



## Kinematics of Terrestrial Snake Locomotion

Bruce C. Jayne

*Copeia*, Vol. 1986, No. 4. (Dec. 23, 1986), pp. 915-927.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%2819861223%293%3A1986%3A4%3C915%3AKOTSL%3E2.0.CO%3B2-Z>

*Copeia* is currently published by American Society of Ichthyologists and Herpetologists.

---

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

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/asih.html>.

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

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

- guinea pigs and rabbits. *Biochemistry* 11:2627–2633.
- SCHMIDT-NIELSEN, K. 1979. *Animal physiology: adaptation and environment*. 2nd ed. Cambridge University Press, Cambridge, United Kingdom.
- SCHNEIDER, H. 1967. Morphology and physiology of sound-producing mechanisms in teleost fishes, p. 135–158. *In: Marine bio-acoustics*. Vol. 2. W. N. Tavolga (ed.). Pergamon Press, New York, New York.
- SEIFTER, S., S. DAYTON, B. NOVIC AND E. MUNTWYLER. 1950. The estimation of glycogen with the anthrone reagent. *Arch. Biochem.* 24:191–200.
- SHENK, W. D. 1972. Terminal innervation pattern in striated muscle of the oyster toadfish, *Opsanus tau*. *Ches. Sci.* 13:139–144.
- SKOGLUND, C. R. 1961. Functional analysis of swim-bladder muscles engaged in sound production of the toadfish. *J. Biophys. Biochem. Cytol.* 10(suppl.): 187–200.
- SOMLYO, A. V., H. SHUMAN AND A. P. SOMLYO. 1977. Composition of sarcoplasmic reticulum in situ by electron probe x-ray microanalysis. *Nature* 268: 556–558.
- TAVOLGA, W. N. 1958. Underwater sounds produced by two species of toadfish *Opsanus tau* and *Opsanus beta*. *Bull. Mar. Sci.* 8:278–284.
- . 1964. Sonic characteristics and mechanisms in marine fishes, p. 195–211. *In: Marine bio-acoustics*. W. N. Tavolga (ed.). Pergamon Press, New York, New York.
- DEPARTMENT OF BIOLOGY, VIRGINIA COMMONWEALTH UNIVERSITY, RICHMOND, VIRGINIA 23284. Accepted 17 Jan. 1986.

*Copeia*, 1986(4), pp. 915–927

## Kinematics of Terrestrial Snake Locomotion

BRUCE C. JAYNE

The lateral undulatory, sidewinding and concertina modes of limbless terrestrial locomotion were analyzed from cinematographic films of five species of snakes and one amphisbaenian crawling on a variety of substrates. For single points on each animal, graphs of  $V$ , (overall velocity),  $V_x$  (longitudinal component) and  $V_y$  (lateral component) vs time were used to characterize locomotor modes and to detect their simultaneous use. Only concertina locomotion was used by the amphisbaenian *Rhineura floridana*. While performing lateral undulation, the constricting colubrid snake *Elaphe obsoleta* did not attain a maximum mean  $V_x$  as great as that of *Nerodia fasciata*, a nonconstricting colubrid. Concertina locomotion is described for the snakes *Acrochordus javanicus* and *N. fasciata*. Sidewinding is described for *N. fasciata*, *Cerberus rynchops* and *Crotalus cerastes*. *Cerberus rynchops* moving on sand combined sidewinding with lateral undulation. The relation between  $V_x$  and frequency of movement is described and compared among each of the terrestrial modes and with aquatic lateral undulation.

**L**ATERAL undulation, concertina locomotion and sidewinding are the three most common modes of snake locomotion which generate propulsive forces by lateral vertebral flexion (Gray, 1946; Gans, 1974). During lateral undulation, the body of the snake pushes against irregularities of the substrate to generate anteromedially directed reactive forces great enough to overcome sliding frictional resistance (Gans, 1974). All points along the body of the snake follow a more or less identical sinusoidal

path and all points on the body move simultaneously (Mosauer, 1932; Gray, 1946). In contrast, during concertina locomotion and sidewinding one portion of the body makes static contact while another moves relative to the substrate (Gans, 1974). Concertina locomotion is often performed in tunnels. Either concertina or sidewinding may be used on flat surfaces lacking projections needed for lateral undulation. During sidewinding, a combination of lateral and dorsal vertebral flexion lifts a portion of

the snake's body from one region of static contact to the next.

