THE JOURNAL OF EXPERIMENTAL ZOOLOGY 252:126–133 (1989)

The Effect of Tail Morphology on Locomotor Performance of Snakes: A Comparison of Experimental and Correlative Methods

BRUCE C. JAYNE AND ALBERT F. BENNETT
Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717

ABSTRACT A combination of experimental and correlative analyses was used to study the effect of tail length on locomotor performance of garter snakes (*Thamnophis sirtalis fitchi*). Correlative analysis was used to determine whether naturally occurring morphological variation was associated with differences in performance, whereas experimental modification of morphology was used to test whether this variation was a causative factor for different performance. Burst speed of snakes performing terrestrial lateral undulation was measured for snakes with experimentally altered tail length and for snakes with partial and complete tails from a natural population. For 445 snakes with complete tails, regression analysis revealed a significant quadratic effect of relative tail length on size-corrected performance, indicating that individuals with intermediate relative tail length had the fastest burst speeds. For 52 snakes that had naturally lost from 0.3% to 80.4% of their tail, there was no significant correlation between size-corrected performance and the extent of the tail that was missing. Experimental ablation of the distal one third of the tail did not affect performance, whereas ablation of the distal two thirds of the tail caused a significant average decrease in speed of only 4.5%. Contrary to the correlative analysis, the experimental manipulation suggests that there is no detectable mechanical effect for minor variations in relative tail length. We conclude that minor deviations from intermediate relative tail length are not the causative factor for a decrement in performance among snakes, and this decrement was a correlated response to some other unmeasured variable.

A primary goal of functional morphology is to determine the functional consequences of morphological variation, and correlative and experimental analyses are two methods widely used to accomplish this objective. For correlative studies, recent innovative applications of multivariate statistical methods employed in population biology appear to be a powerful tool for relating morphology to function (Arnold, '83; Garland, '85). Correlative studies often rely on interspecific differences as a source of morphological variation, but continuing interest in relating morphology to fitness has emphasized the need to also relate intraspecific variation to performance (Bennett, '87). One problem with the correlative approach is the inability to isolate the causative factors for differences in performance. As shown in recent studies of complex morphological systems (Lauder '83; Lauder and Reilly, '88), experimental manipulation of morphology greatly facilitates interpretations based on naturally occurring variation. However, only infrequently are both correlative and experimental approaches applied to a single system.

The relationship between morphology and locomotor performance is a particularly interesting and fruitful area of investigation (Alexander and Goldspink, '77; Garland, '85). The importance of axial morphology and function to locomotion has been discussed for lower vertebrates in general by Gray ('68), and among squamate reptiles one of the most conspicuous sources of morphological variation is in the axial skeleton. This variation is expected to have a significant impact on locomotor capacity. Among different species of lizards, for example, numbers of body vertebrae may range from 16 to 110, and within snakes these may vary from 120 to 320 (Hoffstetter and Gasc, '69). Considerable interspecific variation also exists in the relative length of the tail which may range from about 10% to 75% of total length

Received January 20, 1989; revision accepted May 4, 1989.

of lizards (Smith, '35) and from 2% to 38% among snakes (Broadley, '83). Injuries commonly sustained by lizards and snakes in natural populations are an additional (noninherited) source of variation in relative tail length that might be expected to have a significant impact on locomotor performance and on prospects for survival. Tail injuries may be found in as many as 77% of the individuals in a lizard population (Bellairs and Bryant, '85) and in 32% of a population of the garter snake *Thamnophis sirtalis fitchi* (Arnold and Janzen, personal communication). Although it seems likely that these aspects of axial morphology should affect locomotor performance, the precise functional consequences of this morphological variability are presently unclear. In lizards, correlating interspecific locomotor differences to axial morphology and relative tail length is complicated by different limb lengths and reliance on quadrupedal, bipedal or limbless locomotion. Hence, it is not unexpected that studies on the effects of tail autotomy on lizard locomotion have found that tail loss may (e.g., Punzo, '82) or may not (e.g., Daniels, '83) detrimentally affect locomotor performance. Presently, the effects of tail loss on the locomotor performance of snakes is unknown.

