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Swimming in Constricting (*Elaphe g. guttata*) and Nonconstricting (*Nerodia fasciata pictiventris*) Colubrid Snakes

BRUCE C. JAYNE

The axial skeleton, musculature and the waveform during swimming were examined for *Nerodia f. pictiventris*, a nonconstricting colubrid, and *Elaphe g. guttata*, a constricting colubrid. Both species possess qualitatively similar configurations of the segments of three major epaxial muscles (M. semispinalis-spinalis, M. longissimus dorsi and M. iliocostalis). Segmental lengths of these three muscles of *Elaphe* are slightly less than or equal to those of *Nerodia*, whereas *Elaphe* has 50% more total vertebrae than *Nerodia*. Between the two species examined, no differences were found in waveform or maximum swimming velocity, whereas there were slight differences in the relation between relative swimming velocity and the frequency of wave propagation. For both species the amplitude and wavelength of the lateral undulations increased from anterior to posterior. Within each species, relative amplitude and relative wavelength tended to decrease slightly as swimming speed or snake size increased. For *Nerodia* the maximum absolute swimming velocity scaled with total snake length to the 0.6 power. For all snakes stability in the transverse plane increased with increased swimming speed. Snakes and anguilliform fish exhibited similar burst swimming velocities and a similar relationship between frequency of undulation and relative forward velocity.

OF the four major modes of snake locomotion, three (lateral undulatory, side-winding and concertina) use lateral flexion of the vertebral column to generate propulsive forces (Gray, 1968). Lateral undulatory locomotion is probably the best understood of these three, largely as a result of the classic work by Gray and Lissmann (1950). After examining the ratio of lateral to backward forces that snakes exerted against a series of pegs, Gray and Lissmann (1950) concluded that snakes using the fewest points of lateral contact were the most efficient. Since Gray and Lissmann (1950), much of the study of terrestrial lateral undulatory locomotion has attempted to document further the effects of the number and spacing of lateral points of contact on this mode of locomotion. Heckrote (1965) chased common garter snakes, *Thamnophis s. sirtalis*, of different sizes through an array of regularly spaced pegs. After correcting for the effects of temperature, he concluded that there may be an optimal size for efficient lateral undulatory locomotion. However, as discussed by Gans (1974), this conclusion is suspect because of the likelihood that the spacing of the pegs determined which size of snake could crawl the fastest. Bennet et al. (1974) showed that peg spacing did affect the speed of

individual snakes; however, because of the small numbers of snakes and taxa that were used in this study, the generality of this effect is not clear. Ruben (1977) counted the number of undulations during terrestrial locomotion of *Masticophis flagellum* and *Lichanura roseofusca* and found that *Lichanura* consistently moved with more undulations. Because *Lichanura* also possessed shorter segments of three major epaxial muscles, he suggested that in snakes adaptations for constriction (*Lichanura*) and for locomotor speed (*Masticophis*) may be mutually exclusive. Because of the uncertain effect of the spacing of pivotal points as well as the fact that snakes often simultaneously use two modes during terrestrial locomotion, aquatic lateral undulatory locomotion was chosen for this study.

It is likely that information about terrestrial lateral undulatory locomotion has only limited applicability to swimming (Blight, 1977). Although Hertel (1966) has provided the most quantitative discussion of wave propagation in swimming snakes, he provided few actual measurements and primarily used his data to formulate mathematical models of the waveform of snakes. Hertel (1966) verified that the swimming of snakes was comparable to the anguilliform mode of swimming of fish. This mode of

swimming is most commonly used by long, cylindrical species (Breder, 1926; Gray, 1968; Lindsey, 1978). The anguilliform mode of swimming is characterized by lateral undulations along the entire length of the organism, with these undulations having a relatively large amplitude (ca 30–40% of the body length) and a wavelength less than the body length (Lindsey, 1978). Based upon film analysis, Hertel (1966) found that the water snake (*Natrix natrix*) moves with a constant forward velocity when the body waves travel backwards with a constant speed. Hertel (1966) found that the amplitude of the lateral undulations increased from the head to the tail of the snake, in a fashion similar to the swimming of the eel (Gray, 1968). For the sake of simplicity when mathematically modelling the waveform of the swimming snake, Hertel (1966) assumed the increase in amplitude from head to tail was linear, whereas the wavelength of the undulations remained constant. Finally, using these assumptions Hertel (1966) described the swimming movements for different efficiencies, where efficiency was defined as the ratio of forward velocity divided by wave velocity. Because of the limited data provided by Hertel (1966), it is not clear how the size or velocity of the snake might affect its swimming.

This study compares the locomotor abilities and morphology of *Nerodia f. pictiventris* versus *Elaphe g. guttata*. *Nerodia* and *Elaphe* were chosen for this study for three major reasons. First, segments of the major epaxial muscles are qualitatively similar in these two species. For example, the M. semispinalis-spinalis of both species has two distinct heads, as is characteristic of all colubroid snakes (Mosauer, 1935; Gasc, 1974). The tendinous connection between the M. semispinalis-spinalis and the M. longissimus dorsi is also similar in both species. Second, *Elaphe* possesses nearly twice as many trunk vertebrae as *Nerodia* and hence may be considered more flexible than *Nerodia*. Finally, *Elaphe* constricts, whereas *Nerodia* does not. Furthermore, both *Elaphe* and *Nerodia* naturally utilize all of the major modes of snake locomotion in a wide variety of habitats. In other words, both of these species can be considered locomotor generalists compared to some groups of snakes (e.g., Hydrophiidae) which may be confined exclusively to one type of habitat. Therefore, the comparison of *Nerodia* to *Elaphe* attempts to isolate functional differences which may result from having an axial morphology that is characteristic of constricting colubrid snakes (Jayne,

1982). Hence, the purpose of this study is two-fold. First, the wave propagation of swimming snakes will be quantitatively described in order to document individual and intraspecific variation that may result from different snake size and velocity. Second, the speed and waveform during swimming will be compared for *N. f. pictiventris* versus *E. g. guttata*.

MATERIALS AND METHODS

A Bolex H16 camera was used to make 16 mm movies of the snakes swimming in three different filming arenas. Five *Nerodia s. sipedon* juveniles (22–26 cm total length) captured in east-central Illinois during Oct. 1976 were allowed one month to acclimate to laboratory conditions. They were filmed indoors using a shutter speed of 1/200 sec and 32 fps with spotlights for illumination. The camera was mounted directly above a 45 × 90 cm aquarium with 15 cm of water. A mirror placed along the side of the aquarium permitted simultaneous filming of dorsal and lateral views of the swimming snakes. Water and air temperatures were 25 C and 27 C, respectively. Because the small confines of the aquarium seemed to inhibit the snakes from swimming in a straight path, no additional attempts were made to film with this setup.