Based on extensive movie footage of snake locomotion, Gray (1946) generated models of each of these three locomotor modes. However, quantified kinematic descriptions of them are still scarce or incomplete.

Most species of snakes are capable of using all three of these modes of terrestrial locomotion and individual snakes often appear to use two modes simultaneously (Gans, 1974). For such observations, it is not always obvious whether different regions within a snake are performing discrete locomotor modes or if the entire snake is simultaneously combining characteristics of two modes. This versatility in the locomotor repertoire is a major obstacle to comparative investigations of the terrestrial locomotion of snakes because without cinematography observers are unlikely to distinguish discrete patterns from combinations of locomotor modes.

Comparisons of the maximum speeds attained by snakes have been of interest to many authors who have related speed to differences in species, substrate, snake size and temperature. Mosauer (1935a) timed six species of snakes crawling on substrates similar to those naturally encountered. Heckrote (1967) timed *Thamnophis s. sirtalis* crawling through an array of pegs in order to investigate the influence of temperature and snake size on speed. Bennet et al. (1974) also timed snakes travelling measured distances to investigate the effects of peg spacing on snake speed. None of these studies records the locomotor mode used by the snakes and the lack of cinematographic records prevents their retroactive determination. A few speeds can be determined from some publications which include photographs made from films of snake locomotion (Gray, 1946; Gans and Mendelssohn, 1972). Because of uncertainty regarding locomotor mode, the use of different techniques in determining speed, the complicating effects of snake size and peg spacing and the small number of taxa that have been studied, few valid comparisons can be made of the maximum speeds of snakes.

I investigate lateral undulatory, concertina and sidewinding locomotion with four main objectives: 1) the characteristics of each of these single modes are clarified; 2) an objective method is developed for detecting the simultaneous use of more than one of these modes; 3) vari-

ation in speed and frequency of undulation is quantified; and 4) comparisons are made for the maximum velocities of different locomotor modes and of different species.

#### MATERIALS AND METHODS

Animals were chosen based on availability and their ability to perform different locomotor modes. Like all amphisbaenians, *Rhineura floridana* is an extremely specialized burrower (Gans, 1974) and my preliminary observations of this species suggested that lateral undulation could not be elicited. Filming *Rhineura* presented an opportunity to determine the mode it used on a substrate that should allow lateral undulation. *Acrochordus javanicus* is generally considered an aquatic snake; however, I had observed the individual used in this study readily performing concertina locomotion both underwater and on land. The viperid *Crotalus cerastes* is behaviorally and to some extent morphologically specialized for sidewinding (Gans and Mendelssohn, 1972; Jayne, 1982). All other filmed species are colubrids. The homalopsine *Cerberus rynchops* is mostly aquatic with the relatively short segmental lengths of epaxial muscles characteristic of most aquatically specialized snakes (Jayne, 1982). The natricine *Nerodia fasciata pictiventris* is a semi-aquatic to terrestrial species whose epaxial musculature is characteristic of nonconstricting terrestrial colubrids, whereas *Elaphe obsoleta quadrivittata* is a terrestrial to semi-arboreal species of colubrine morphologically representative of constricting colubrids (Jayne, 1982).

Animals were filmed on substrates which most readily elicited the locomotor mode desired for study. *Nerodia* were filmed on a layer of sand about 5 cm deep covering a 46 × 110 cm area, whereas a layer of sand 1.5 cm deep over a 120 × 120 cm area was used for *Crotalus* and *Cerberus*. Straight-sided tunnels, used for eliciting concertina locomotion, had a floor of glass placed over a 1 cm grid which provided points of reference. Pieces of wood 4.4 cm high formed the sides of these 8–10 cm wide tunnels. For some sequences, strips of dense rubber matting lined the tunnel walls. For other sequences, the bare surfaces of the wood served as the sides of the tunnel. If animals attempted to crawl out of the tunnel, a sheet of glass was placed over the top. Because the colubrids of this study would not perform concertina on flat substrates, *Ac-*

TABLE 1. MOTION ANALYSIS SAMPLE GROUPED BY SUBSTRATE. Figures in parentheses after species indicate range in total length of animals in cm. lu = lateral undulatory, c = concertina and sw = sidewinding. Distances listed after substrate indicate widths of tunnels or distances between pegs used. See text for more complete explanation.