Correlating differences in axial morphology with locomotor function in snakes is potentially simplified because of the absence of limbs and the entire length of snakes commonly appears to be used for propulsion during locomotion. By comparing the locomotion of snake taxa (*Nerodia* vs. *Elaphe*) with great differences in vertebral number, rather subtle differences in function have been found (Jayne, '86, '88a, '88b). Furthermore, when Arnold and Bennett ('88) recently used correlative methods to study neonatal garter snakes (*Thamnophis radix*) sampled from a single population, they described a significant interactive effect of numbers of body and tail vertebrae on the speed of locomotion. Unfortunately, because many physiological and morphological traits relevant to locomotion could be correlated with the traits that have actually been measured, it is difficult to determine if the traits used for either interspecific or intraspecific comparisons of function are in fact the causative factors.

This study examines the effects of relative tail length on the speed of locomotion in garter snakes with different experimental and correlative approaches. First, for one group of snakes, the relative tail length was experimentally altered and locomotor performance was measured. Second, using snakes from a single natural population, the locomotor performance was measured and correlated with variation in relative tail length both for individuals with complete tails and for individuals with partial tails resulting from natural injuries. Finally, the congruence between these two analytical approaches is examined to obtain insight into the function of the tail during snake locomotion. This is part of a larger study examining the effect of body size on locomotor performance in this species (Jayne and Bennett, in press).

MATERIALS AND METHODS

Subjects

For the experimental treatments, forty-eight juveniles of *Thamnophis sirtalis fitchi* were captured from a site in Lassen County, California in July 1987 (California Scientific Collecting Permit 985). Snout-vent (SVL) and tail (TL) lengths were determined to the nearest mm and mass was measured to the nearest 0.1 gm. The snakes were then sorted into three groups of 16 individuals such that there were no significant among-group differences in means and variances of snout-vent length and mass of the snakes (Table 1).

For the correlative analysis, additional information was used from 497 snakes, with a large range in size (16.5 cm $<$ SVL $<$ 67.6 cm), captured between 15 June and 24 August 1986 from a nearby (within 10 km) population of *T. sirtalis fitchi* that was being studied for other purposes. These animals have naturally occurring variation in tail length and about 10% of them had from 0.3% to 80.4% of their tails missing as a result of natural damage.

Performance testing and analysis

All performance tests were conducted on snakes at a body temperature of 30°C (±0.5°C). After capture and before testing, the snakes were manually forced to regurgitate any stomach contents. A track 3 m long by 10 cm wide was used to determine speed of the crawling snakes. The bottom of the track was covered with artificial turf to facilitate rapid lateral undulatory locomotion, and the overall design of the track was similar to that described by Huey et al. ('81). Photodetectors, spaced at 25 cm intervals over the middle 2 m of the track, were interfaced to an IBM XT computer with programs that determined time between adjacent stations to the nearest msec and calculated the speed of the fastest 50 cm interval

TABLE 1. Summary of size and performance of snakes before and after tail removal[1]

	Mass (gm)	SVL (cm)	Initial tail length (cm)	% Tail length removed (%)	% Total mass removed (%)	After tmt. tail residual (log units)	Initial V (cm/s)	After tmt. % change V (%)	After tmt. V residual (log units)
Control									
Mean	7.7	27.3	9.2	0	0	0.011	69.5	2.5	0.039
Range	2.7, 14.7	20.7, 36.7	6.8, 12.6	0	0	−0.010, 0.034	47.5, 91.3	−5.4, 26.3	−0.062, 0.109
Std. dev.	4.1	5.1	1.9	0	0	0.012	11.9	7.7	0.047
Group 2									
Mean	7.6	27.8	9.2	33.4	0.6	−0.171	70.5	1.4	0.033
Range	2.8, 15.2	20.8, 36.3	7.0, 12.7	29.9, 42.3	0.3, 1.5	−0.193, −0.133	48.1, 84.9	−5.6, 15.5	−0.016, 0.090
Std. dev.	4.0	5.2	1.9	2.9	0.29	0.024	11.6	4.7	0.027
Group 3									
Mean	8.2	28.3	9.6	65.0	2.4	−0.447	71.8	−4.5	0.007
Range	3.6, 17.0	21.8, 35.7	7.3, 12.4	63.0, 68.0	1.6, 3.2	−0.486, −0.413	55.6, 91.7	−9.8, 5.3	−0.047, 0.047
Std. dev.	4.4	5.0	2.0	1.5	0.35	0.020	11.6	4.5	0.022