Nerodia f. pictiventris and *Elaphe g. guttata*, captured from areas in west-central Florida, were used for all subsequent filming (Dec. 1979–March 1980). All of the remaining footage was made outdoors with available light, using a shutter speed of 1/300 sec and 48 fps. Film was exposed with the camera centered above a circular swimming pool with a diameter of 2.1 m and a water depth of 40 cm. To provide fixed points of reference, a 25 cm grid was drawn on a cloth and placed on the bottom of the pools. The water and air temperatures were 22 C and 27 C, respectively. Because the largest snakes seemed to be inhibited from swimming fast and straight in the circular pool, the three largest *Nerodia* and *Elaphe* were filmed again in a 3 × 6 m reflecting pool with a water depth of 30 cm. The water and air temperatures approximated 22 C and 25 C, respectively. The camera was not centered directly over this reflecting pool.

After the completion of filming, the snakes were killed with an injection of Nembutal. Before preservation, snakes were weighed to the

nearest 0.1 gm. Body length, tail length and distance from the snout to the posterior end of the lung were then measured to the nearest 0.5 cm. Numbers of trunk and caudal vertebrae were estimated by counting the numbers of ventral and subcaudal scales. Each freshly killed, intact snake was placed with its side on a flat horizontal surface and pins were stuck into the body and tail to mark intervals equal to 10% of the total length. At each pin, the mid-dorsal to mid-ventral distance was measured to the nearest 0.1 mm with vernier calipers. For each of these intervals along the body and tail, the mid-sagittal areas were calculated and then summed to yield an estimate of total midsagittal area. Midsagittal areas also were calculated in a similar fashion from preserved specimens until a total of 15 individuals of each species was measured. Snakes killed for this study were then preserved in 10% formalin. After fixation of the specimens, segments of the *Mm. semispinalis-spinalis*, *longissimus dorsi* and *iliocostalis* were dissected in the three largest *Nerodia* and *Elaphe*. Because the two smallest *Elaphe* were borrowed pets, they were not preserved and they were only weighed, measured for body and tail length, and examined for numbers of ventral and subcaudal scales.

The films were projected on a Vanguard motion analyzer and images from single frames were traced with pencil on sheets of matted acetate. Usually fifteen tracings were made at regular intervals for each sequence of swimming. When possible, tracings were made from five sequences per snake, including the sequence with the greatest forward velocity. Every attempt was made to obtain footage in which the snakes were swimming at constant forward velocity in a straight line. In order to confirm whether or not the forward velocity varied significantly ($P < .05$) with time within a sequence the velocities were analyzed with one-way analysis of variance. The forward velocities were grouped into three successive time intervals and an F test was used to compare variance among and within the time intervals. On each series of tracings, a line indicating the direction of travel was drawn by bisecting the distance between points of maximum lateral displacement from two images that were 180° out of phase. This swimming direction then was used as the abscissa for constructing a Cartesian coordinate plane in which the snakes swam in the negative x direction (Fig. 1). For each tracing, the x coordinates were measured for the position of the snake's snout and

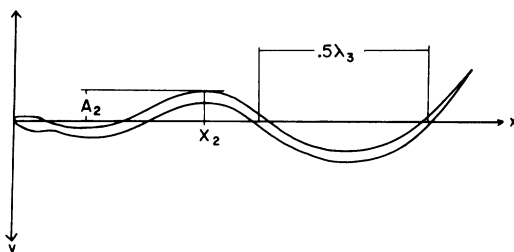


Fig. 1. Method of measuring waves. A_2 = amplitude of second half wave. X_2 = distance of the second half wave from the snake's snout. $.5\lambda_3$ = half of the wavelength of the third half wave.

for the nodes of the waves. For each point of maximum lateral displacement, the x and y coordinates measured the position and amplitude of the wave, respectively.

In order to calculate regressions for amplitude and wavelength, all x coordinates were adjusted so that the snakes' snouts were at $x = 0$ (Fig. 1). All amplitudes were converted to positive values. Internode distances were multiplied by two to calculate the wavelength (λ) of each half wave (undulation). Measurements then were converted to % of the snake's total length (TL). Finally, least squares regressions were calculated for amplitude and wavelength as a function of x (distance from the snout of the snake). Regressions of amplitude as a function of wavelength also were calculated as an indicator of the amount of vertebral flexion. A Hewlett-Packard plotter was used to draw regressions with their 95% confidence limits (CL). Paired comparisons of the regressions were made by superimposing two graphs and noting, for regions not showing overlapping 95% CL, which regression $\pm 95\%$ CL was greater. The period of the waves (T) was measured as the amount of time needed for the waves to undergo a 360° phase shift. The snake's mean forward velocity during one sequence was calculated as the average distance travelled between successive tracings divided by time between tracings. Because of parallax, footage of the largest snakes in the reflecting pool could not be used for measuring waveform; however, it was used to determine forward velocities and frequencies of wave propagation.

RESULTS

Anatomy.—Table 1 summarizes the basic anatomical measurements of the experimental *Ner-*

TABLE 1. BASIC ANATOMICAL DATA FOR *Nerodia f. pictiventris* AND *Elaphe g. guttata* (ABBREVIATED N AND E, RESPECTIVELY). * INDICATES THAT THE MEASUREMENT WAS AFFECTED BY AN INCOMPLETE TAIL AND THAT IT WAS NOT USED TO CALCULATE AN AVERAGE. SNAKES ARE ORDERED BY INCREASING TOTAL LENGTH. THE NUMBER AFTER THE LETTER ABBREVIATION FOR A SPECIES IS ONLY TO FACILITATE RECOGNITION OF INDIVIDUALS.

