizards have demonstrated correlations between maximal measures of stamina and individual differences in various physiological and morphological characters (Garland, 1984; Garland and Else, 1987).

Treadmill Endurance.—Endurance capacity at a relatively low, controlled speed was measured as snakes crawled on a motorized treadmill. To provide adequate traction, adhesive-backed stairway safety tape was applied to the rubberized cloth belt surface in a checkerboard pattern covering almost half of the belt surface. The effective belt surface was 79 cm long by 21 cm wide.

I wished to measure endurance at a work load that would be supported largely by aerobic metabolism. Preliminary tests indicated that a speed of 0.4 km/hr for new-

born snakes would yield average endurance times of approximately 6 min, a length of time during which aerobic production of ATP must contribute significantly to muscular contraction (see Ruben, 1976; Pough, 1977; Howald et al., 1978; Bennett, 1982; Feder and Arnold, 1982; Arnold and Bennett, 1984). Most individuals crawled readily at this speed, matching belt speed smoothly until they were near exhaustion.

Snakes were removed from their individual plastic containers, placed on the moving treadmill, and induced to crawl by gentle tapping about the tail and posterior body with a foam-rubber-tipped pointer (total length 19.5 cm, tip approximately 1.5 cm diameter). Taps were used as necessary to keep the snake moving, although many individuals matched tread speed with little prodding. As animals neared exhaustion, tapping frequency was increased to approximately four taps/sec.

After some time on the treadmill, snakes failed to maintain tread speed and fell off the rear of the belt. When fall-offs occurred, snakes were picked up, placed immediately back on the center of the belt, and again induced to crawl by tail tapping. Exhaustion was defined as when a snake fell off the belt for the third time (cf. Huey et al., 1984). Total time on the treadmill until exhaustion was rounded to the nearest 1 sec for statistical analyses. Each individual was tested on two days. Values on both days were analyzed for repeatability; the higher of the two values was employed in subsequent analyses.

Antipredator Displays.—As *Thamnophis sirtalis* individuals reached exhaustion on the treadmill, they would adopt characteristic antipredator displays, similar to those described by Arnold and Bennett (1984) for *T. radix*. I also used an open-ended catalog to record displays as they occurred, noting separately the behaviors involving the tail, body, and head. I used a scoring system modified from that of Arnold and Bennett (see Appendix), stemming from their observation that the displays seem to fall on a more-or-less continuous scale of "defensive" (passive) to "offensive" (or aggressive) displays, with the most defensive behaviors scored as 0. I analyzed tail, body, and head scores separately to test for correlations

among these components of overall behavior. In addition, following Arnold and Bennett (1984), I computed a simple sum of tail, body, and head scores for each individual, and term this "antipredator display." (Arnold and Bennett [1984] discuss the use of both simpler and more complicated weighting schemes, none of which yielded better results than the simple sum.) Values on both days were analyzed for repeatability; their average was analyzed subsequently.

Attempts to Reduce Nongenetic Maternal Effects.—As in previous studies (Arnold, 1981a, 1981b, 1981c; Arnold and Bennett, 1984), newborn garter snakes used in the present study are presumed to represent sets of full siblings (Devine, 1977; Ross and Crews, 1977). A limitation of full-sib analyses for estimating heritabilities is that they can yield only broad-sense heritabilities. These probably overestimate narrow-sense heritabilities, because dominance, nongenetic maternal effects, and common family environment are confounded with estimates of the additive effects of genes (Arnold, 1981a; Falconer, 1981; Stearns, 1984). On the other hand, J. M. Schwartz (pers. comm.) has used electrophoretic evidence to demonstrate multiple paternity in some eastern populations of *T. sirtalis*. As noted by Stearns (1984 p. 370), assuming that families contain only full sibs, if they actually contain unknown half sibs, could lead to underestimates of heritabilities. In any case, presumed full sibs are presently the only sets of relatives readily available for reptiles (at least for characters that may change ontogenetically, such as locomotor performance) and can provide an important first step in genetic analyses of natural populations (Arnold, 1986).

Many nongenetic maternal effects in reptiles may be mediated through maternal size and condition, which should depend, in part, on age and on past nutritional (and perhaps thermal) history. In turn, maternal size and condition might affect locomotor performance of offspring in two ways. First, dams that were larger and/or in better condition might produce larger offspring, and both speed and stamina are usually positively correlated with body size in ontogenetic series of reptiles (Huey, 1982; Garland and

Arnold, 1983; Garland, 1984, 1985; Huey and Hertz, 1984; Garland and Else, 1987 [and references therein]); such effects were also found in the present study (see below). Second, larger dams and/or those in better condition might produce offspring of higher quality, in the sense of having, for example, more glycogen in their muscles and livers, or perhaps a higher enzyme content per gram wet weight of tissue. Such variation in offspring would in turn be expected to affect their performances (e.g., Garland, 1984; Garland and Else, 1987).