[1]Mass, SVL, and Tail are pretreatment mass, snout-vent, and tail lengths of snakes. Initial V is burst speed measured before the treatment. After Tmt. % change is the percentage change of V within individuals after the treatment.

within a single test. The experimenter's hand was used to chase the snake the entire length of the track, and tapping and scraping the bottom of the track immediately behind the snake elicited maximal speed (for more detail see Jayne and Bennett, in press).

Snakes were tested twice each morning and afternoon of days 2 and 3 after capture. On day 4, the distal one third and two thirds of the tail was removed from the snakes in the experimental groups two and three, respectively. Four post-treatment trials were conducted on days 6 and 7 with the exception of two snakes that were allowed to complete ecdysis before final testing. Using the fastest speed from each pair of replicates within a trial, mean burst speed (V) was calculated by averaging results from the four trials per treatment. For the individuals tested during 1986, a protocol identical to days 2 and 3 was used.

Information from the snakes collected during 1986 was used to calculate the least squares regression of the scaling equations of log V and log TL as a function of log SVL (all log transforms are base 10). Regressions for log TL as a function of log SVL were calculated separately for males and females, and taking the antilog of these predicted values of log TL yielded expected tail length in cm. The difference between these expected and observed values was then converted to a percentage of expected tail length to provide one of the estimates of the amount of the tail that was missing in injured snakes. The difference between log of the observed values and the values predicted by the least squares regressions yielded size-corrected values (residuals), which were used for further analysis. Another variable analyzed for the experimental group was the percent change in mean burst speed within an individual before and after the treatment. A microcomputer version of SPSS was used to perform analysis of variance to determine significant ($P < 0.05$) differences among groups, and Scheffe's test was used to determine which groups were significantly different.

RESULTS

Experimental analysis

In the tail amputation experiment, six of sixteen snakes in the control group were slower after the treatment. In group two (33% removal), five snakes were slower whereas 13 of 16 snakes in group three (67% removal) were slower after the treatment. Analysis of variance revealed no significant difference in the size-corrected burst speed among the three groups before the treatment ($F = 0.027$; df = 2, 45; $P = 0.973$). After the treatment, there was a significant difference in the burst speed residuals among the three groups ($F = 3.89$; $P = 0.028$), and the only significant difference was that group three was significantly slower than the control group. Analyzing the change in each individual's performance after the treatment accounts for variation in performance among individuals and this decreased the

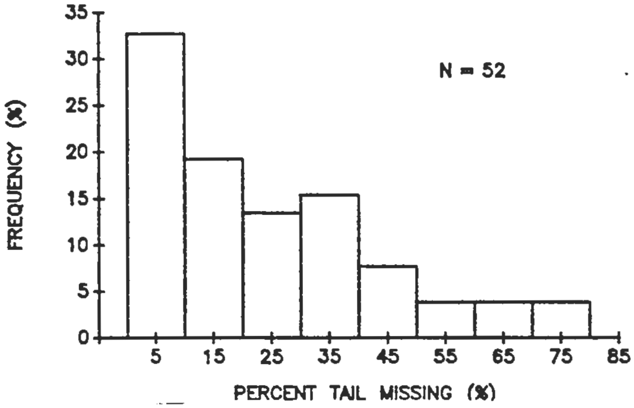

Fig. 1. Frequency distribution of the percent of tail missing among the 52 individuals with partial tails captured in 1986.