Snake	Sex	Weight (gm)	TL = Total length (cm)	Tail length (% TL)	Number of vertebrae		Position lung end (% TL)	Total midsagittal area (cm ²)	Caudal midsagittal area (cm ²)
					Body	Caudal			
N2	F	4.4	22.0	25.0	125	60	54.5	11.0	1.3
N1	F	5.1	24.0	25.0	128	75	52.1	11.4	0.7
N3	F	9.9	28.0	23.2	124	75	53.6	17.8	1.1
N4	M	20.6	39.0	24.4	128	68	53.8	29.6	2.4
N5	M	143.5	71.0	25.4	124	71	52.1	89.6	8.8
N6	F	242.0	77.0*	18.2*	125	46*	57.1*	153.2	8.9
N7	F	510.0	99.0*	20.2*	125	58*	53.0*	224.6	13.2
Average				24.6	126	70	53.0		
E1	?	8.0	33.5	16.4	221	76	—	—	—
E2	?	17.0	41.0	17.1	217	68	—	—	—
E4	F	220.0	99.5*	8.0*	229	29*	80.4*	162.2	4.5
E3	M	460.5	126.5	16.6	224	68	75.1	244.4	11.2
E5	M	803.1	142.0	14.1	215	61	75.4	386.9	18.5
Average				16.0	221	68	75.2		

odia and *Elaphe*. The mean number of body vertebrae of *Nerodia* was 126 compared to 221 in *Elaphe*. *Nerodia* and *Elaphe* possessed nearly equal numbers of caudal vertebrae, with respective means of 70 and 68. However, the tail of *Nerodia* accounts for a significantly greater percentage of the total length (24.6%) than that of *Elaphe* (16.0%). The lung of *Nerodia* extends for a smaller percentage of the total length compared to *Elaphe* (53% vs 75.2%). For a series of 15 *Nerodia* and *Elaphe*, regressions were calculated for log of total midsagittal (ms) area (cm²) as a function of log of total length (cm). Regression statistics for *Nerodia* are: slope = 2.05, intercept = -1.76, and $r^2 = .993$; for *Elaphe* the statistics were, respectively, 2.01, -1.80 and .987. The slopes of these regressions do not differ significantly ($t = 1.90$, $P > .05$); however, for *Nerodia* the regression plus and minus the 95% confidence limits had a significantly greater elevation than that of *Elaphe*. This indicates that *Nerodia* is proportionately stouter than *Elaphe*. Regressions were also calculated for log of the ms body area as a function of log body (snout-vent) length. Regression statistics for *Nerodia* are: slope = 1.98, intercept = -1.45, and $r^2 = .998$; for *Elaphe* the statistics were, respectively, 1.97, -1.60, and .998. Once again the slopes do not differ significantly ($t = 0.80$, $P > .40$). Because *Nerodia* possesses a relatively long, thin tail, however, an even greater differ-

ence exists between the two regressions than in the previous comparison. In both *Nerodia* and *Elaphe* the tail generally accounts for a small portion (~6%) of the total midsagittal area.

The following descriptions of muscles are based on the average measurements taken from three individuals each of *Nerodia f. pictiventris* and *Elaphe g. guttata*. In both *Elaphe* and *Nerodia* the muscular segments of the Mm. semispinalis-spinalis, longissimus dorsi, and iliocostalis each receive muscle fibers from two adjacent vertebral units (e.g., see spinalis origin on vertebrae 19 and 20 in Fig. 2). Despite this, certain tendinous portions of all three muscles exhibit a 1:1 correspondence with the number of vertebrae. These tendinous portions are 1) the long anterior tendon of the M. semispinalis-spinalis, 2) the anterior tendinous arch of the M. longissimus dorsi, and 3) the intermediate tendon between the medial and lateral heads of the M. iliocostalis (Fig. 2).

To facilitate comparisons, the vertebra onto which the anterior tendon of the M. semispinalis-spinalis inserted was counted as number one and the subsequent numbering of vertebrae proceeded posteriorly. The thin anterior tendon of the M. semispinalis-spinalis extends posteriorly to end lateral to the 14th vertebra of *Nerodia* and to the 11th vertebra of *Elaphe*. The muscle tissue of the dorsomedial head (spinalis) of the M. semispinalis-spinalis continues poste-

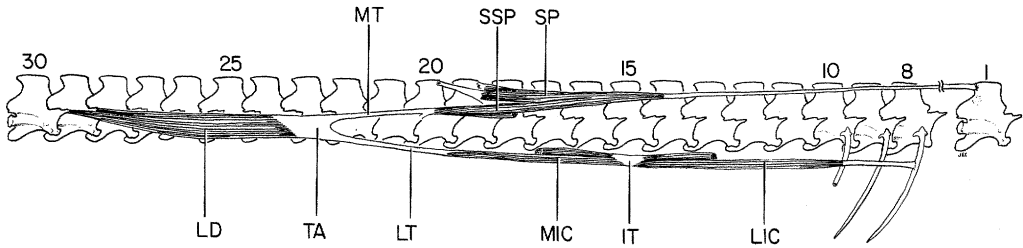


Fig. 2. Simplified right lateral view of the major epaxial muscle segments of *Nerodia f. pictiventris*. Anterior is to the right of the figure. SP and SSP respectively indicate the spinalis and semispinalis portions of the M. semispinalis-spinalis. LD represents the M. longissimus dorsi and MT, TA, and LT are the medial tendon, tendinous arch, and lateral tendon of LD. MIC and LIC respectively are the medial and lateral heads of the M. iliocostalis and IT is the intermediate tendon of this muscle. See text for more detailed descriptions.

riorly for 5 vertebrae in *Nerodia* and for 4 vertebrae in *Elaphe*. The muscle fibers then terminate on the posterior tendons of the segments of the M. multifidus, which extend posteriorly for an additional 1 or 2 vertebrae in *Nerodia* and for 2 vertebrae in *Elaphe*, to attach to the lateral surface of the neural spine. Thus, the resulting span of vertebrae for one segment of the spinalis is 20 in *Nerodia* and 17 in *Elaphe*. Muscle fibers from the ventrolateral head (semispinalis) of the M. semispinalis-spinalis terminate on a tendinous sheet at the 20th vertebra of *Nerodia* and at the 17th vertebra of *Elaphe*. In both *Elaphe* and *Nerodia*, part of this tendinous sheet contributes to an intermuscular septum (between the Mm. semispinalis-spinalis and longissimus dorsi). This septum forms a diffuse connection to the vertebra in the region of the prezygapophysis. Another portion of the tendinous sheet extends ventrolaterally to form the medial tendon of the M. longissimus dorsi.

Muscle tissue from a single segment of the M. longissimus dorsi extends anteriorly from its origin on the 30th vertebra to insert into a tendinous arch lateral to the 24th vertebra of *Nerodia*; in *Elaphe* the muscular tissue of the M. longissimus dorsi extends from the 27th to the 21st vertebra. The tendinous arch gives rise to a dorsomedial tendon that connects with the semispinalis and a ventrolateral tendon that connects with the medial head of the M. iliocostalis. Between the lateral and medial heads of the iliocostalis, both *Nerodia* and *Elaphe* possess an intermediate tendon that is less than one vertebra long; this tendon is lateral to the 15th vertebra of *Nerodia* and the 11th vertebra of *Elaphe*. The muscle tissue of one segment of the M. iliocostalis extends anteriorly from the 20th to 10th vertebra of *Nerodia* and from the 17th

to 7th vertebra of *Elaphe*. The tendon from the lateral head extends anteriorly until it attaches to the rib of the 8th vertebra of *Nerodia* and the 5th vertebra of *Elaphe*. Hence the total number of vertebrae spanned by a single unit of the M. longissimus dorsi–M. iliocostalis is 23 in both *Nerodia* and *Elaphe*.