I therefore sought to remove statistically the effects of body size and condition, maternal body size and condition, and litter size, on the characters of primary interest. Thus, before conducting the genetic analyses, I conducted stepwise multiple-regression analyses of speed, stamina, and antipredator displays on a series of potentially significant covariates: mass, snout-vent length, age, age², dam mass, dam snout-vent length, and litter size. (I also examined plots of each character versus the various covariates to check for obvious nonlinearities. Except for the relationships between speed and stamina and age [see below], none was apparent.) After determining which of these were statistically significant as independent variables, I computed residuals from multiple-regression equations for further analyses.

In spite of the foregoing arguments, some nongenetic maternal effects may have persisted. On the other hand, effects of heritable variation in body size may also have been removed by taking residuals. Estimating nongenetic versus heritable effects of body size would require information on other sets of relatives (e.g., a full-sib, half-sib breeding design; Falconer, 1981). As noted above, common family environments were disrupted on the day of birth.

Statistical Analyses.—Prior to computation of residuals, I examined visually the distribution of each character and used procedures outlined by Sokal and Rohlf (1981 Ch. 7) to test for significant deviations from normality. Where appropriate, I tried various transformations (log, square, square root, inverse, inverse square root; Sokal and Rohlf, 1981 p. 425) and then used the one that most closely approached normality. In

practice, no transformation was used for speed, but endurance and antipredator display were transformed to logarithms. For a comparative measure of the variability of all three characters, I \log_{10} -transformed each character, regressed them on the appropriate significant covariates (see Results), then compared SD's of residuals (multiplied by 2.3026, since variables were \log_{10} - rather than \log_e -transformed). This quantity is approximately equivalent to a coefficient of variation (Garland, 1984).

I used Shaw's (1987) program for restricted maximum-likelihood estimation and significance testing of quantitative-genetic parameters. One advantage of the maximum-likelihood approach is that it allows tests of significance for genetic and environmental correlations, which are not available with ordinary least-squares approaches. However, the power of the likelihood tests may be relatively low (see Shaw, 1987). Point estimates of genetic and environmental variances and covariances (and, hence, heritabilities and correlations) were based on parameter estimates for the complete (three character) data set, with no parameters constrained to zero. (Because only data for sets of presumed full sibs were available, dominance variances and covariances could not be estimated independently of additive genetic variances and covariances.) Significance tests involved comparing the likelihood of a constrained model (one or more parameters constrained to zero, as appropriate) with that of the unconstrained model. Twice the difference in likelihoods is distributed approximately as chi-square, with *d.f.* = the number of parameters constrained to zero (Shaw, 1987).

To facilitate comparisons with previous studies, I also estimated genetic parameters in the usual least-squares fashion (formulas in Arnold [1981a] and Falconer [1981]) and calculated 95% confidence intervals for heritabilities using Bulmer's (1980 p. 84) algorithm. SPSS/PC+ (Norusis, 1986) was used for most calculations. Statistical significance was judged at $P < 0.05$ in all cases.

RESULTS

The 46 dams gave birth between 2 August and 6 September 1984. Litter size ranged from one to 26 ($\bar{x} \pm SD = 12.2 \pm 5.15$). Of

the 562 offspring produced, 23 were born dead (frequencies were 10, 5, 2, 2, 1, 1, 1, and 1 individuals born dead in each of eight different families); another 13 were born with obvious deformities (eight with kinked tails, bodies, or necks; one with deformed ventral scales; four with one or both eyes small or absent); there were no more than two deformed individuals in any one family). Dam mass following birth ranged from 30.7 to 94.4 g ($\bar{x} \pm SD = 60.8 \pm 13.66$); snout-vent length ranged from 467 to 763 mm ($\bar{x} \pm SD = 585 \pm 53.4$). The 249 neonates measured (representing a random sample of those born alive and with no obvious deformities) ranged in mass from 1.68 to 3.57 g ($\bar{x} \pm SD = 2.52 \pm 0.374$) and in snout-vent length from 160 to 207 mm ($\bar{x} \pm SD = 187 \pm 9.2$). Speed trials were conducted when snakes were 4–53 ($\bar{x} \pm SD = 23.7 \pm 13.98$) days old; endurance and antipredator displays were scored when snakes were 6–56 ($\bar{x} \pm SD = 28.6 \pm 14.74$) days old. Body masses following endurance trials ranged from 1.22 to 3.34 g ($\bar{x} \pm SD = 2.22 \pm 0.357$); thus, on average, snakes lost less than 12% of birth weights. Five individuals died for unknown reasons before all trials were completed and are not included in the analyses ($N = 249$).

Repeatability.—Measurements for all characters were significantly ($P < 0.0001$) repeatable between trials (days), and none differed significantly between trials. Intra-class correlations were 0.803 for speed ($n = 275$), 0.685 for \log_{10} endurance ($N = 231$), and 0.668 for antipredator display ($N = 248$). Corresponding Pearson product-moment correlations between trials 1 and 2 were 0.802, 0.696, and 0.674.