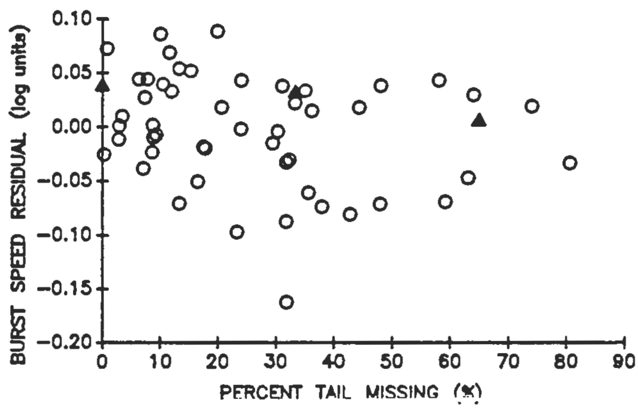

Fig. 2. Size-corrected locomotor performance versus the percent of tail missing for the 52 individuals with partial tails captured in 1986 (circles). Triangles indicate mean values for the three experimental groups.

P values dramatically. The difference between burst speed residuals before and after treatment was calculated for each individual and then used for ANOVA which revealed highly significant differences among groups (F = 7.37, *P* = 0.002) with group three being significantly slower than both group two and the controls. Similarly, the percent change in speed calculated from absolute speeds had significant differences among groups (F = 6.66; *P* = 0.003) with group three being significantly slower than both of the other groups. The average percent change in speed of group three was surprisingly small (−4.5%).

Correlation with natural tail loss

Fifty-two (10.5%) of the 497 snakes collected and tested in 1986 were missing from 0.3% to 80.4% of their tails. Figure 1 illustrates the frequency distribution of the extent of the tail that was missing in these 52 animals. Only 16 of these snakes were missing more than one third of their tails. For snakes with incomplete tails, there was not quite a significant correlation between locomotor performance (burst speed residuals) and the extent of the tail loss whether tail loss was expressed either as a percent (r = −0.257, *P* = 0.066; Fig. 2) or as a residual value (r = 0.226, *P* = 0.108; Table 2). However, the trend was consistent with greater tail loss detrimentally affecting performance.

Once an individual has sustained a tail injury, its health could decline and cause a decrease in performance rather than the mechanical effect of a shortened tail. The residuals of log mass, predicted from a regression using log SVL, indicate the relative heaviness of an individual, and this variable can roughly indicate health by detecting emaciated individuals (Jayne and Bennett, in press). For the 52 snakes with natural tail injuries, mass residuals were not significantly correlated either with the V residuals (r = 0.207, *P* = 0.14) or TL residuals (r = 0.218, *P* = 0.12), suggesting poor health was not a confounding factor in this particular test, at least according to this analysis.

Correlation with natural variation

Figure 3 illustrates the variation in the relative tail length among the 445 snakes with complete tails captured in 1986. However, this source of variation is small compared to that which originated from injuries. A tail length residual of about −0.17 indicates a relatively short tail equal to about one third of the tail "missing" and only one individual of this group had a more negative value than this for the tail residual. The value of the second smallest tail residual was −0.089 (= 18% of tail "missing"). Hence, 99.8% of the observed naturally occurring variation in relative length of complete tails was less than that which was used as the treatment for group two.

Table 2 summarizes regression statistics relating burst speed (V) residual to tail length (TL) residual. For snakes with complete tails, there is a regression with a significant positive slope predicting V residual as a function of TL residual alone (*P* = 0.021). However, the regression of V residual with a second degree polynomial of TL residual (Table 2) also produces a highly signifi-

TABLE 2. Least squares regression statistics for the equation $Y = a_0 + a_1X + a_2X^2$ [1]

Sample	Y	X	N	Multiple r^2	a_0	a_1	a_2	P_1	P_2
All 1986	log(V)	log(SVL)	497	0.854	−3.7668	6.7326	−1.9760	<0.0001	<0.0001
Males	log(TL)	log(SVL)	214	0.951	−0.5095	1.0288	—	<0.0001	—
Females	log(TL)	log(SVL)	231	0.966	−0.5301	1.0238	—	<0.0001	—
Complete tail	V resid.	TL resid.	445	0.051	0.0017	0.1171	−3.929	<0.0001	0.038
All 1986	V resid.	TL resid.	497	0.010	0.0001	0.0713	ns	0.027	—
Partial tail	V resid.	TL resid.	52	0.051	0.0075	0.0767	ns	0.108	—
Partial tail	V resid.	TL resid.	52	0.003	0.0004	ns	−0.0996	—	0.191

[1] P_1 and P_2 indicate the significance levels of the coefficients a_1 and a_2, respectively. ns indicates a variable was entered into the regression and then removed after determining that it was not significant.