Waveform.—Fig. 3 illustrates the listing that occurs during swimming of juvenile *Nerodia s. sipedon*. For this study, listing is defined as changes in orientation between the surface of the water and the plane containing the snake. In other

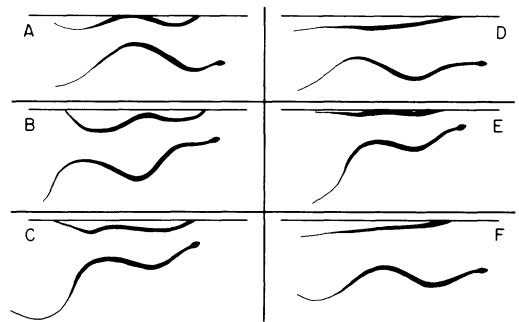


Fig. 3. Simultaneous lateral and dorsal views of swimming juvenile *Nerodia s. sipedon*. Figures were made from tracings of films. The horizontal line at the top of each figure represents the surface of the water and the tracing touching the line is the lateral view of the snake. The dorsal view is immediately below each lateral view. Because of distortions at the surface of the water, illustration of those portions of the snake above the surface was not possible. The snakes shown had total lengths ranging from 22–26 cm. Forward velocities in figures A–F are respectively 8.9, 14.0, 30.8, 43.9, 56.6 and 77.2 cm/sec.

TABLE 2. SELECT WAVEFORM DATA FOR SWIMMING *Nerodia f. pictiventris* AND *Elaphe g. guttata*. The snakes are numbered as in Table 1 in addition to the number in parentheses identifying the film footage sequence. N = sample size. V_m and V_n respectively indicate the mean forward velocities in cm/sec and tl/sec. SD = standard deviation. T = period of the waves. AMP = amplitude of the waves, λ = wavelength, and X = distance from the snout of the snake along the direction of travel (all are in units of % tl). r^2 = coefficient of determination. * Indicates significant variation with time (see text).

Snake (seq)	V_m	V_n	V_n	V_n SD	T (sec)	Reg N	Regression AMP = mX + b			Regression $\lambda = mX + b$			Regression AMP = mX + b		
							Slope	Intercept	r^2	Slope	Intercept	r^2	Slope	Intercept	r^2
N2(4)	13	42.1	1.91	.54	.250	25	.0870	3.47	.47	.456	40.5	.65	.189	-4.15	.70
N1(6)	15	60.4	2.52	1.18	.188	33	.144	1.46	.66	.649	31.8	.68	.213	-5.11	.88
N1(2)	14	35.9	1.50	.70	.313	27	.141	3.06	.59	.592	37.9	.55	.212	-4.32	.83
N1(3)	13	24.6	1.02	.24	.500	28	.117	3.02	.69	.686	34.4	.75	.160	-2.20	.81
N1(5)	14	12.4	0.52	.13	.917	35	.180	.769	.85	.898	22.2	.76	.179	-2.54	.89
N3(5)	14	71.0	2.54*	.36	.208	28	.147	1.24	.83	.274	46.7	.57	.289	-9.51	.57
N4(1)	14	76.2	1.95	.39	.208	38	.107	1.29	.88	.439	31.4	.47	.120	-4.95	.45
N5(1A)	6	113.2	1.59	.27	.333	19	.0564	2.21	.63	.578	23.4	.78	.104	-.327	.91
N5(1B)	7	80.9	1.14	.11	.417	22	.0832	2.61	.68	.664	22.7	.91	.130	-.468	.80
N6(3)	14	113.2	1.47	.13	.333	31	.101	1.86	.70	.765	18.8	.64	.123	-.232	.95
N7(3)	14	97.0	0.98	.17	.375	38	.0491	3.95	.56	.281	35.3	.50	.149	-1.03	.82
E1(1)	14	47.1	1.41	.31	.417	25	.109	3.25	.56	.276	51.1	.47	.224	-6.27	.39
E1(2)	14	36.5	1.09	.11	.500	25	.117	2.71	.65	.403	49.2	.51	.212	-6.37	.68
E1(4)	14	18.3	0.55	.06	.833	23	.0993	3.33	.51	.603	35.0	.64	.154	-1.80	.71
E2(1)	11	46.1	1.12	.30	.333	34	.133	-.390	.80	.540	24.1	.52	.182	-3.45	.83
E3(1)	14	72.0	0.57	.11	.750	35	.0578	2.28	.81	.158	41.4	.22	.130	-.152	.45

TABLE 3. SUMMARY OF CHANGES IN WAVEFORM WITH CHANGES IN FORWARD VELOCITY. The number of pairs used for comparisons was the number of sequence pairs of one snake with significant differences in forward velocity. <, =, and > indicate the relation between predicted values of the sequence with the greater forward velocity versus that with the smaller forward velocity. Abbreviations are as in Table 2.

Snake	Number pairs	Paired comparisons of predicted values								
		Regression AMP = mX + b			Regression $\lambda = mX + b$			Regression AMP = m λ + b		
		<	=	>	<	=	>	<	=	>
N2	8	2	6	0	3	5	0	1	7	0
N1	12	0	11	1	0	12	0	1	9	2
N3	9	3	1	5	0	6	3	2	4	3
N4	5	3	2	0	3	2	0	2	3	0
N5	11	5	6	0	3	8	0	4	7	0
N6	7	5	1	1	3	4	0	2	4	1
N7	4	2	0	2	2	1	1	1	3	0
E1	9	0	8	1	2	5	2	0	9	0
Total	65	20	35	10	16	43	6	13	46	6

words, when the snake lists, the plane determined by the body of the snake rotates about the axis indicating the direction of travel. *N. s. sipedon* is closely related to *N. f. pictiventris* and seems to have a similar distribution of buoyant forces. For example, the lung of *N. s. sipedon* extends to approximately 50% of the snake's total length, and this is very similar to the length of the lung in *N. f. pictiventris* (Table 1). Listing is not readily quantified; however, three major conclusions can be made. 1) Maximal listing generally occurs at the points of maximal lateral displacement. 2) The magnitude of the listing decreases as forward velocity increases. 3) At maximum forward velocity, *N. s. sipedon* juveniles swim in a plane approximately 5.5° below the surface of the water.