Correlations Among Components of Defensive Displays.—Correlations among the three separate components of overall antipredator display were not strong but were all positive and significant ($N = 249$) (tail \times body: $r = 0.174$, $P < 0.01$; tail \times head: $r = 0.225$, $P < 0.001$; body \times head: $r = 0.398$, $P < 0.0001$). This suggests that the ordering of scores for each component was consistent with a common underlying continuum (of defensive-offensive; see discussion in Arnold and Bennett [1984]). Percentages of individuals scored in each category are noted in the Appendix.

TABLE 1. Descriptive statistics for organismal performance traits ($N = 249$). Speed was approximately normally distributed on an arithmetic scale; endurance and antipredator display were approximately log normally distributed. The scoring system for antipredator display and the percentages of individuals scored in each category are presented in the Appendix.

Character (units)	Mean (SD)	Range	CV (%)	SD of logs	SD of residuals
Speed (km/hr)	1.40 (0.207)	0.87–2.01	14.8	15.0	12.4
Treadmill endurance (sec)	363 (211.2)	59–1,394	58.3	59.6	47.8
Antipredator display	4.4 (1.56)	1.5–9.6	35.9	32.5	31.6

Descriptive Statistics, Variability, and Scaling.—Speed, stamina, and antipredator displays all were quite variable (Table 1). As in previous studies (Bennett, 1980; Garland and Arnold, 1983; Garland, 1984; Garland and Else, 1987), treadmill endurance (range: 59 sec–23.2 min) was considerably more variable than was maximal crawling speed (range: 0.87–2.01 km/hr). This relative variability was maintained (Table 1: “SD of residuals”) after removing the effects of several significant covariates, including body size and age at testing (see next section). Coefficients of variation for antipredator displays (32–36%) are considerably lower than those reported by Arnold and Bennett (1984) (65–80%, computed from their table II), who used a more compressed scoring scale (see Appendix).

Coefficients of static allometry were computed as the partial regression of \log_{10} (speed) or \log_{10} (stamina) on \log_{10} (body mass), holding age and age² (see next section) constant. Speed scaled as $\text{mass}^{0.289 \pm 0.111}$ ($\pm 95\%$ confidence interval; partial r^2 for mass = 12.2%); stamina scaled as $\text{mass}^{1.798 \pm 0.421}$ (partial r^2 for mass = 23.8%). Excluding age and age² from the analyses increased the slopes: speed scaled as $\text{mass}^{0.350 \pm 0.117}$ ($r^2 = 12.2\%$); stamina scaled as $\text{mass}^{1.919 \pm 0.430}$ ($r^2 = 23.8\%$). A stronger scaling of stamina than of speed has been noted within other species of reptiles (Garland, 1984, 1985, unpubl.; Garland and Else, 1987) and may result in part from the generally much higher variance in stamina, as compared with speed. \log_{10} (antipredator display) did not vary in relation to body mass ($r^2 = 0.1\%$).

Variation Among Families.—Analysis of variance indicated highly significant components of variance among families for raw values of all three characters ($d.f. = 45, 203$; all $P < 0.0001$) (speed: 50.5%, $F = 8.50$; \log_{10} (endurance): 53.8%, $F = 7.30$;

\log_{10} (antipredator display): 24.6%, $F = 2.76$). As shown in the next two sections, these estimated proportions of variance among families were reduced when the effects of various covariates were factored out statistically. For example, for residuals of speed regressed on age² only, 42.2 of the variance was among families; and for residuals of \log_{10} (endurance) regressed on both age and age², 49.5% of the variance was among families (antipredator displays did not vary significantly with age).

Effects of Covariates.—Several of the potential covariates were intercorrelated (Table 2). Larger dams gave birth to both greater numbers of offspring and larger offspring than did smaller dams. Offspring size and litter size, however, were uncorrelated.

As expected, several covariates explained significant amounts of the variance in speed, stamina, and antipredator displays. The intercorrelations noted above may confound attempts to interpret the independent effects of each covariate (multicollinearity confounds estimates of partial regression coefficients; review in Slinker and Glantz [1985]), but such interpretation is not of prime concern here. Rather, I wished simply to remove as much of the variation that might probably be related to nongenetic maternal effects and/or common family environments as possible.

Speed did not deviate significantly from normality and was not transformed prior to further analyses. Stepwise multiple regression indicated that \log (snout–vent length) (partial $r^2 = 17.1\%$), age² (partial $r^2 = 13.1\%$; age was standardized prior to being squared to reduce multicollinearity between age and age²), \log (dam snout–vent length) (partial $r^2 = 1.3\%$), and \log (dam mass) (partial $r^2 = 1.0\%$) were all significant predictors of speed (multiple $r^2 = 32.5\%$). Thus, longer individuals were faster, those tested at older ages