Species	No. animals	No. trials	Mode	Substrate
<i>Acrochordus javanicus</i> (74)	1	3	c	linoleum
<i>Nerodia f. pictiventris</i> (84–110)	2	13	c, c + lu	tunnel 8, 10 cm
<i>Crotalus cerastes</i> (33–36)	3	17	sw	sand
<i>Cerberus rynchops</i> (46–50)	2	10	sw, lu, lu + sw	sand
<i>Nerodia f. pictiventris</i> (30)	2	4	sw, lu + sw	sand
<i>Elaphe o. quadrivittata</i> (120–147)	3	27	lu	pegs 7.5, 12.5 cm
<i>Nerodia f. pictiventris</i> (70–91)	9	49	lu, lu + sw	pegs 7.5, 10, 12.5 cm
<i>Rhineura floridana</i> (29)	1	9	c	pegs 2.5, 5.0 cm

*rochordus* was filmed on a smooth floor primarily to document the surface mode of concertina locomotion.

Several trials were filmed using 5 mm diameter wooden pegs which were arranged on a square grid pattern. These pegs were inserted through the holes of 3 mm thick tempered pegboard into an underlying sheet of styrofoam that was 2.5 cm thick. About 3.5 cm of each 5 cm peg protruded above the surface of the pegboard. All peg distances given in Table 1 refer to the shortest straight-line distance between centers of adjacent pegs. To reduce frictional resistance, sheaths of glass tubing 5 cm long, with an inside diameter of 6 mm and an outside diameter of 8 mm, were placed over the pegs. Because *Rhineura* seemed to slip when the glass sheaths were in place, they were removed during filming. A piece of pegboard 60 × 240 cm was used during filming all snakes, whereas the *Rhineura* was filmed in a 45 × 60 cm arena. For all animals not moving on sand, supplementary notes recorded whether dorsiflexion of the vertebrae occurred.

A Bolex H16 movie camera operated at 50 f.p.s. with an exposure time of 1/300 sec was used for 16 mm black and white films. All animals (Table 1) were filmed indoors with the camera positioned directly above the test surface. Flood lights provided illumination and the air temperature at the time of filming approximated 25 C. Paint marks along the mid-dorsal line of each animal provided points of reference.

The films were projected with a Lafayette stop-action movie projector and a single paint

mark (usually from the middle one-third of the animal's body) was traced through time. The resulting record of displacement was then placed on a graphics tablet interfaced with an Apple II+ microcomputer for digitizing. Tracings were oriented so that the overall direction of travel was in the positive x direction (Fig. 1). The overall direction of travel was determined by drawing a straight line through two points that were 360° out of phase. After digitizing, changes in displacement were divided by the time between traced points to calculate velocities. Each resultant velocity,  $V_r$ , was then resolved into longitudinal ( $V_x$ ) and lateral ( $V_y$ ) components. Hence, positive and negative values of  $V_x$  indicate forward and backward movements, respectively. Positive and negative values of  $V_y$  respectively indicate movement to the right and left. All velocities were converted to total animal lengths/sec to facilitate comparisons among individuals of different size. For each film sequence,  $V_x$ ,  $V_y$ , and  $V_r$  were plotted against time.

Velocity profiles of film sequences were compared with those predicted from descriptions and models proposed by Gray (1946). Gray's models of lateral undulation and sidewinding were digitized in a fashion similar to that of the film tracings. A photocopy of Fig. 10 from Gray (1946) was placed on the digitizing tablet with the orientation of axes as indicated in Fig. 2. For both models, the point at one end of the line representing segment XV provided the record of displacement. This point was digitized for two cycles of activity, assuming the period of motion was equal to 1 sec. The length of the