A complete list of the regression statistics that were used to detect changes in waveform for all forty-three film sequences can be found in Jayne (1980). Table 2 lists representative regression statistics for waveform and includes the absolute and relative forward velocities (V_{cm} and V_{cl}) and the period of wave propagation (T) for a film sequence. One-way analysis of variance detected only three sequences that had significant variation in V_{cl} with time. For N2(2) $F = 4.18$ (.025 < P < .05). For N6(4) $F = 5.52$ and for N3(5) $F = 6.49$, with .01 < P < .025 for both sequences. In order to determine whether or not waveform changes with V_{cl} of each snake, paired comparisons of the regressions $\pm 95\%$ CL were made for all pairs of film sequences of one snake for which there were significant differences in the mean V_{cl} (two-tailed

t-test, $P < .05$). Table 3 summarizes the results of these comparisons. As snakes swam faster both the amplitude of the waves and the wave length usually decreased. The ratio of AMP/ λ also tended to decrease with greater speeds, indicating that amplitude decreases more quickly than wavelength with increasing speed.

Comparisons among different film sequences are complicated by error in determining the orientation of the axes of the coordinate system. Hence, subtle changes in waveform resulting from changes in swimming speed may have been obscured. *Nerodia* 5 swam one particularly interesting sequence in which it decelerated significantly. Because of this deceleration, data from this sequence were subdivided (into 1A and 1B) for analysis after they had been gathered using a single set of axes. Sequence 1A possessed a greater V_{cl} than 1B (two-tailed t-test, $P < .05$) and the regression for amplitude ($\pm 95\%$ confidence limits) was less than that of 1B (for 22 < X < 66). Although the regression for wavelength was slightly less for 1A compared to 1B, this was not a significant difference, as the 95% confidence limits overlapped completely. The regressions for amplitude as a function of wavelength also displayed complete overlap of their 95% confidence limits. Therefore, these data further suggest that there are significant decreases in amplitude as speed increases, whereas changes in wavelength with speed are less obvious.

Because drag is proportional to the surface area of a snake and marked differences in surface area exist among different sizes of conspe-

TABLE 4. SUMMARY OF WAVEFORM AMONG DIFFERENT SIZES AND SPECIES. For the comparisons among different sized *Nerodia* all possible pairs of the listed sequences were utilized (* except N2(3) vs N6(5) because of their different V_{cl} 's). For comparisons with constant V_{cl} , symbols indicate predicted values of the smaller snake versus the larger snake. For comparisons between species, symbols indicate the values of *Nerodia* vs. *Elaphe*.

Comparison and sequences used	Number pairs	Paired comparisons of predicted values								
		Regression AMP = $mX + b$			Regression $\lambda = mX + b$			Regression AMP = $m\lambda + b$		
		<	=	>	<	=	>	<	=	>
V_{cl} 0.5										
N1(5), N3(2), N5(3), N7(1)	6	1	2	3	1	2	3	1	2	3
V_{cl} 1.0*										
N2(1), N1(3), N4(4), N5(2), N6(5), N7(3)	14	3	2	9	2	5	7	2	9	3
V_{cl} 1.5										
N1(2), N3(4), N4(2), N5(1A), N6(3)	9	2	2	5	0	3	6	2	0	7
Total	29	6	6	17	3	10	16	5	11	13
<i>Elaphe</i> , constant V_{cl}										
E1(4) vs E3(1); E1(2) vs E2(1)	2	0	0	2	0	0	2	0	2	0
<i>Elaphe</i> vs <i>Nerodia</i> , constant V_{cl}										
E1(1) vs N4(2), N3(4), N1(4), N1(2); E1(2) vs N1(3), E1(3) vs N4(5); E1(4) vs N1(5), E2(1) vs N4(4)	8	3	4	1	2	3	3	2	6	0

cific snakes, comparisons of waveform were made among different sizes of snakes within each species. In order to minimize the variation of waveform while comparing different sizes of snakes, paired comparisons were confined to sequences with insignificant differences in V_{cl} (t-test, $P > .05$). Table 4 summarizes the changes in waveform that occur with changes in the size of the snake. In 17 of 29 comparisons of *Nerodia*, smaller snakes had greater values of the regressions for relative amplitude. Smaller *Nerodia* also tended to possess greater estimated values for λ and AMP/ λ . Unfortunately, only two comparisons of different sizes of *Elaphe* with comparable relative velocities were possible. In both comparisons, relative to the large *Elaphe*, the smaller *Elaphe* possessed smaller relative amplitudes and wavelengths and comparable AMP/ λ ratios.

Comparisons between species were confined to snakes with the most similar lengths and equal V_{cl} (Table 4). Consistent differences of waveform were not discernable. Only 2 of 8 paired comparisons displayed different AMP/ λ ratios.

Velocity.—For both *Nerodia* and *Elaphe*, the relative forward velocity (V_{cl}) usually increased with increased frequency ($f = 1/T$) of wave propagation (Table 2). Regression statistics for V_{cl} as

a function of f are summarized in Table 5. Because the smallest snakes consistently attained the highest frequencies, separate regressions were calculated for small (N1–N4; E1–E2) and large (N5–N7; E3–E5) snakes, as well as combining the data for all snakes of each species. For both species, the slopes of the regressions of the small versus the large snakes were larger; however, this was not a significant difference for *Nerodia* ($t = .457$, $P > 0.2$), whereas it was significant for *Elaphe* ($t = 2.82$, $P < .01$). For both species, when these regressions $\pm 95\%$ CL

TABLE 5. REGRESSION STATISTICS FOR $V_{cl} = mf + b$. f = FREQUENCY OF WAVE PROPAGATION IN Hz. The numbers in parentheses are the standard errors of the slopes. Other symbols are as in Table 2. Explanation of samples is in text.

Sample	n	r^2	Slope	Intercept
Small <i>Nerodia</i>	21	.845	.459 (.045)	-.087
Large <i>Nerodia</i>	15	.769	.450 (.068)	.056
All <i>Nerodia</i>	36	.844	.434 (.032)	.033
Small <i>Elaphe</i>	18	.620	.383 (.075)	.101
Large <i>Elaphe</i>	17	.925	.329 (.024)	.141
All <i>Elaphe</i>	35	.730	.338 (.036)	.161

were compared between different sizes of snakes, the CL overlapped completely. When the regressions for small, large, and all snakes were compared for *Nerodia* versus *Elaphe*, the slope of the *Nerodia* regression was always larger by a highly significant ($P < .001$) amount (small $t = 3.94$, large $t = 6.88$, and all $t = 10.57$). The regressions $\pm 95\%$ CL for small *Nerodia* versus small *Elaphe* exhibited complete overlap. In contrast, the regression $\pm 95\%$ CL was greater both for large *Nerodia* versus *Elaphe* (where $2.0 \text{ Hz} < f < 3.0 \text{ Hz}$) and for all *Nerodia* versus all *Elaphe* (where $2.5 \text{ Hz} < f < 4.0 \text{ Hz}$).