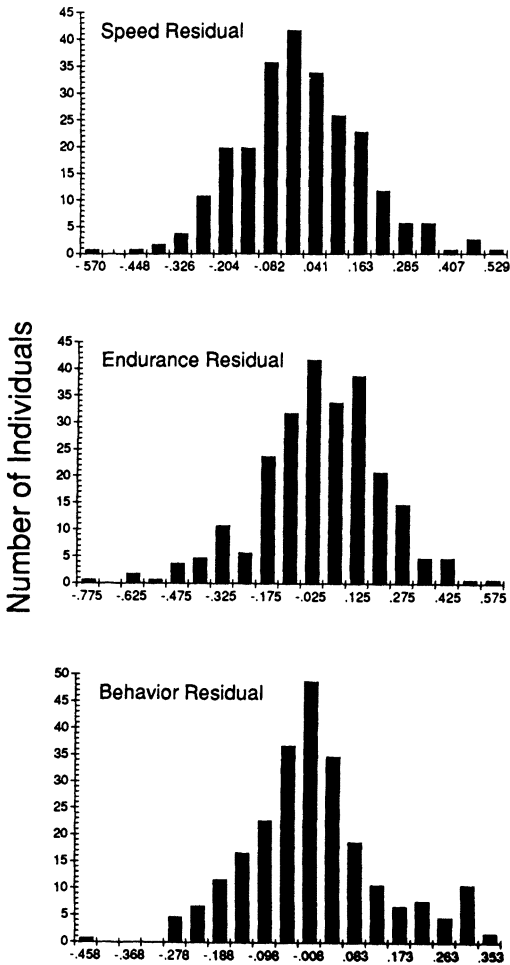


FIG. 1. Distributions of residuals ($N = 249$) from multiple-regression equations (see text). Independent variables (all statistically significant) were: $\log(\text{snout-vent length})$, age^2 , $\log(\text{dam snout-vent length})$, and $\log(\text{dam mass})$ for maximal sprint crawling speed; $\log(\text{body mass})$, $\log(\text{snout-vent length})$, age , age^2 , and litter size for treadmill endurance time; and litter size for antipredator display. These residuals were used for estimates of quantitative-genetic parameters.

were somewhat slower (and this relationship was curvilinear downward), and longer and/or heavier dams produced offspring that were slightly faster. Computed residuals were approximately normally distributed (Fig. 1).

Endurance times were positively skewed. A log transformation yielded a distribution that was somewhat negatively skewed (coefficient of skewness, $g_1 = -0.341$, $t_s = -2.21$, $P < 0.05$). $\log(\text{body mass})$ (partial $r^2 = 23.8\%$), $\log(\text{snout-vent length})$ (partial $r^2 = 1.9\%$), age (partial $r^2 = 1.5\%$), age^2 (partial $r^2 = 4.3$), and litter size (partial $r^2 = 4.1\%$) explained significant amounts of the variation in $\log(\text{endurance})$ (multiple $r^2 = 35.7\%$). Longer individuals and those that were heavy for their length had greater stamina; individuals from larger litters also had somewhat greater stamina. Stamina increased slightly up to approximately three weeks of age, then declined. Residuals from this multiple regression (Fig. 1) were somewhat leptokurtotic (coefficient of kurtosis, $g_2 = 0.743$, $t_k = 2.42$, $P < 0.02$) and negatively skewed ($g_1 = -0.426$, $t_s = -2.77$, $P < 0.01$).

The negative effect of age at testing on both speed and stamina is not surprising, because newborns were not fed. The slight increase in stamina up to approximately three weeks of age, followed by decreasing stamina, is also not unexpected. Increases in stamina during early ontogeny, which are in turn related to changes in blood oxygen-carrying capacity, have been documented in both garter snakes (Pough, 1977, 1983 [and references therein]) and lizards (Garland and Else, 1987).

Antipredator displays were leptokurtotic and positively skewed; a few individuals were very aggressive. A log transform al-

TABLE 2. Correlations among potential covariates of organismal performance characters ($N = 249$). Significant correlations ($P < 0.05$) are indicated by asterisks.

Variable	Variable				
	$\log(\text{body mass})$	$\log(\text{snout-vent length})$	Litter size	$\log(\text{dam mass})$	$\log(\text{dam snout-vent length})$
$\log(\text{body mass})$	—	0.798*	0.003	0.463*	0.367*
$\log(\text{snout-vent length})$		—	0.036	0.337*	0.389*
Litter size			—	0.466*	0.512*
$\log(\text{dam mass})$				—	0.849*
$\log(\text{dam snout-vent length})$					—

most eliminated the kurtosis and reduced (but did not eliminate) the skewness ($g_2 = 0.455$, $t_k = 1.48$, $P > 0.10$; $g_1 = 0.444$, $t_s = 2.86$, $P < 0.01$). Antipredator displays were uncorrelated with either measure of body size, either measure of dam size, or age. The only significant covariate of log (antipredator display) was litter size, which explained 4.8% of the variance. Individuals from larger litters exhibited slightly more offensive (aggressive) displays. Residuals of antipredator displays (Fig. 1) were somewhat positively skewed ($g_1 = 0.317$, $t_s = 2.058$, $P < 0.05$).

