

Behavioural variation in natural populations. V. Morphological correlates of locomotion in the garter snake (*Thamnophis radix*)

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A series of morphological and locomotor performance variables was measured in a population of newborn garter snakes to determine whether performance capacity has a significant morphological basis in these animals. Morphological traits measured were body length and mass, number of body and tail vertebrae and numbers of vertebral abnormalities. Locomotor performances included burst and mid-distance speed and distance and time crawled before anti-predator displays were assumed. All performance variables were repeatable in daily replicate trials ($P < 0.001$). Individual burst speed, mid-distance speed, and distance crawled were significantly correlated pairwise ($P < 0.01$). Most morphological and performance variables had a significant mass dependence (static allometry), although the effects were rather weak ($r^2 < 0.1$, except for body length): larger animals performed better and had fewer abnormalities. There were significant associations between some morphological traits and locomotor performance. Morphological factors accounted for 19% of the variation in mid-distance speed and 14% of the variation in antipredator behavior by multiple regression analysis. Canonical correlation of all performance and morphological variables simultaneously accounted for 24% of the observed variation in performance. Numbers of body and tail vertebrae (assayed by scale counts) had an interactive effect on speed of locomotion.

KEY WORDS:—Antipredator behaviour – burst speed – crawling performance – locomotion – scalation – static allometry – *Thamnophis* – vertebral numbers.

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INTRODUCTION

It is generally accepted that form reflects functional capacities, particularly in regard to locomotion and locomotor behaviours (e.g. Gans, 1974; Hildebrand, 1982; Hildebrand, Bramble, Liem & Wake, 1985). For example, different locomotor capacities for burst speed in antelopes and elephants are reflected in and dependent upon limb design. Most comparative studies of form and function are based on inter-familial, -generic or -specific comparisons. The extent to which these correlations also apply within populations is much less clear. Intrapopulational relationships have a particular evolutionary significance because populations are the locus of adaptive shifts in response to natural selection. The statistical relationship between individual differences in morphology and performance has been termed the "performance gradient" (Arnold, 1983). It forms an important link in relating morphology and physiology of individual organisms to fitness. Do individual differences in locomotory capacity reflect differences in individual morphology? Such assumptions are often made (e.g. Kramer, 1951; Dodson, 1975; Pounds, Jackson & Shivley, 1984) but rarely tested. A recent study that specifically examined this issue in the lizard *Amphibolurus nuchalis* found no mass-independent correlation between limb morphology (e.g. limb length and muscle mass) and locomotor performance (e.g. burst speed) (Garland, 1985). Consequently, *a priori* associations between locomotor structures and performance should be tested experimentally instead of simply being assumed.

We used a sample of newborn garter snakes from a single natural population to test for a relationship between morphology and performance. This test case is of interest from a number of viewpoints. First, the sample of newborns is relatively unpruned by selection and so offers a good opportunity to measure intrinsic population variability in performance and morphology. Second, we can test for the relationship between performance and size in a sample of uniform age. No such test for static allometry (Cock, 1966) seems ever to have been conducted with reptiles. Usually allometry is studied in animals of diverse size and unknown age (cross-sectional allometry—Cock, 1966), so that static allometry is confounded with the effects of growth and selection. Third, some of the morphological variables in our study have been implicated as functional elements in the locomotory system of snakes, yet their statistical impact on locomotion has never been tested using intrapopulational variability. Numbers of ventral and subcaudal scales are the two morphological variables of particular functional interest. These scale counts correspond, respectively, to the numbers of vertebrae in the body and tail (Alexander & Gans, 1966; Voris, 1975). These two scale counts have played an important role in snake systematics since the time of Linnaeus.

Ideally, a study of intraspecific correlation between morphology and performance should be rooted in functional analysis of the morphological traits.

Unfortunately, however, the functional connections between vertebral numbers and snake locomotion are incompletely understood. Functional studies do not yet provide predictions about intraspecific correlation. Nevertheless, available studies do provide strong motivation for seeking links between vertebral variation and crawling performance.

Vertebral numbers are part of a functional complex that affects locomotion in snakes. The complex includes the axial musculature, vertebrae and their associated ribs, the skin, including the enlarged ventral scales, and neural circuitry (Gasc, 1981; Jayne, 1982; Cundall, 1987). This complex produces the four major modes of locomotion used by snakes: lateral undulation, rectilinear locomotion, concertina locomotion and sidewinding (Gans, 1962, 1974). Lateral undulation is the mode generally employed by *Thamnophis*, and it was the predominant mode used by *T. radix* in our test apparatus. During terrestrial lateral undulation the snake moves forward by pressing the sides of its body against objects in its environment. In contrast to the other modes, all parts of the snake's body are constantly moving as the snake weaves between points of lateral contact.