The absolute maximum forward velocity (V_{\max} , cm/sec) increases with increased total length (tl, cm) both for *Nerodia* and *Elaphe*. With the exception of the largest snakes, mean maximum velocities and sample sizes are listed in Table 2. For the large snakes N7, E3, E4 and E5 sample sizes are 10 and the mean values of V_{\max} (and standard deviation) are, respectively, 103.1(13.3), 114.4(16.9), 155.5(15.3) and 132.4(28.4) cm/sec. Regressions for V_{\max} as a function of tl were calculated and for *Nerodia* slope = 0.817, intercept = 40.4, $r^2 = .575$; for *Elaphe*, the regression statistics were, respectively, 0.877, 21.1 and .662. Comparisons using the 95% confidence limits of slope and elevation of these two regressions showed no significant differences between these two quantities for *Nerodia* versus *Elaphe*. Regressions were also calculated for $\log(V_{\max})$ as a function of $\log(\text{tl})$. For *Nerodia* the slope, y-intercept, and r^2 were .602, .890 and .49, respectively. For *Elaphe* these respective quantities were .829, .378 and .78. As before no significant differences were found between either the slopes or the elevations for *Nerodia* versus *Elaphe*.

DISCUSSION

Three major sources of error are apparent in this study. First, although no significant differences existed between the regressions for maximum forward velocity of *Nerodia* and *Elaphe*, the error, as indicated by the 95% CL, about the regression for *Elaphe* was much larger. This difference may be attributable to varying durations of captivity. Zug (1978) conducted an extensive study on the jumping abilities of frogs and found that maximum jumping ability often decreased with increased time in captivity. With the exception of N4, all *Nerodia* were filmed after the same amount of time in captivity. All of the *Nerodia* also displayed sim-

ilar temperament when handled. In contrast, for *Elaphe* times in captivity before filming ranged from about three years (E3 and 5) to one month (E4). *Elaphe* 4 swam with the fastest absolute velocity of any snake and it was also the only snake of either species that bit a handler during filming. Thus, behavioral or motivational differences may affect the determination of maximum performance.

Second, examination of the coefficients of determination (r^2) in Table 2 illustrates that the errors of the regressions for amplitude and wavelength were consistently greater than those for the regressions of amplitude versus wavelength. Difficulty in measuring X (the distance of an undulation from the snout) most likely accounts for this discrepancy. When a curve has a long radius of curvature, it is difficult to discern the exact location of the intercept of a tangent and the curve. In contrast, it is relatively easy to measure wavelength and amplitude. Therefore, one would expect less error when calculating the regression of amplitude versus wavelength.

Finally, the regression data are not always a very accurate summary of the complex waveform of the swimming snakes. In an attempt to qualitatively determine how accurately the calculated regressions of wave parameters (Table 2) could reconstruct the waveform of a swimming snake, the linear regressions for AMP and λ were substituted into the model $Y = \text{AMP} \sin(X/\lambda - t/T)$ where X = distance from the snout, t = time, and T = period of the wave. The resulting plots (Fig. 4) could then be compared to the original tracings of the films (Fig. 5). Fig. 4 illustrates one rather accurate reconstruction (N3(5)) and one rather inaccurate reconstruction (N1(6)) for two snakes of nearly equal sizes swimming at comparable velocities. As indicated in Figs. 3, 5, as well as in previously published figures of swimming snakes (Taylor, 1952; Hertel, 1966) snakes generally swim with three undulations (half waves). Therefore, the generation of only about two lateral undulations for N1(6) in Fig. 4 is most likely the result of inaccurate predicted values from the regression for wavelength. Because higher order polynomials of the independent variable of the regression model increase the goodness of fit, an attempt was made to determine if the regressions for wavelength and amplitude might be better modelled by including an X^2 term in the regression in addition to the linear X term. Ten data sets were fitted to this regression model

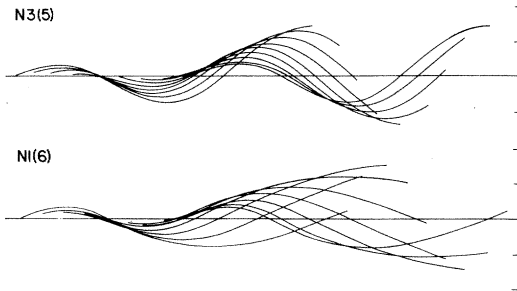


Fig. 4. Plots of waves generated with the model: $Y = \text{AMP}(\sin((X/\lambda) - t/T))$. AMP = amplitude and λ = wavelength and both are defined by linear regressions of X . X is distance from the snout of the snake in % of total length. t = time; T = period and both are in seconds. Waves were generated in the first quadrat for $t = 0, T/8, 2T/8, \dots T$ and then translated to the left an amount equal to V_{u1} times t . The ordinate and abscissa are to the same scale and the tick marks on the ordinate equal 10% of the total length. The length of each curve is equal to total length (100%). Regression statistics, forward velocities, and periods of the waves for these two film sequences are listed in Table 2.

that was a second order polynomial of X . However, the coefficient of the X^2 term of different data sets had both positive and negative values. Because of this lack of consistency in the influence of the quadratic terms (i.e., a coefficient always of the same sign), no further attempts were made to use nonlinear regressions.