Heritabilities.—Analysis of variance indicated highly significant components of variance among families for all three residual characters ($d.f. = 45, 203$; all $P < 0.0001$) (speed: 28.8%, $F = 3.18$; endurance: 34.8%, $F = 3.88$; antipredator display: 20.8%, $F = 2.42$). As expected, all of these proportions of variance among families are lower than those computed for raw values or for residuals from regressions on age and/or age² only (see *Variation Among Families* above). Corresponding heritabilities are 0.58, 0.70, and 0.42. Estimates and 95% confidence intervals using Bulmer's (1980) algorithm were $0.33 < 0.58 < 0.88$ for speed, $0.44 < 0.70 < 1.00$ for endurance, and $0.19 < 0.41 < 0.70$ for antipredator display. Heritabilities, estimated with Shaw's (1987) restricted maximum-likelihood program were 0.58 for speed ($X^2 = 35.3$, $P < 0.0001$), 0.70 for endurance ($X^2 = 46.2$, $P < 0.0001$), and 0.42 for antipredator display ($X^2 = 19.7$, $P < 0.0001$) ($d.f. = 1$, in each case).

Heterogeneity of Variance Among Families.—Homogeneity of variance among families is assumed in both least-squares and maximum-likelihood significance tests. Moreover, as noted by Mitchell-Olds and Rutledge (1986), heterogeneity of variances among families may suggest something about the number of genes underlying a quantitative character and the magnitude of their effects. In particular, major-gene effects are suggested if families with intermediate scores are more variable than are extreme families. I therefore computed Cochran's C , Bartlett-Box F , and Hartley's F_{\max} statistics with procedure ONEWAY in SPSS/PC+ (Sokal and Rohlf, 1981; Norusis, 1986). Apparent statistical significance

was attained only for residual endurance (Cochran's $C = 0.0898$, approximate $P = 0.047$; Bartlett-Box $F = 1.322$, approximate $P = 0.078$; Hartley's $F_{\max} = 42.2$, approximate $P < 0.01$). I also conducted Levene's test, which is based on an ANOVA of the absolute deviations of each individual's value from its corresponding family mean (Conover et al., 1981). Results for all three characters were statistically significant (all P 's approximately = 0.01), but the magnitude of heterogeneity among families was only approximately 10% for each character. The extent to which this amount of heteroscedasticity may have biased significance tests is unknown (R. G. Shaw and T. Mitchell-Olds, pers. comm.), although the moderate-to-high magnitude of all calculated heritabilities suggests that each is actually significantly greater than 0.

Plots of the absolute deviations for individuals versus family means of absolute deviations and corresponding quadratic regressions were examined for patterns in the heterogeneity of variances among families (T. Mitchell-Olds, pers. comm.). No obvious patterns were apparent, but the quadratic term explained 4.7% of the variance in absolute deviations for speed ($P = 0.0006$), with extreme families being somewhat more variable. Since intermediate families were not more variable for any character, these analyses do not suggest major-gene effects.

Phenotypic, Genetic, and Environmental Correlations.—Phenotypic correlations among the residual characters were all positive and significant, though of relatively low magnitude (Table 3). Thus, fast snakes tended to exhibit high endurance and to adopt relatively offensive antipredator displays. The positive correlation between residual speed and residual stamina (Fig. 2) is contrary to expectations based on physiological considerations (see Introduction).

In all cases, genetic correlations are of the same sign but stronger in magnitude than are phenotypic correlations (Table 3). The genetic correlation between speed and endurance is highly significant ($X^2 = 8.76$, $P < 0.005$; see also Fig. 2 for correlation between speed and endurance for litter means), while that between speed and antipredator display is marginally nonsignificant ($X^2 = 3.31$,

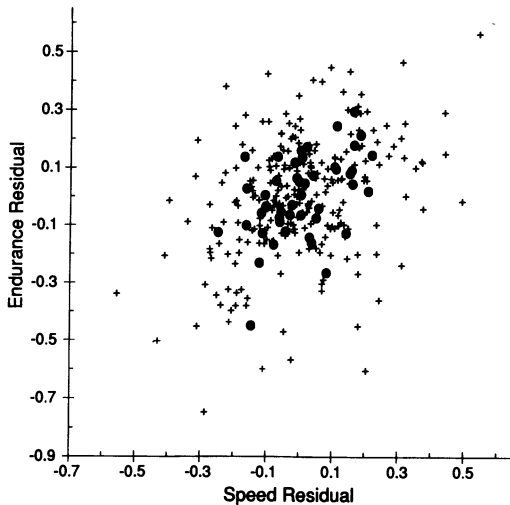


FIG. 2. Positive phenotypic correlation between endurance residuals and speed residuals ($N = 249$, $r = 0.359$, $P < 0.0001$). Solid circles represent family means, illustrating that the two characters tend to run together in families; this pattern suggests a positive genetic correlation (see Table 3 for estimates of genetic correlations).