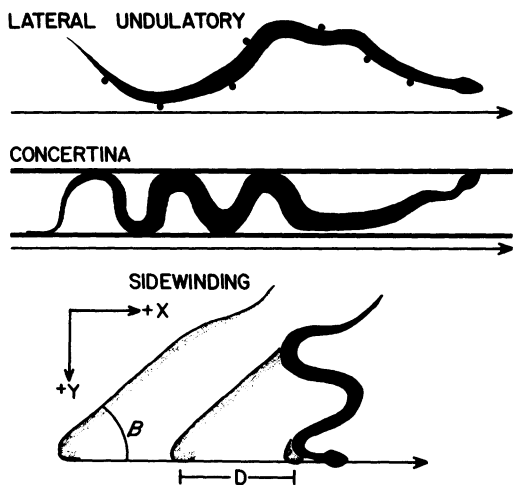


Fig. 1. Orientation of axes for digitizing displacements of snakes. The large horizontal arrows indicate the overall direction of travel for each of the locomotor modes. The thick horizontal lines surrounding the snake performing concertina represent the sides of the tunnel.

24 segment line representing a snake was used to convert velocities into lengths/sec. Operational definitions of each mode were then developed based on the observed patterns of  $V_x$ ,  $V_y$  and  $V_r$  and previous definitions (Gray, 1946; Gans, 1974). After determining the locomotor mode of each trial, mean forward velocity was calculated for one or more complete periods of motion.

Two procedures were used to estimate errors associated with the digitizing process. First, to assess error resulting from inaccurate placement of the digitizing pen on the graphics tablet, various series of eight equal displacements on graph paper were digitized. The range of displacements for different trials represented the range in values found in the tracings made from the films. This kind of error produced a coefficient of variation (CV) of less than 5% in  $V_r$ . Second, eight different tracings were made from the same film sequence, which contained a range of displacements comparable to those observed among all of the sequences. For each equivalent estimate of  $V_r$ , the CV was calculated for the eight replicates. This yielded CV values of less than 13% for  $V_r$ .

## RESULTS

Figure 2 illustrates Gray's (1946) mathematical model of lateral undulatory locomotion

which was digitized for analysis;  $V_x$  and  $V_y$  behave sinusoidally (Fig. 3). The period of the sinusoidal function of  $V_x$  is one-half the period for  $V_y$ , and the absolute value of  $V_x$  is always at a maximum when  $V_y$  equals zero. For the first period,  $V_r$  had little variation (CV = 10%). Considering the error of the digitizing procedure,  $V_r$  is effectively constant.

Figure 4 illustrates velocity profiles for lateral undulation of the snakes I filmed. A slight difference can be seen in the pattern of  $V_x$  for *Nerodia* compared to *Elaphe* and *Cerberus*. The *Nerodia* was not travelling in a regular sinusoidal path as were the *Elaphe* and the *Cerberus*. Hence,  $V_x$  shows a somewhat irregular pattern which reflects these rather irregular changes in direction. However,  $V_x$  is still always at a maximum when  $V_y$  equals zero. For this sequence of *Nerodia*,  $V_r$  also showed only slight variation (CV = 27%). For the sequences of *Elaphe* and *Cerberus* CV of  $V_r$  was 11% and 28%, respectively. For other sequences of lateral undulatory locomotion, there was not always a clear periodic pattern of variation in  $V_x$ . However, for many of the sequences with no clear pattern of  $V_x$ ,  $V_r$  was effectively constant which indicates that the mode was lateral undulation.

Gray (1946) did not provide sufficient detail in his model of concertina locomotion to allow digitizing. However, his model did suggest that a single point on the snake would move left, then right and then stop ( $V_r = 0$ ) during one cycle of activity.

Figure 5 illustrates velocity profiles for three sequences of concertina locomotion that I filmed. For all three sequences, the snakes stopped periodically causing high coefficients of variation for  $V_r$  (103–122%). In the period from 4–6 sec into the sequence of *Acrochordus* performing concertina locomotion on the floor, the snake moved to the left (L), stopped, moved to the right (R) and then stopped. For the middle diagram of *Nerodia* performing concertina locomotion in a tunnel, a similar pattern of R, stop, L, stop was used from 6–10 sec. However, during earlier points in time for these sequences of *Acrochordus* and *Nerodia*, a pattern of R, L, stop was used. The right diagram of Fig. 5, showing concertina locomotion of *Nerodia* in a tunnel, has three bimodal curves for  $V_r$  in the three periods from 2–10 sec. A close examination of the film of this sequence revealed that the first and second peaks corresponded to pushing and pulling phases, respectively. In other words, the observed body portion of the snake was first pushed forward from a more posterior