The superficial epaxial muscles of snakes (Mm. spinalis, semispinalis, longissimus, and iliocostalis) attach between vertebrae, sometimes spanning many vertebrae (Gasc, 1967, 1974; Jayne, 1982). During lateral undulation, alternating blocks of these epaxial muscles contract on the right and left sides and play a major role in producing propulsive forces (Gray, 1953; Jayne, 1985a). Terrestrial species of nonconstricting colubroid snakes (e.g. *Thamnophis*) show a positive interspecific correlation between the average number of vertebrae spanned by the spinalis and the number of body vertebrae. Constricting colubroids generally have more body vertebrae than non-constrictors, which suggests that greater vertebral number promotes flexibility of the vertebral column (Jayne, 1982). Studies of performance showed that a nonconstricting colubroid (*Nerodia fasciata*) could attain faster crawling velocities than a constrictor (*Elaphe obsoleta*) that had 50% more vertebrae in the body and tail (Jayne, 1986). The two genera did not differ in swimming performance (Jayne, 1985b). These results suggest that selection for constricting and crawling performance may produce conflicting pressures on vertebral numbers (see also Ruben, 1977).

Our aim is to explore the unknown issue of intraspecific correlation between vertebral number and crawling performance in the hope that this new perspective on morphology will motivate additional functional analysis and experimentation. This report is part of a broader study that includes both phenotypic and genetic analyses of morphology, locomotion and antipredator behaviours in this population (Arnold & Bennett, 1984, and in prep.)

MATERIALS AND METHODS

Animals

One hundred and seventy-four laboratory-born garter snakes (*Thamnophis radix*) were used in this study. They were the progeny of 15 gravid females collected in July 1981 at Wolf Lake, Cook Co., Illinois. Females were maintained individually in the laboratory on a natural (Chicago) photoperiod

and given access to a natural thermal gradient (20 to $> 30^{\circ}\text{C}$ during the day, 20°C at night). Newborn snakes were housed in individual containers (Arnold, 1981) within 16 h after birth, at a temperature of 27°C on a natural photoperiod schedule. Animals were tested on days 14 and 15 after birth. They were not fed until after completion of experiments, because feeding may affect performance (Garland & Arnold, 1983).

Morphological variables

Numbers of body vertebrae were determined by counting ventral scales from photographs (Kodak Panatomic X) of the ventral surface, using the conventions of Dowling (1951). Numbers of tail vertebrae were determined by counting numbers of subcaudal scales on the same photographs. The number of body abnormalities refers to the total number of ventral scutes that extended only halfway across the venter or that were divided into two for half the width. Such abnormal ventral scales apparently correspond to vertebrae with an extra rib on one side (King, 1959; Plummer, 1979). The number of tail abnormalities refers to the total number of undivided subcaudal scales. It is not known whether this undivided condition corresponds to an osteological deviation. Body mass was determined the day after birth by weighing each snake on an electronic top-loading balance to the nearest 0.01 g. Body length (in millimetres, from snout to vent) was determined at the completion of the performance trials (in order to eliminate trauma before the tests) by stretching the snake along a metric ruler.

Performance testing

Locomotor performance was measured on a rectangular racetrack 116×45 cm on the inside lane, 10.5 cm wide, with 14 cm high walls, lined with artificial (plastic) grass matting (Garland & Arnold, 1983; Arnold & Bennett, 1984). The surface provided excellent traction for the snakes. At the beginning of each trial an animal was introduced to the starting line by sliding it from its box on a short 45° cardboard ramp without handling it directly. The snake was chased around the track by gently prodding its tail with a cotton-tipped swab every 5 s until it assumed a defensive posture and would not locomote further in response to ten rapid consecutive taps on its tail. An individual was tested only once a day on two consecutive days between 13.00 and 17.00 hours local time. Average body temperature was 26.5°C (± 0.1 s.e.), an ecologically relevant activity temperature for this species (Brattstrom, 1965).

The following performance variables were measured: (1) burst speed—the speed in traversing the first 1.00 m from the starting line; (2) mid-distance speed—the crawling speed between metre 1.00 and 2.50; (3) distance crawled—the total distance before the snake ceased crawling; (4) duration of crawl—the total time elapsed from initiation to cessation of crawling; and (5) defensive behaviour—the posture adopted by the snake after cessation of locomotion (see Arnold & Bennett, 1984). Crawling times were measured with a digital stopwatch to 0.1 s. Defensive behaviours were scored on a numerical scale of aggressiveness (0–6) described by Arnold & Bennett (1984).