$P > 0.05$), and that between endurance and antipredator display is nonsignificant ($X^2 = 1.28$, $P > 0.20$) ($d.f. = 1$ in each case). All environmental correlations are nonsignificant, as indicated by maximum-likelihood tests.

DISCUSSION

Heritabilities.—Speed, stamina, and antipredator displays all show significant additive genetic variance. Heritability of antipredator displays (0.41 by Bulmer's algorithm) is statistically indistinguishable from Arnold and Bennett's (1984) estimate for newborn *T. radix* (0.45). Heritability of speed (0.58 by Bulmer's algorithm) is very similar to that estimated for hatchling lizards by van Berkum and Tsuji (1987): 0.59 for their "physiological measure." All of these values are in turn similar to estimates of various indices of racing ability in horses (Hintz, 1980; Langlois, 1980; Tolley et al., 1983) and greyhounds (Ryan, 1975). The foregoing suggests that natural selection acting on any of the characters measured in the present study would result in genetic response.

The foregoing conclusions are based on estimates of broad-sense heritabilities (see

Materials and Methods). It would therefore be highly desirable to know by what extent these values overestimate true narrow-sense heritabilities. Unfortunately, no comparisons are presently available for garter snakes, and few exist for any natural populations of vertebrates. Stearns (1984), for example, reports differences between full-sib (broad-sense) and parent-offspring estimates of heritabilities. Boag (1983), on the other hand, reports values that are virtually identical. Although many studies of domesticated vertebrate populations quantify differences between broad- and narrow-sense heritabilities (Falconer, 1981), their relevance for the present study is unclear.

Genetic Constraints on the Evolution of Locomotor Performance?—The response to selection depends on genetic correlations, in addition to the heritability of individual characters. As discussed in the Introduction, several empirical observations suggest a necessary trade-off between capacities for speed versus stamina. The positive genetic correlation between speed and stamina found in the present study (Table 3, Fig. 2) is therefore surprising. One possible explanation is that family differences in overall physical (nutritional) condition influenced both speed and stamina in similar ways. Analogous concerns have been raised in studies of life-history components, e.g., "good environments" may increase both survivorship and fecundity (Reznick et al., 1986). Such effects seem unlikely to explain the present results, however, because covariates (mass and snout-vent length) that should index differences in condition were factored out statistically before calculation of genetic parameters.

Alternatively, perhaps most of the variation among families is not in percentage distribution of fiber types, but rather, in overall muscle mass per unit body mass (that is, snakes differ in shape or "physique"). In humans, world-class sprinters are usually built more robustly than are marathoners; in the lizard *Ctenosaura similis*, thigh-muscle mass correlates positively with treadmill endurance (Garland, 1984). In the present study, $\log(\text{body mass})$ and $\log(\text{snout-vent length})$ were factored out statistically prior to genetic analyses; this should have factored out some differences in shape. How-

TABLE 3. Correlations among speed, treadmill endurance, and antipredator displays (based on residuals from multiple regression equations). Phenotypic correlations are standard Pearson product-moment correlations. Genetic correlations are restricted maximum-likelihood estimates, followed in parentheses by 1) least-squares estimates, obtained by partitioning covariance among versus within families and 2) correlations among weighted litter means, computed as in Arnold (1981a). Environmental correlations are restricted maximum-likelihood estimates, followed in parentheses by least-squares estimates, computed by equation 19.1 of Falconer (1981) (also, eq. 2 of Arnold [1981a]). Significance of phenotypic correlations was tested in the usual way (Sokal and Rohlf, 1981). Significance tests for likelihood estimates of genetic and environmental correlations were made by comparing the likelihood of the full model with the likelihood of a model with the corresponding parameter constrained to zero (Shaw, 1987). Significance tests for least-squares estimates of genetic and environmental correlations were not attempted. Significant correlations ($P < 0.05$) are indicated by asterisks.

Variable	Correlation	Variable	
		Endurance	Antipredator display
Speed	Phenotypic	0.359*	0.185*
	Genetic	0.588* (0.583, 0.489)	0.426 (0.219, 0.312)
	Environmental	-0.034 (-0.027)	-0.046 (0.157)
Endurance	Phenotypic		0.204*
	Genetic		0.257 (0.255, 0.230)
	Environmental		0.162 (0.158)

ever, snakes that were heavy for their length may have been fat, muscular, or both, so some body shape effects may have remained in the residual characters.

Another factor that might account for positive covariation between speed and stamina is variation in overall patterns of muscle recruitment. Perhaps snakes differ in the total percentage of muscle that can be recruited during both speed and endurance trials. Finally, ratios of body:tail vertebrae correlate in complex ways with individual differences in locomotor performance in *T. radix* (Arnold and Bennett, 1988). It is also possible that snake locomotion is fundamentally so different from terrestrial locomotion with legs (Hildebrand et al., 1985; Jayne, 1986) that predictions from the latter may be irrelevant for the former.