Taylor (1952) and Hertel (1966) used the forward velocity (V) over wave velocity (W) to indicate the efficiency of swimming with lateral undulations. The calculations of both Taylor and Hertel were derived from models with the simplifying assumption that wavelength and W were constant. As Table 2 emphasizes, wavelength is not constant for a swimming snake, but rather increases as waves are propagated posteriorly. For example, for N1(6) from Table 2, wavelength = 7.6 cm at $X = 0$ and 19.3 cm at $X = 75$. Frequency times wavelength equals wave velocity; therefore, $W = 40.4$ cm/sec at $X = 0$ and $W = 102.7$ cm/sec $X = 75$. The corresponding efficiencies (V/W) at these two points on the same snake are .67 and .59, respectively. For E1(1), $V/W = 1.15$ where $X = 0$, but it is impossible for an efficiency to be greater than one. Thus V/W appears only minimally useful as an indication of snakes' swimming efficiencies, because 1) it is not constant

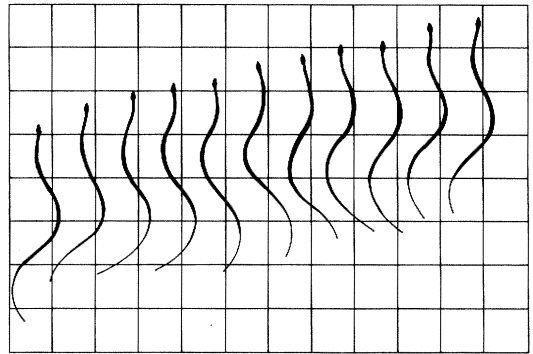


Fig. 5. Dorsal view of surface swimming of *Nerodia f. pictiventris*. These tracings of N1(6) are from successive frames of film taken at .021 sec intervals. Each successive image has been displaced to the right by one square of the grid (5 cm).

for one snake and 2) it does not always stay within realistic values (0–1). More recently, Froude efficiency has been commonly used for discussions of fish locomotion (e.g., Lighthill, 1970, 1971; Webb, 1975). Froude efficiency is calculated by dividing the estimated useful power (used to overcome drag) by the estimated total power (useful power + power lost to the fluid) generated by the swimmer. Given a number of assumptions, this ratio reduces to $(W + V)/2W$, which is equal to $\frac{1}{2} + \frac{1}{2}(V/W)$. Therefore, although this quantity varies from $\frac{1}{2}$ to 1, it is still dependent on the same variables. Because both Froude efficiency and V/W utilize a constant wave velocity (W), it is not clear if the actual efficiency of elongate swimmers with variable wavelength (hence variable W) is greater or less than the values generated by these two estimates of efficiency.

The fact that forward velocity can exceed wave velocity in the anterior regions of the snake indicates that very little real propulsion is generated anteriorly. In other words, the larger and faster posterior waves are pushing the anterior region through the water. It is interesting to note that some sea snakes (e.g., *Microcephalophis gracilis*, *Hydrophis fasciatus* and *H. brookii*) have evolved a microcephalic morphology which includes an extreme reduction in the diameter of the cervical region. For example, in a *Microcephalophis gracilis* about one meter long, the diameter of the head and neck is only about 7 mm, compared to a height greater than some 22 mm for the laterally flattened posterior region of the body. Perhaps a relatively insignif-

icant contribution of the neck region to propulsion has allowed the evolution of such an extreme morphology. Observations of swimming speed and waveform of these species could prove to be extremely informative as to the relative importance of the different regions of the snakes's body for generating propulsive forces.

The instability (listing) that occurs during the low speed swimming of *Nerodia* (Fig. 3) seems likely to reduce the actual efficiency of this movement compared to swimming at faster speeds. The two smallest *Elaphe* seemed to exhibit similar instability, despite the fact that they had proportionately longer lungs. Varde (1951) surveyed the morphology of the lung in a wide variety of snakes. Two species of sea snakes (Hydrophiinae) were included in her sample, and they possessed saccular extensions of the lung that extended all the way to the cloaca. I examined the lung in additional species of sea snakes and in *Lapemis hardwickii*, *Pelamis platurus* and *Hydrophis melanosoma* the lung also extended to the cloaca. In the remaining species of sea snakes that I examined (*Thalassophina viperina*, *Enhydrina schistosa*, *Acalyptophis peronii* and *Aipysurus eydouxi*) the lungs extended to 92–98% of the body length. For all of the sea snakes that I examined the lung averaged 84.4% of the total length. Varde (1951) suggested that such lung morphology either acts as a reservoir for air or serves as an organ of buoyancy. Sea snakes are highly specialized for a fully aquatic existence. In light of the considerable instability experienced by two terrestrial forms (*Nerodia* and *Elaphe*) with shorter lungs, sea snakes have a much more advantageous distribution of bouyant forces for efficient low speed swimming.

Taylor (1952) considered the waveform of elongate swimmers as idealized flexible cylinders immersed in water, with waves of constant amplitude travelling down the cylinder at a constant velocity. He then calculated the average values of AMP/λ and efficiency (V/W) for a swimming water snake and found they were quite similar to his theoretical estimates of the values of AMP/λ and V/W that would enable maximum speed to be obtained for a given energy output. Additional discussions of anguilliform swimming of vertebrates have emphasized the similarity of waveform (Hertel, 1966; Gray, 1968) and implied that this similarity is the result of the hydrodynamic constraints encountered by elongate swimmers. Perhaps hydrodynamic constraints are the reason that no

consistent differences were found when comparing the waveform of *Elaphe* to that of *Nerodia*. Among the most substantial anatomical differences between *Elaphe* and *Nerodia* is that *Elaphe guttata* possess approximately 297 vertebrae, compared to 196 in *Nerodia fasciata*. The segmental lengths of the major epaxial muscles of *Elaphe* were less than or equal to those of *Nerodia*, and the segmental lengths of the actual contractile tissue were similar in both species; therefore, for a given number of vertebrae, one might expect equal amounts of lateral flexion during swimming. Because *Elaphe* has about 50% more vertebrae than *Nerodia*, one might also expect about a 50% greater number of lateral undulations along the body. This increased number undulations would decrease the predicted values of the regression for relative wavelength (versus X); however, this was not the case. Fishes also exhibit tremendous variation in the numbers of vertebrae, but the effects of this variation on locomotion are not clearly understood (Lindsey, 1978). Despite the external similarity in waveform between these two species of snakes, the differences in the numbers of vertebrae and muscle segments within the undulations seem quite likely due to differences in the muscular mechanism for wave propagation. Grillner and Kashin (1976) have conducted electromyographic studies of the swimming of the European eel. They found that the axial muscles generally contracted on the concave side of the eel's undulating body. However, they also discovered that there was a significant phase lag between the wave of muscular contraction and the mechanical wave of flexion in the body of the eel. Grillner and Kashin (1976) suggested that this phase lag, which increased from anterior to posterior, may be the result of the changing influences of active and passive properties of this system of the eel plus the water. These differences in phase lag and the presumably variable significance of active and passive properties within the body of an anguilliform swimmer may also support the earlier suggestion that different anteroposterior regions of the snake's body make substantially different contributions to the propulsion of the snake. Furthermore, if this relationship between muscle contraction and mechanical effect within a body is caused by differing balances between active and passive properties, then it seems even more likely that such morphological differences as the number of vertebrae will affect the mechanism of wave propagation.