Not all the snakes completed runs on the racetrack at each trial. Incomplete runs were caused by mistrials, or by snakes stalling at the starting gate or

crawling less than 2.5 m. Mistrials were infrequent (1% at the first trial, 4% at the second) and were caused by snakes crawling under the track surface or observer failure to record times correctly. Snakes that refused to leave the starting gate (8% and 28% at the two trials) could not be given burst speed or distance scores. In addition some snakes stopped crawling and assumed anti-predator displays before crawling 1 m or 2.5 m, eliminating one or both burst speed scores. In order to retain as many snakes as possible in data analysis, all snakes were used that had a score in one or both trials for each of the performance measures. If scores were available for both trials, the average score was used. Thus while 172 snakes were scored for anti-predator displays (Arnold & Bennett, 1984), only 100 achieved a score in all performance measures, using one or both trials. This subset of 100 snakes was used in all multivariate analyses.

Statistical analyses

Several variables were normally distributed or closely approximated this distribution (checked by fitting a normal distribution and testing the fit with the Kolomogorov D statistic): body length, body mass, log body vertebrae, log tail vertebrae, the two measures of burst speed, log total distance and log total time. Numbers of body and tail abnormalities were Poisson distributed with modes at zero. These two variables were log transformed. The behavioural score showed a trimodal distribution (Arnold & Bennett, 1984).

Multivariate statistics were calculated using the Statistical Analysis System (SAS User's Guide, 1982). Multivariate analysis of variance was used to check for sexual differences in morphology and performance. No sexual differences in performance were detected. Males had on the average 4.1 more body vertebrae and 7.4 more tail vertebrae than females. Males and females were adjusted to the same means for these meristic variables (by adding or subtracting the average sexual difference to the trait values of the appropriate sex, see Table 1) and the sexes were pooled for all subsequent analyses.

A potential statistical problem arises when correlations are computed between two measures of performance that are assessed on the same trial. Thus the correlation between the two performance scores may be inflated by correlated errors in measurement. In the present case, the procedure of taking the correlation between the score averages at two trials lessens the contribution of correlated measurement errors. To test for a lingering contribution, we computed the correlation between one kind of performance assessed at the first trial and the other performance score measured at the second trial. These cross-correlations were generally similar to the correlations between score averages. Thus, the cross-correlations for burst speed and mid-distance speed averaged 0.47 *vs.* 0.44 for the correlation between average scores. The two largest discrepancies were for mid-distance speed and distance crawled (0.34 *vs.* 0.53) and for distance crawled and duration of crawl (0.64 *vs.* 0.78). Thus correlated measurement errors may have made a small but negligible contribution to performance correlations in one or two cases.

Directional and stabilizing performance gradients (Arnold, 1983; Lande & Arnold, 1983) were computed using the general linear model (GLM) subroutine in SAS. The directional performance gradients describe the effects of each

morphological character on average performance while holding the other characters constant. This gradient is a partial regression of relative performance (mean equals one) on the characters. The stabilizing performance gradient describes the effects of squared deviations from character means and pairwise products of deviations from character means on performance. The directional gradients test for a linear effect of morphology on performance, while the stabilizing gradients test for improved performance at intermediate character values (squared variables) and for interactive character effects on performance (product variables). Two runs were required to compute the coefficients that describe these performance gradients because skewness of trait distributions causes correlations between trait values, on the one hand, and squared and product values, on the other, that distort estimates of the directional coefficients. The directional (linear) coefficients were computed in one run by doing a multiple regression of relative performance on the five morphological traits. In a second run, a multiple curvilinear regression was computed that included two squared variables (each divided by two) and a product variable—i.e. $z_1^2/2$, $z_2^2/2$, z_1z_2 ; where z_1 is \log_e number of body vertebrae and z_2 is \log_e number of tail vertebrae—as well as the original nine morphological variables. The coefficients corresponding to the squared and product variables are the stabilizing performance gradients. The factor of 2 converts the coefficients for the squared variables into measures of curvature of the performance surface. The computed coefficients for the linear variables in this second run do not coincide with the correct directional gradients computed in the first run. This discrepancy arises because skewness in trait distributions causes distortion of directional gradients when squared and product variables are included in the regression (Lande & Arnold, 1983).

RESULTS

Morphology

Univariate statistics for the morphological variables are reported in Table 1. Our sample of newborn snakes showed a considerable relative size range, with the largest snake 50% longer than the smallest snake and weighing 150% more.

TABLE 1. Basic statistics for the morphological traits (sample size = 174 for all variables)

	Mean	Range	s.d.	Coefficient of variation (c.v.)
Body vertebrae*†	153.53	142–166	0.02	2.3%
Tail vertebrae*†	74.25	66–82	0.04	4.0%
Body abnormalities‡	0.23	0–22	0.53	396.3%
Tail abnormalities‡	0.08	0–3	0.27	368.5%
Body length (mm)	155.59	119–177	9.89	6.4%
Body mass (g)†	1.72	0.93–2.48	0.15	14.2%

*Sexual dimorphism in body and tail vertebrae was pronounced and significant. For these variables the female mean was adjusted to coincide with the male mean.