A positive correlation between speed and stamina may not be as unusual as suggested by the foregoing arguments. Ford and Shutlesworth (1986) noted a positive phenotypic correlation between speed and stamina among juvenile *Thamnophis marcianus*, although Garland and Arnold (1983) found no significant correlation for juvenile *T. elegans*. Interspecific comparisons of speed and stamina are almost nonexistent for snakes (Ruben, 1976, 1977; Jayne, 1986); however, Mosauer's (1935) "maximum" and "prowling" speeds for six species are posi-

tively correlated ($r = 0.817$, $P < 0.05$). Unfortunately, Mosauer (1935) reports neither measurement temperatures nor locomotor modes, either of which could have affected both speed and stamina (Jayne, 1986). Interestingly, a trade-off between speed and constricting abilities has also been suggested (Ruben, 1977; Jayne, 1986).

Among individual lizards, speed and stamina do not appear to be negatively correlated at the phenotypic level (Bennett, 1980; Garland, 1984; Garland and Else, 1987). Moreover, human decathletes are relatively good at both sprint and sustained activities. Similarly, some species of lizards are both fast and have good stamina (Garland, 1988), as is true for some mammals (e.g., horses and dogs). Recognized "cursorial" adaptations (e.g., changes in limb bone lengths and proportions) may enhance both speed and stamina (Howell, 1944; Hildebrand, 1982; see also Hildebrand et al. [1985]). Finally, maximal sprint running speeds and maximal aerobic speeds (speed at which maximal oxygen consumption is attained) of 18 species of mammals are uncorrelated ($r = 0.135$ after removing correlations with body mass; Garland et al., 1988). Clearly, the phenotypic relationship between speed and stamina is complex and deserves further study.

Correlations Between Locomotor Performance and Defensive Displays.—Phenotypic

ically, antipredator display was positively and significantly correlated with both speed (0.185) and stamina (0.204); snakes exhibiting offensive (aggressive) displays tended also to be relatively fast and to have relatively high stamina. Therefore, selection on either performance or behavior will result in some correlated selection on the other (Lande and Arnold, 1983). Moreover, in nature, one might predict that the success of different antipredator displays will depend in part on an individual's inherent capacity for locomotion. For example, a snake that "chose" to crawl away from a predator at top speed would presumably be more successful if it were actually a fast individual. The effectiveness of striking and biting repeatedly might be facilitated by high stamina.

Thamnophis sirtalis exhibited considerably more offensive (aggressive) displays than did the *T. radix* studied by Arnold and Bennett (1984). (Nevertheless, estimated heritabilities are strikingly similar.) The adaptive significance of these interspecific differences in antipredator displays is unknown but worthy of further ecological and comparative studies (e.g., Greene, 1979, 1987; Kephart, 1982; Kephart and Arnold, 1982; Herzog and Burghardt, 1986).

Implications for Theory.—The actual physiological and/or morphological mechanisms that result in an apparent positive genetic correlation between speed and stamina in garter snakes are currently unknown. Nevertheless, the existence of such a correlation, if general, has important implications for future theoretical studies.

Although no theory concerning the evolution of locomotor performance (and associated antipredator behaviors) has yet been developed, such a theory will likely be based on optimality considerations (e.g., Alexander, 1982) and, hence, would rely in part on some assumptions concerning necessary trade-offs between various components of performance (cf. theories of life-history evolution: Rose, 1984; Reznick, 1985; Giesel, 1986; Reznick et al., 1986). As noted above, one might be tempted to predict such trade-offs based on patterns of phenotypic correlation or existing knowledge of the physiology and biomechanics of locomotion. However, the present results demonstrate that genetic analyses of loco-

motor performance may suggest evolutionary predictions contrary to those based on comparative physiology and morphology. Finally, even if elements of locomotor performance are themselves positively intercorrelated, it should be noted that higher-level trade-offs may exist. For example, overall locomotor performance (some index of capacities for speed and stamina) might be negatively genetically correlated with growth rate or perhaps relative clutch size. Such a possibility has yet to be explored.

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APPENDIX

The scoring system used for antipredator displays is modified from that of Arnold and Bennett's (1984) for two reasons. First, *T. sirtalis* exhibited certain behaviors (biting and holding onto the pointer) not observed in *T. radix*. Second, treadmill endurance trials (continually moving substrate leading to snakes falling off) are different from Arnold and Bennett's (1984) race-track trials. If a snake adopts any stationary antipredator display, it will quickly fall off a moving belt. Therefore, complete displays of stationary behaviors (e.g., coiling into a tight ball) were somewhat inhibited in treadmill trials. Moreover, many behaviors were exhibited during the trial, rather than at the defined end point (when a snake fell off for the third time). I therefore made mental notes of all behaviors occurring during trials, in addition to their final behaviors, and recorded these after snakes were exhausted. Scores were based on all behaviors noted both during and at the end of trials. All of the individual components of overall "antipredator display" (sum of head, body, and tail scores) were significantly repeatable between trials (all $P < 0.0001$: $r = 0.480$ for tail scores; $r = 0.380$ for body scores; $r = 0.658$ for head scores). Categories corresponding with those used by Arnold and Bennett (1984) are indicated by asterisks; percentages of individuals in each category are listed in parentheses for trials 1 ($N = 249$) and 2 ($N = 248$), respectively.