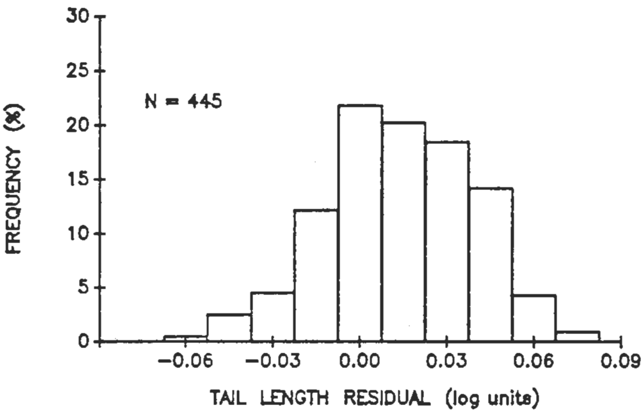

Fig. 3. Frequency distribution of the relative tail lengths of the 445 individuals with complete tails that were captured during 1986. Two individuals with extreme values of TL residual (−0.25 and 0.14) are not illustrated.

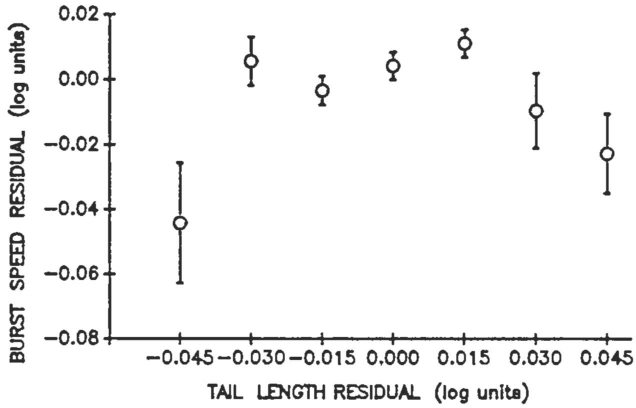

Fig. 4. Mean size-corrected performance (± one standard error) for 445 snakes with complete tails, pooled by relative tail length (see text). Sample sizes for groups from left to right are 21, 31, 94, 147, 108, 28, and 16, respectively.

cant relationship with the coefficient of the quadratic term having a much greater level of significance ($P < 0.0001$) than the coefficient of the first degree term ($P = 0.038$). For the sake of illustration (Fig. 4), V residuals were pooled into seven groups by TL residuals (less than −0.0375, greater than 0.0375 and for interval widths of 0.015 between these extreme values). The regression analysis and Figure 4 clearly illustrate that for snakes with complete tails, animals with relative tail lengths deviating farthest (either positive or negative) from the mean are most likely to have decreased locomotor performance. A similar result for snakes with complete tails was found by an additional multiple regression for performance containing the square of TL residuals, which showed that $\log V = -3.6898 + 6.6250(\log SVL) - 1.9366(\log SVL)^2 - 4.0948(TL\ resid.)^2$. All three of these coefficients were very highly significant ($P < 0.0001$), but comparing the multiple r^2 (0.858) with that of the scaling equation of V in Table 2 (0.854) also indicates that (TL residual)^2 is explaining a relatively small portion of the total variance in performance.

If the V residuals are analyzed by combining the data for the 497 snakes with complete and partial tails, the regression for V residual versus TL residual does not have a significant coefficient for the quadratic term of TL residual (Table 2). The positive coefficient of TL residual indicates that the regression predicts individuals with relatively shorter tails will be slower. No significant coefficient for (TL residual)^2 suggests that the effect of natural tail loss is sufficiently large to obscure the quadratic effect of TL residual for snakes with complete tails.

On average, female snakes have relatively shorter tails than males (Table 2). Yet, when the initial multiple regressions were calculated for V as a function of size, a coded variable for sex did likely. One would also expect that one-third tail removal would change speed less than two-thirds removal (−4.5%), and it is not clear whether such a small change would be biologically important.