†Mean is back transformed from the \log_e scale; range and c.v. are for the raw scale. Reported standard deviation is for the \log_e scale.

‡Transformed by adding one to raw count and taking natural logarithm. Reported standard deviation is for the \log_e scale.

Variations in the meristic characters are typical of values routinely reported for snake populations (e.g. Klauber, 1941). Coefficients of variation for body and tail vertebrae, for example, fall in the range typical for snakes (Kerfoot, 1970; Kerfoot & Kluge, 1971). Incidences of body and tail abnormalities are infrequently reported. In our sample, 18% of the newborn snakes had one or more body abnormalities and 9% had one or more tail abnormalities. Coefficients of variations for these two counts are large relative to the other two vertebral counts and reflect modes at zero with distribution tails extending to moderate numbers.

There were surprisingly few correlations among the morphological traits. The largest correlations were of body size with body vertebrae ($r = 0.28$), tail vertebrae ($r = 0.29$), body abnormalities ($r = -0.33$) and tail abnormalities ($r = -0.32$). Body and tail abnormalities were also correlated with each other ($r = 0.25$). All of these correlations were significant at the 0.01 level ($N = 174$). Principal component analysis, which included body size, confirmed the independence of meristic variables. The first principal component explained only 41% of the total trait variance and four principal components were required to explain 93% of the variance in the five variables.

Performance

Mean values and variation of locomotor performance variables are presented in Table 2. Snakes crawled fastest ($\bar{x} = 0.19 \text{ m s}^{-1}$) over the first 1 m interval, slowed appreciably ($\bar{x} = 0.15 \text{ m s}^{-1}$) during the next 1.5 m, and averaged less than 0.04 m s^{-1} during the remainder of the run, resulting in an average speed of 0.09 m s^{-1} over a total average distance of 6.13 m. Individual variability in performance was high: coefficients of variation ranged from 38 to 83% (Fig. 1). The fastest snake was over ten times as quick as the slowest; the animal that covered the longest distance went nearly twenty times as far as the one that travelled the shortest distance. Individual variability in performance was repeatable: individual correlations for all locomotor performances are significant at $P < 0.001$ in comparisons of the first and second trials (Table 2). Defensive behaviours also were previously reported to be repeatable during these trials ($r = 0.65$, $N = 172$, $P < 0.001$) (Arnold & Bennett, 1984). We did not detect any obvious variation in modes of locomotion.

Correlations among performance variables are reported in Table 3. These are either insignificant or positive. There were no indications of a trade-off between

TABLE 2. Means, variation and repeatability of performance ($N = 100$)

	Mean	Range	s.d.	Coefficients of variation	Repeatability†, r (sample size)
Burst speed (m s^{-1})	0.19	0.03–0.35	0.07	38.0%	0.60 (88)
Mid-distance speed (m s^{-1})	0.15	0.01–0.23	0.05	31.2%	0.71 (39)
Distance crawled (m)*	6.13	1.61–31.82	0.57	78.5%	0.55 (139)
Duration of crawl (m)*	67.61	25.53–411.58	0.61	83.3%	0.62 (141)

*The standard deviations for distance crawled and duration of crawl are on the \log_e scale, whereas the means, ranges and coefficients of variation are for the original scale.

†Repeatability is measured by the correlation between replicate trials on two consecutive days. All correlations are significant at the 0.001 level.