- Tail: 0* = waves tail vigorously (8.8, 10.5)
 1 = waves tail (62.7, 63.3)
 1.5 = waves tail a little (15.7, 10.9)
 2* = never waves tail (scored as 1 by Arnold and Bennett) (12.9, 15.3)

Arnold and Bennett (1984) recognized only two categories; tail-wave (scored as 0) and tail-flat (=no tail-wave, scored as 1); this inadequately describe the range of tail-waving seen in *T. sirtalis*.

- Body: 0* = body rolled into ball or tight coil not followed by strike (2.4, 2.0)
 0.5 = slight coil or slight extended body (14.5, 14.1)
 1* = snake stops crawling and extends body rigidly on belt (6.0, 6.9)
 1.5 = snake reverses direction repeatedly (1.2, 3.6)
 2 = no notable defensive behavior; snake simply keeps crawling until defined point of exhaustion is reached (68.7, 64.5)
 3* = snake coils and strikes (scored as 2 by Arnold and Bennett) (7.2, 8.9)

Again, I have expanded the scale and added some categories. Snakes that did nothing with their bodies except to continue to crawl (score = 2) seem clearly to represent a behavioral category that is intermediate to defensive (coiling into a ball [score = 0]) versus offensive (striking at the pointer [score = 3]) extremes. Similarly, snakes that reversed direction frequently could be considered to be exhibiting more defensive (as opposed to offensive) behavior than were those that simply continued to crawl.

- Head: 0* = head hidden under body or in center of coil (1.2, 0.4)
 0.5 = head at edge of coil (0.0, 1.6)
 1* = head exposed (83.1, 75.0)
 2* = closed-mouth attack (0.0, 0.4)
 3* = open-mouth attack (4.4, 8.9)
 3.3 = plus 1–10 open-mouth attacks during trial (1.2, 0.8)
 3.6 = plus 11–20 open-mouth attacks during trial (0.0, 0.4)
 3.9 = plus > 20 open-mouth attacks during trial (0.0, 0.0)
 4 = snake bites and holds onto pointer (7.6, 10.1)
 4.3 = plus 1–5 bites and holds during trial (2.0, 2.0)
 4.6 = plus 6–20 bites and holds during trial (0.4, 0.0)
 4.9 = plus > 10 bites and holds during trial (0.0, 0.4)

I have added a fourth category, "bite and hold," that was not observed by Arnold and Bennett (1984). This difference may be partially attributable to the larger area of my pointer tip as compared with the cotton-tipped swabs used by Arnold and Bennett (cf. Herzog and Burghardt, 1986). Scores 3 and 4 refer to a snake's behavior at the end of a trial; however, snakes that exhibited the behavior only once during a trial also received these scores. In addition, I noted how many open-mouth attacks ($N \leq 27$) and bites and holds ($N \leq 11$) occurred during a run. Snakes that exhibited these aggressive displays additional times during a trial were given slightly higher scores, as listed above. Note that my scale is adjusted such that any snake that ever bit and held received a higher score (≥ 4 ; suggesting a more offensive behavior) than did any snake that never bit and held (≤ 3.9).

The above scale for head behavior may seem somewhat more detailed than necessary. Its use is justified, however, because 1) it does not obscure details of individual differences and 2) it should accommodate future studies on other populations (or species) that may differ in antipredator displays (cf. Arnold and Bennett, 1984; Herzog and Burghardt, 1986). Moreover, using the percentages listed above, others can recalculate the numbers of *T. sirtalis* exhibiting broader categories (e.g., 3 plus 4) for comparison with studies using simpler scoring systems.

Using the above scale, a snake that coiled into a ball with its head hidden and waved its tail vigorously would receive a composite score of 0 for its antipredator display (see Arnold and Bennett, 1984 fig. 1). At the opposite end of the apparent defensive-offensive scale, a snake that coiled, struck at, bit, and held onto the pointer at the end of the trial, bit and held onto the pointer > 10 times during the trial, and never waved its tail, would receive a score of 9.9.

Neither the above components nor their sum ("antipredator display") varied in relation to body size (or dam size). Herzog and Bailey (1987) also found no correlation between defensive behaviors and body size in juvenile *T. sirtalis*. G. M. Burghardt (pers. comm.) reports that "a maturational increase in defensive behavior (occurs) over the first few weeks" in some pop-

ulations of *T. sirtalis*. In the present study, approximately equal numbers of snakes were tested at approximately 1, 2, 3, 4, 5, 6, and 7.5 weeks of age. However, regression analysis revealed no significant linear or curvilinear relationship between antipredator

displays and age. The only possible trend noted by visual inspection of the data was a slight tendency for the youngest snakes tested (approximately 1 week old) to exhibit fewer strikes and bites than did older snakes.