There have been only two previously published reports on the speed of swimming snakes based on film analysis. Taylor (1952) used unpublished data from Gray and measured a forward velocity of 32 cm/sec for a *Natrix* with a total length approximating 27 cm. Hertel (1966) recorded a forward velocity of 52 cm/sec for a *Natrix natrix* with a total length of 105 cm. The European *Natrix* is closely related to *Nerodia* and it also has similar habitat preference; therefore, one would expect *Natrix* and *Nerodia* to have similar maximum swimming speeds. Thus, as Table 2 and regressions for V_{\max} suggest, these two previously recorded speeds of *Natrix* are much less than the maximum attainable swimming velocity. In this study the fastest relative velocity and the highest frequency were attained by *Nerodia* (Table 2), but the fastest absolute velocity (155 cm/sec) was of a 99.5 cm *Elaphe*. Furthermore, comparison of the regressions for maximum absolute velocity as a function of snake length failed to show any significant differences between the two studied species despite the fact that the musculoskeletal morphology of *Elaphe* is representative of constricting colubroid snakes (Jayne, 1982). Thus, Ruben's (1977) suggestion that adaptations for constriction and locomotor speed may be mutually exclusive does not appear to hold for aquatic locomotion in *Elaphe*. Until the relation between swimming and terrestrial lateral undulatory locomotion is better understood, it would be premature to speculate about the relative terrestrial locomotor abilities of *Nerodia* and *Elaphe*. However, although *Nerodia* and *Elaphe* have similar burst swimming velocities, this need not imply that both species have equal energetic costs of transport. If the muscular mechanisms of wave propagation are different between these two species, it is likely that there are differences in the cost of transport and the true efficiency of locomotion. Hence, although direct measurements of metabolic rate during the swimming of snakes would be rather difficult to obtain, this information would be extremely useful.

Although data are limited, many similarities exist between the maximum velocities of swimming snakes and "anguilliform" fish. Beamish (1978) provided a convenient summary of fish speeds. A 60 cm *Anguilla vulgaris* exhibited a burst velocity of 1.9 tl/sec. The maximum velocities of snakes were attained from short time intervals (1–2 sec) and should correspond to the

"burst" swimming speeds of fish. The predicted maximum velocity of a 60 cm *Nerodia* is 1.5 tl/sec. Lampreys (*Petromyzon marinus*) with total lengths from 14–39 cm are able to sustain maximum velocities from 1.1–1.7 tl/sec for ten min (Beamish, 1978). The predicted maximum velocity of a 25cm *Nerodia* is 2.4 tl/sec.

For fish, the correlation between velocity and frequency of the tailbeat is well documented (e.g., Bainbridge, 1958). For carangiform swimmers such as dace and carp, Bainbridge found that $V = .75f - 1.33$, where V is the velocity in lengths/sec and f is frequency of the tailbeats/sec. For an eel, Grillner and Kashin (1976) found that relative forward velocity (tl/sec) approximated one-half the frequency of wave propagation. Gray (1933) listed the forward velocity and frequency both for a glass eel (*Anguilla vulgaris* = *A. anguilla*) and for a butterfish (*Certonotus gunnellus*), both of which are anguilliform swimmers. For *A. vulgaris* $V = .55$ tl/sec where $f = 1.55$ /sec, whereas for *Certonotus* $V = .94$ tl/sec where $f = 2.00$ /sec. The regression of relative velocity versus frequency of *Nerodia* predicts velocities of .71 and .90 tl/sec, when f is 1.55 and 2.00/sec, respectively. Thus, the relation of relative velocity to frequency is quite similar between snakes and fish (particularly those using the anguilliform mode). For trout swimming at different speeds, Grillner and Kashin (1976) stated that the amplitude of lateral displacement increased with velocity up to a point and then amplitude remained fairly constant. However, in their discussion of eel swimming, it is not clear how amplitude varied with speed. In this study the amplitude of swimming snakes usually did not change with speed, or if it did change, it was more likely to decrease with increased speed. In light of the high correlation between frequency and relative velocity, perhaps only minimal changes in waveform should be expected. In addition, relative amplitude of the undulations of the snakes and maximum frequency of undulation tended to decrease with increased size of the snake. Decrease in the maximum frequency with increase in size has also been found in fish (Bainbridge, 1958), and this is presumed to be the result of greater inertia of the larger animals, as well as absolute limits on velocities of muscle contraction. For *Nerodia* and *Elaphe*, maximum absolute velocity scaled with length to the .602 and .829 power, respectively. Wu (1977) suggested that absolute velocity of maximally active streamlined fish

scaled with length to the .6 power, and this figure agrees very closely with the regression data for *Nerodia*. Hence, similar effects of size are evident when comparing swimming in snakes and fish.

Despite the similarities between anguilliform swimming of fish and the swimming of snakes, a striking contrast exists in the morphology of the locomotor apparatus. The musculature of fish is characteristically arranged in myomeres with connective tissue confined mainly to the myosepta (Bone, 1978). Muscles of snakes also are arranged segmentally, but a tremendous elongation of connective tissue (tendons) exists (Mosauer, 1935; Gasc, 1974). In some specialized snake species, tendons of the *M. semispinalis-spinalis* extend more than 30 vertebrae (Jayne, 1982). The locomotor muscles of fish may comprise 40–60% of the total body mass (Bone, 1978). Although Willemse (1979) did not state specifically the % body mass of the locomotor muscle of the European eel, his illustrations suggest a value greater than 50%. After examining a series of cross sections of the coach-whip snake (*Masticophis flagellum*), Ruben (1977) estimated that the *Mm. semispinalis-spinalis*, *longissimus dorsi* and the *iliocostalis* composed 65% of the major axial muscle mass. Because these three muscles also are believed to be among the most important for lateral undulatory locomotion (Gasc, 1974), I removed them from both sides of a freshly killed *Nerodia taxispilota* (703.4 gm, tl = 110 cm) in order to estimate their mass directly. The *Mm. semispinalis-spinalis*, *longissimus dorsi* and the *iliocostalis* weighed 25.1, 60.0 and 38.3 gm, respectively. Together, these three muscles constituted about 17.5% of the total mass of the snake, and this is substantially less than the available corresponding measurements of fish. Hence, snakes seem to possess burst locomotor capabilities that are comparable to "anguilliform" fish while possessing a relatively smaller associated muscle mass. The action of the axial muscles is still not clearly understood, but perhaps the long tendons of ophidian muscular segments convey a mechanical advantage by effectively increasing the lever arm length of the portions of the body undergoing flexion. In light of the interspecific differences in anaerobic and aerobic metabolism among snakes (Ruben, 1976), studies combining electromyography with measurements of active metabolism should shed considerable light on the different locomotor abilities among

snakes, as well as the differences and similarities between swimming in fish and snakes.

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