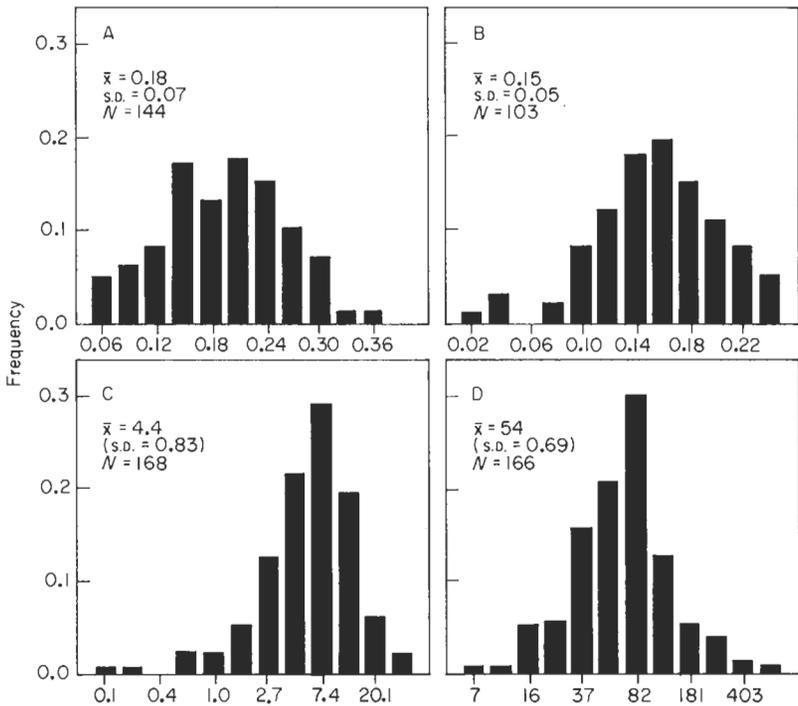


Figure 1. Frequency distributions showing intrapopulation variation in the four performance variables: A, burst speed (m s^{-1}); B, mid-distance speed (m s^{-1}); C, distance crawled (m); D, duration of crawl (s). Standard deviations for distance crawled and duration of crawl are for the \log_e scale, whereas the mean is back transformed to the original scale.

speeds and distance crawling capacity. Burst and mid-distance speeds were positively related, and both were positively correlated with distance travelled. The latter results indicate that animals that were fast on the initial stretch also crawled the furthest. Not surprisingly, distance and time crawled are also positively associated. Defensive behaviours were generally unrelated to crawling performance. The one exception is the positive correlation between mid-distance speed and aggressiveness. Some aggressive snakes did not leave the starting line. However, even when these animals are included, the correlations between behaviour and distance crawled ($r = -0.07$, $N = 165$) or duration of crawl ($r = 0.14$, $N = 163$) are still insignificant. Positive correlations among

TABLE 3. Correlations among the performances, r ($N = 100$), above the main diagonal. Partial correlations holding body length constant are shown below the main diagonal

	Burst speed	Mid-distance speed	Distance crawled	Duration of crawl	Behaviour
Burst speed		0.441**	0.292**	-0.056	0.022
Mid-distance speed	0.420**		0.531**	0.058**	0.386**
Distance crawled	0.268**	0.507**		0.783**	0.021
Duration of crawl	-0.076	0.032	0.781**		-0.144
Behaviour	-0.013	0.353**	-0.027	-0.175	

** $P < 0.01$; otherwise, $P > 0.05$.

performances were not due to common correlation with body size. Partial correlations holding body length constant were almost identical to the raw correlations (Table 3). Likewise, principal components for the matrix of partial correlations were nearly identical with principal components for the raw correlation matrix.

Principal component analysis (Table 4) revealed a general performance factor (PC1), but also a tendency for burst speed to be inversely related to endurance (PC2). Thus, there seems to be a trade-off between speed and total duration of crawl or distance crawled that is masked by positive correlations between the two kinds of performance. The third principal component indicates that aggressive snakes tend to show slow burst speed during the first meter. This relationship was also reflected by the fact that 90% of the snakes ($N = 28$) that never left the starting gate in the second trial adopted the most aggressive mode of display (score = 6). At the first trial the figure was 100% of eight snakes. Body length showed weak loadings on the first two principal components, again reflecting virtual size-independence of performance.

Static allometry

Relationships between the variables and body mass are reported in Table 5, which gives coefficients of static allometry. Burst speed, distance crawled and duration of crawl all showed statistically significant but weak dependence on body mass. Body mass explained only 3–9% of the variation in these performance measures and an insignificant fraction of variation in mid-distance speed. Behaviour showed no significant static allometry. Body vertebrae showed no mass dependence, but body and tail abnormalities showed an inverse relationship, and numbers of subcaudals showed a positive relationship. Mass dependence of meristic traits was slight, explaining less than 10% of variation. Body length was highly correlated with body mass ($r = 0.855$).

Morphology and performance

Correlations between morphology and performance were weak although a fair number of them were statistically significant (Table 6). These significant

TABLE 4. Principal components of the performances ($N = 100$). Entries are component correlations; squares of the entries represent the proportion of variance in each performance measure explained by each principal component

	Principal components					
	PC1	PC2	PC3	PC4	PC5	PC6
Burst speed	0.51	0.34	-0.69	0.21	0.03	0.10
Mid-distance speed	0.76	0.42	-0.13	-0.26	-0.40	0.09
Distance crawled	0.89	-0.39	-0.01	-0.13	-0.02	-0.19
Duration of crawl	0.58	-0.74	0.22	-0.06	0.18	0.16
Behaviour	0.27	0.66	0.52	-0.37	0.31	-0.01
Body length	0.46	0.25	0.43	0.74	-0.07	-0.00
Eigenvalues	2.25	1.49	0.99	0.81	0.39	0.07
Cumulative proportion of variance explained	0.37	0.62	0.79	0.92	0.99	1.00