Comparison of experiments and correlations

The results of the experimental and correlative analyses in this study are apparently at odds at first examination. Correlative studies on locomotion in snakes with complete tails suggest that tail length is important to locomotion and that intermediate tail lengths are associated with greatest speeds. In contrast, experiments on tail removal suggest that tail length is relatively unimportant until over half of the tail is lost.

Arnold and Bennett ('88) have made one of the first attempts to relate naturally occurring variation in snake axial morphology to performance statistically by measuring 174 neonatal *Thamnophis radix*. In a multiple regression analysis, the product of body and tail vertebrae (used to indicate a combined effect) had a significant positive relationship with speed. They concluded that minor variations in body and tail vertebrae have detectable impact on performance and that snakes with either too many or too few tail vertebrae in relation to body vertebrae had the worst performance. Similar to Arnold and Bennett ('88), the present study found a correlation of morphology with size-corrected performance of intact snakes, such that animals with abnormally long or short tails for their body length had significantly poorer performance (Fig. 4). However, we differ from Arnold and Bennett ('88) in the interpretation of this correlation.

Removing one third of the tail effectively exceeds all of the naturally occurring variation in relative length of complete tails, but this removal did not detectably affect performance. This result refutes the suggestion that minor variations in relative tail dimensions cause a decrement in performance for purely mechanical reasons. There may be an alternative explanation for the discrepancy between these experimental and correlative findings. Arnold and Bennett ('88) found a significant negative correlation between number of developmental abnormalities and performance, and the magnitude of two different developmental abnormalities (body and tail) was significantly correlated ($r = 0.25$). Hence, extreme deviations in complete tail length could be correlated to a higher probability of other developmental anomalies or detrimental morphologies that in turn might cause the observed decrement in performance. Although the functional basis of this decrement in performance remains to be determined, this example does show the utility of correlative analysis as an exploratory tool for revealing trends which often can be analyzed further by experimental methods.

The potential drawbacks of a strictly correlational analysis are further illustrated by the results relating natural tail loss to performance. This correlation could have been confounded easily by vagaries of sampling and/or by indirect effects of natural tail loss. Among the factors potentially affecting the characteristics of the sample of 52 snakes with incomplete tails are 1) interactions between an individual's locomotor performance and the probability of tail injury (e.g., slow individuals may be more likely to get injured), 2) the frequency distribution of the relative amount of the tail that was missing (see preponderance of snakes missing a small fraction of the tail in Fig. 1), and 3) interactions between tail injury and consequent health (discussed earlier) and survival.

Because experimentally induced morphological variation will almost inevitably differ in some way with naturally occurring morphological variation, statistics correlating performance and morphology will continue to be a valuable form of analysis. However, inferences from such correlative analyses should be strongest if the actual morphology of each individual is related to its performance. Related to this point are some aspects of the analysis performed by Arnold and Bennett ('88) that may have complicated their interpretation are as follows. 1) The significance of the product of body times tail vertebrae is difficult to interpret functionally because it does not yield a unique quantity for different ratios of body to tail vertebral counts. 2) The actual morphology (vertebral numbers) of each individual was not entered into the regression predicting performance, but instead a quantity (adjusted for sexual differences) was used which artificially altered the relation of body to tail vertebrae. 3) Although the actual numbers of tail vertebrae relative to body vertebrae differed significantly between males and females, Arnold and Bennett ('88) found no significant difference in performance between males and females. Consequently, relating performance to the least derived measure of morphological variation in their study argues against a body-tail relationship as being the causative factor affecting performance.

The present study illustrates the desirability of using experimental rather than correlative methods for relating morphology to performance. Furthermore, a surprising diversity of conclusions resulted from correlative analyses performed on different samples from a natural population. Depending on the sample, one might have concluded that there was no significant effect (natural tail loss), a significant linear effect (complete + natural loss), or a significant quadratic effect (complete tails) of relative tail length on locomotor performance. Although it is clearly not always possible or practical to measure performance of individuals before and after an experimental treatment, this study provides a striking example of the power of such methodology and the misleading conclusions that may result from a purely correlative analysis of morphology and function.

ACKNOWLEDGMENTS

We thank Dr. P. Wainwright, Dr. G. Lauder, and Dr. S. Reilly for helpful discussions and comments on an earlier draft of the manuscript. This research was supported by National Science Foundation grant number BSR 8600066 to AFB.