TABLE 5. Coefficients of static allometry for morphology and performance of newborn snakes. For each variable, y , the coefficients are given for the following allometric equation are given: $y = aM^b$, where M is body mass. The reported squared correlations (r^2) are for \log_e transformed variables

	N	Intercept a	Slope b	Standard error of b	r^2
Burst speed	144	0.099	0.957**	0.259	0.087
Mid-distance speed	102	0.102	0.520 n.s.	0.354	0.021
Distance crawled	168	1.891	1.586**	0.400	0.086
Duration of crawl	166	34.988	0.801*	0.346	0.032
Behaviour	171	5.028	0.357 n.s.	0.392	0.005
Body vertebrae	173	152.170	0.016 n.s.	0.012	0.010
Tail vertebrae	173	72.313	0.048*	0.021	0.029
Body abnormalities	174	1.964	-0.874**	0.254	0.064
Tail abnormalities	174	1.470	-0.561**	0.130	0.097
Body length	173	2.220	56.208**	2.597	0.732

n.s. Denotes $P > 0.05$ that slope equals zero.

*Denotes $0.05 > P > 0.01$ that slope equals zero.

**Denotes $P < 0.01$ that slope equals zero.

correlations ranged, in absolute value, from 0.20 to 0.24. Snakes with the best mid-distance speed had fewer body abnormalities ($r = -0.24$). There were no significant correlations between body and tail vertebrae and performance. All of these associations might reflect indirect effects through correlated morphologies or physiology. Indirect effects could produce a spurious correlation or mask a real effect (Lande & Arnold, 1983). We used the multivariate techniques of canonical correlation and multiple regression to help resolve these ambiguities of simple correlation.

Canonical correlation provides an overall test for effects of morphology on performance (Table 7) (Harris, 1975). Thus the maximum variance in the performances that can be explained by the measured morphological characters is 24% (canonical correlation = 0.49, $P < 0.02$). Only the first pair of canonical variables (linear combinations of morphologies and of performances) produced a statistically significant canonical correlation. The coefficients for this first pair of variables are shown in Table 7. The best compound measure of performance gives high positive weights to mid-distance speed and to total time and negative weight to total distance. Thus the best performance measure predicted by the morphologies is a tendency for high mid-distance speed and long crawl time but

TABLE 6. Correlations (r) between morphology and performance ($N = 100$)

Morphology	Performance				
	Burst speed	Mid-distance speed	Distance crawled	Duration of crawl	Behaviour
Body vertebrae	0.069	0.108	0.116	0.104	0.065
Tail vertebrae	0.130	-0.019	0.065	-0.002	0.043
Body abnormalities	0.017	-0.240*	-0.115	-0.078	-0.100
Tail abnormalities	-0.087	0.062	-0.104	-0.138	0.150
Body length	0.159	0.232*	0.210*	0.116	0.219*

*Denotes $0.01 < P < 0.05$.

TABLE 7. Standardized coefficients for the first pair of canonical variables ($N = 100$). The morphologies and performances are standardized to unit variances, as are the canonical variables

	First canonical performance variable
Performances	
Burst speed	-0.29
Mid-distance speed	1.28
Distance crawled	-0.96
Duration of crawl	0.80
Behaviour	0.25
Morphologies	
Body vertebrae	0.09
Tail vertebrae	-0.43
Body abnormalities	-0.77
Tail abnormalities	0.67
Body length	0.60
	$R_c = 0.49^*$
	$R_c^2 = 0.24^*$

*Denotes $P < 0.05$.

short overall distance. The compound measure of morphology that best predicts this performance is composed of large body length, few body abnormalities and tail vertebrae. Surprisingly, tail abnormalities received positive weight.

The individual effects of each morphological character on each performance measure are shown in Table 8. The standardized directional performance gradients in this table indicate the increase in performance that would result if a particular morphology were increased by one standard deviation, without changing any of the other morphologies (Lande & Arnold, 1983). All of the directional effects are small. Thus the largest effect (aside from relations with behaviour) is that an increase in body abnormalities by a standard deviation

TABLE 8. Standardized directional performance gradients ($N = 100$). Partial regression coefficients for relative performances regressed on morphology (with unit variances), holding all other morphologies constant

	Performance				
	Burst speed	Mid-distance speed	Distance crawled	Duration of crawl	Behaviour
Morphology					
Body vertebrae	-0.013	0.004	0.011	0.014	-0.074
Tail vertebrae	0.028	-0.036	-0.007	-0.010	-0.011
Body abnormalities	0.029	-0.088*	-0.024	-0.008	-0.078
Tail abnormalities	-0.012	0.079*	0.003	-0.018	0.228**
Body length	0.053	0.096*	0.056	0.004	0.264**
Multiple R^2 with only linear terms	0.04	0.16**	0.05	0.03	0.14**
Multiple R^2 with linear and quadratic† terms	0.09	0.19**	0.07	0.05	0.14

*Denotes $P < 0.05$, **denotes $P < 0.01$.