LITERATURE CITED

Alexander, R.McN., and G. Goldspink eds. (1977) Mechanics and Energetics of Animal Locomotion. Chapman and Hall, London.

Arnold, S.J. (1983) Morphology, performance and fitness. Amer Zool., *23*:347–361.

Arnold, S.J., and A.F. Bennett (1988) Behavioural variation in natural populations. V. Morphological correlates of locomotion in the garter snake (*Thamnophis radix*). Biol. J. Linn. Soc., *34*:175–190.

Bellairs, A.d'A., and S.V. Bryant (1985) Autotomy and regeneration in reptiles. In: Biology of the Reptilia. C. Gans and F. Billett, eds. John Wiley and Sons, New York, Vol. 15, pp. 301–410.

Bennett, A.F. (1987) Interindividual variability: an underutilized resource. In: New Directions in Ecological Physiology. M.E. Feder, A.F. Bennett, W.W. Burggen and R.B. Huey eds. Cambridge University Press, Cambridge, pp. 147–165.

Blight, A.R. (1977) The muscular control of vertebrate movements. Biol. Rev., *52*:181–218.

Broadley, D.G. (1983) Fitzsimon's Snakes of Southern Africa. Delta Books (pty) Ltd., Johannesburg.

Daniels, C.B. (1983) Running: an escape strategy enhanced by autotomy. Herpetologica, *39(2)*:162–165.

Gans, C. (1974) Biomechanics. An Approach to Vertebrate Biology. University of Michigan Press, Ann Arbor.

Garland, T. Jr. (1985) Ontogenetic and individual variaton in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. J. Zool., *207*:425–439.

Gray, J. (1953) Undulatory propulsion. Q. J. Microsc. Sci., *23*:101–120.

Gray, J. (1968) Animal Locomotion. Weidenfield and Nicholson, London.

Gray, J., and H.W. Lissmann (1950) The kinetics of locomotion of the grass snake. J. Exp. Biol., 26:354–367.

Hoffstetter, R., and J.P. Gasc (1969) Vertebrae and ribs of modern reptiles. In: Biology of the Reptilia. C. Gans, ed. Academic Press, New York, Vol. 1, pp. 201–310.

Huey, R.B., V. Schneider, G.L. Erie, and R.D. Stevenson (1981) A field portable racetrack and timer for measuring acceleration and speed of small cursorial animals. Experientia, *37*:1356–1357.

Jayne, B.C. (1985) Swimming in constricting (*Elaphe g. guttata*) and nonconstricting (*Nerodia fasciata pictiventris*) colubrid snakes. Copeia, *1985*:195–208.

Jayne, B.C. (1986) Kinematics of terrestrial snake locomotion. Copeia, *1986*:915–925.

Jayne, B.C. (1988a) Muscular mechanisms of snake locomotion: an electromyographic study of lateral undulation of the Florida banded water snake (*Nerodia fasciata*) and the yellow rat snake (*Elaphe obsoleta*). J. Morphol., *197*:159–181.

Jayne, B.C. (1988b) Muscular mechanisms of snake locomotion: an electromyographic study of the sidewinding and concertina modes of *Crotalus cerastes*, *Nerodia fasciata* and *Elaphe obsoleta*. J. Exp. Biol. *140*:1–33.

Jayne, B.C., and A.F. Bennett (in press) Scaling of speed and endurance in garter snakes: A comparison of cross-sectional and longitudinal allometries. J. Zool.

Lauder, G.V. (1983) Prey capture hydrodynamics in fishes: experimental tests of two models. J. Exp. Biol., *104*:1–13.

Lauder, G.V., and S.M. Reilly (1988) Functional design of the feeding mechanism in salamanders: causal bases of ontogenetic changes in function. J. Exp. Biol., *134*:219–233.

Punzo, F. (1982) Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. J. Herpetol., *16*:329–331.

Smith, M.A. (1935) The Fauna of British India. Reptilia and Amphibia vol. II Sauria. Taylor and Francis, London.

Wassersug, R.J., and K.V.S. Hoff (1985) The kinematics of swimming in anuran larvae. J. Exp. Biol., *119*:1–30.