†The quadratic variables $z_1^2/2$, $z_2^2/2$ and z_1z_2 where z_1 is (\log_e) number of body vertebrae and z_2 is (\log_e) number of tail vertebrae.

would decrease mid-distance speed by 9%. These gradients show much the same pattern as the covariances between morphology and performance (Table 6), reflecting the general lack of correlations among morphologies.

Curvilinear relationships between morphology and performance were examined by calculating stabilizing performance gradients. These are equivalent to quadratic coefficients in a curvilinear multiple regression (Lande & Arnold, 1983). Quadratic coefficients for each performance measure were calculated for the squares of the two vertebral counts as well as for the product of body and tail vertebrae. The coefficients for the squared variables were not statistically significant. However, the coefficient describing the joint effect of body and tail vertebrae on burst speed was significant ($\gamma_{12} = 0.073 \pm 0.035$ s.e., $P = 0.04$). The proportions of variance in performance explained by the five linear terms, and by the combination of five linear and three quadratic terms, are shown at the bottom of Table 8 (squared multiple correlation coefficients). Despite the small individual contributions of the morphologies to performance, a significant fraction of variance in mid-distance speed (16–19%) could be attributed to the morphological variables measured in this study.

The coefficients for the product of body length with body vertebrae and with tail vertebrae are also of interest because they might indicate whether the best number of body or tail vertebrae varies with body length. Accordingly, another multiple curvilinear regression was computed that included the products of body length with body vertebrae and with tail vertebrae, as well as the five linear and three quadratic variables used in the preceding analysis. None of the coefficients for variables involving products with body length were statistically significant.

No quadratic variables involving body or tail abnormalities were included in any of the analyses because we had no *a priori* expectation that intermediate values or interactions with other variables would affect performance.

The effects of vertebral numbers on burst speed are shown graphically in Fig. 2. Surprisingly, numbers of body and tail vertebrae are not correlated

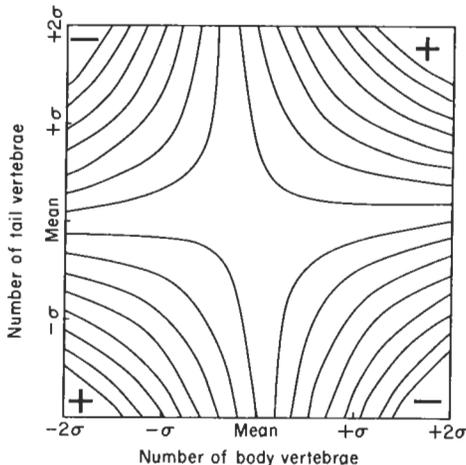


Figure 2. Burst speed as a function of numbers of body and tail vertebrae assayed by scale counts. The axes are in units of phenotypic standard deviation. Burst speed is shown in contours calculated from a multiple quadratic regression equation (see text). The bivariate mean of the population is located at the centre of the graph.

($r = -0.03$, $N = 174$, $P = 0.6$). The figure portrays the equation, relative burst speed $= \alpha + \beta_1 z_1 + \beta_2 z_2 + \gamma_{11} z_1^2/2 + \gamma_{22} z_2^2/2 + \gamma_{12} z_1 z_2$, where α is a constant, $\beta_1 = -0.013$, $\beta_2 = 0.029$, $\gamma_{11} = -0.040$, $\gamma_{22} = 0.016$, $\gamma_{12} = 0.073$, z_1 is the (\log_e) number of body vertebrae and z_2 is the (\log_e) number of tail vertebrae. The coefficients were calculated as outlined above. Only the quadratic coefficient, $\gamma_{12} = 0.073$, was statistically significant and that coefficient completely dominates the visualization of the performance surface. Thus Fig. 2 indicates that the best performance was achieved by two classes of snakes: those with numerous tail and body vertebrae or with low numbers of body and tail vertebrae. The worst performance was by snakes with too few or too many tail vertebrae in relation to body vertebrae.

The visualization shown in Fig. 2 is robust to estimation of the separate coefficients for body and tail vertebrae. Thus if we set the coefficients for $z_1^2/2$ and $z_2^2/2$, (i.e. γ_{11} and γ_{22}) to zero or reverse their signs, we do not make any qualitative change in the surface portrayed in Fig. 2. For example, stabilizing performance on both vertebral numbers (achieved by using γ_{11} as calculated and by giving γ_{22} a negative sign) merely steepens the slope downhill from the saddle.

DISCUSSION

Garland (1987) studied individual variation in crawling performance in 46 families of *T. sirtalis* (249 neonates) and obtained results similar to our results. Garland found that burst speeds, endurance (measured on a treadmill) and antipredator behaviours were moderately repeatable. Using the fastest burst speed in a set of four trials on each of two consecutive days, he obtained a repeatability of 0.80 (versus 0.60 for single trials on two days for *T. radix*). Treadmill endurance ($r = 0.67$) and behaviour ($r = 0.62$) in *T. sirtalis* gave repeatabilities that were extremely similar to repeatabilities for analogous variables in *T. radix*. Likewise, size-corrected values of speed, endurance and behaviour showed similar patterns of correlation in *T. sirtalis* and *T. radix*. In addition, Garland estimated heritabilities and genetic correlations (using among-family components of variance and covariance) and found performances and behaviour to be heritable with moderate, positive genetic correlations.

Can the morphological variables we measured predict locomotor performance capacities in these snakes? Yes, but generally only when several variables are considered simultaneously. Correlations between single morphological traits and single performance measures are insignificant or account for less than 6% of variation in performances (Table 6). Description of single performance variables by the best linear combination of morphological traits can account for a significant fraction of the variation in mid-distance speed (19%) and in antipredator behaviour (14%) (Table 8). The best prediction of the overall effect of all morphological variables on all performance characters considered simultaneously is provided by canonical correlation. This explains a moderate but significant 24% of the variation in performance capacity (Table 7). We conclude therefore that there are weak but statistically significant associations between vertebral numbers and locomotor performance in this population of snakes.

There are two aspects of this correlation, however, that may be cautionary for

other studies attempting to relate minor morphological variations to performance. First, many of the effects demonstrated were of only borderline significance, even with a large sample size ($N = 100$). Experimental designs involving fewer individuals might fail to uncover real but weak correlations. Second, demonstration of these associations may have been easier in our study because our population sample had not been exposed to postnatal selection. It might be impossible to demonstrate these correlations in a sample that had already been exposed to postnatal selection that eliminated extreme classes of ventral abnormality.

Our study demonstrated an effect of body and tail vertebral numbers on crawling performance. We were able to demonstrate an interactive effect between body and tail vertebral numbers on burst speed (Fig. 2.). In contrast, differences in numbers of body or tail vertebrae *per se* neither improved nor impeded performance. Nor could we demonstrate best performance at intermediate vertebral numbers, as might be inferred from Kerfoot's (1970) observations of strikingly low intrapopulation variation in these counts in snakes. Instead, we found that the relative proportion of body to tail vertebral numbers had an impact on speed.

The dependence of the measured variables on body mass deserves particular comment, as there was a considerable range of sizes among the snakes at birth (Table 1) and many morphological, physiological and behavioural factors are expected to scale significantly with body mass (Pough, 1977, 1978; Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1984). Our measures of the static (single age) allometry of the performance characters indicate that they are indeed significant but rather weak, accounting for at most 9% of the variation observed in the sample (this figure for burst speed and for distance crawled) (Table 5). Larger animals perform better, however marginally, and this size differential performance may constitute part of the selection acting on neonates. Larger animals also had significantly fewer scale abnormalities. Because mass effects are so weak, they did not contribute to correlations among performance variables (see Table 3).

Performance of the kind we measured in this study is likely to be favoured in natural populations of garter snakes. The most common predators of *Thamnophis* are probably raptorial and wading birds, as well as carnivorous mammals. *Thamnophis* commonly bask within one metre of a refuge, such as a bramble thicket or rock pile, into which they retreat immediately when disturbed. When startled by a predator in such circumstances, there is probably a premium on rapid acceleration and high burst speed. Foraging garter snakes, however, may venture several metres from cover. Predatory attack under these circumstances may favour rapid distance movement of the kind we measured because of premiums on ability to sustain both locomotion and, in the event of actual attack, a vigorous struggle. Garter snakes are sometimes able to thwart ingestion by birds, for example, by wrapping the body around the bird's beak or by knotting the tail around vegetation. Such intense bursts of activity in reptiles are fuelled primarily by anaerobic metabolism (Bennett, 1978, 1982), and we established that the snakes in our study were at the limits of their anaerobic capacities when they assumed anti-predator displays at the end of their performance trials (Arnold & Bennett, 1984). Field observations and experiments are needed to test these inferences.

Our results suggest that the minor variations in body and tail vertebral numbers that characterize snake populations may have a detectable impact on locomotory performance. In order to generalize the results and interpret them more completely we will need additional experimental work on other species (including functional analyses), assays of vertebral impact on other aspects of whole animal performance, longitudinal studies of the ontogeny of performance, and direct measurement of selection on performance in natural populations.

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