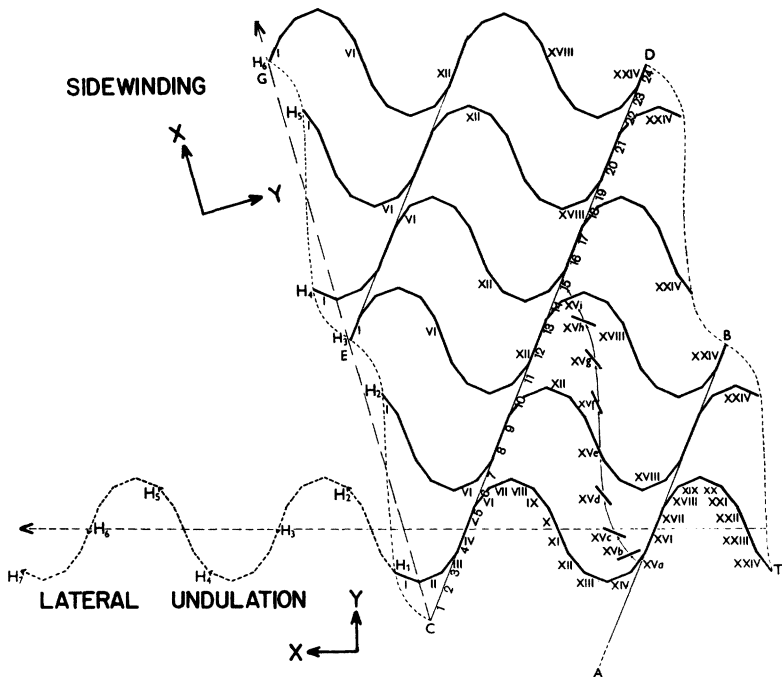


Fig. 2. Modified Fig. 10 from the models of Gray (1946) predicting the displacements of a hypothetical snake 24 segments long performing sidewinding (top) and lateral undulation (bottom). Displacements of segment XV are shown for equal intervals of time within one cycle of activity (XVa–XVi).

point of static contact and then pulled forward from a more anterior point of static contact. In most other sequences of concertina locomotion, two regions of the snake usually touched the walls of the tunnel simultaneously. Consequently, for all points between these anterior and posterior regions of lateral contact, it was not obvious at any one time if they were being pushed or pulled.

Figure 6 illustrates the velocity profiles for Gray's (1946, Fig. 10) model of sidewinding. Gray verbally indicated there was static contact during this mode. However,  $V_r$  never equalled zero in his illustration (Figs. 2, 6). Presumably, the reason for this discrepancy is that the time of static contact in the model is shorter than the time interval that was used to generate the displacements of segment number 15 (Fig. 2). Hence, despite the illustration, in Gray's model the snake should periodically stop ( $V_r = 0$ ), causing the range in  $V_r$  during one cycle to be larger than that illustrated in Fig. 6. Consequently, the CV of  $V_r$  values for Gray's model should exceed the 37% that was calculated from digitizing Fig. 2. The period of  $V_x$  equals the period of  $V_y$  and  $V_r$  with R, L, R movements occurring between times of static contact.

Figure 7 shows the velocity profiles for *Crotalus*, *Cerberus* and *Nerodia* sidewinding on sand. Because of periodic stopping in all three of these trials, the coefficients of variation of  $V_r$  were rather large (46–63%). *Cerberus* stopped at the 1 sec point of its sequence, but the time of static contact was shorter than the time interval that was used for making tracings. During one cycle of activity for each of these sequences, there are R, L, R movements between times of static contact. *Crotalus cerastes* consistently attained maximum speeds ( $V_r$ ) approximately midway between times of static contact (Fig. 7). In contrast, *Cerberus rynchops* always decelerated about midway between times of static contact followed by a second acceleration before stopping (Fig. 7). The sidewinding of *N. f. pictiventris* was the most variable of the three species. *Nerodia* occasionally decelerated midway between times of static contact, but most often the maximum speed was attained at this point (Fig. 7). *Nerodia* and *Cerberus* often remained briefly in static contact (Fig. 7) as predicted in Gray's model (Fig. 6). In contrast, *Crotalus* generally had longer times of static contact.

For at least one sequence of each locomotor mode or combination of modes performed by

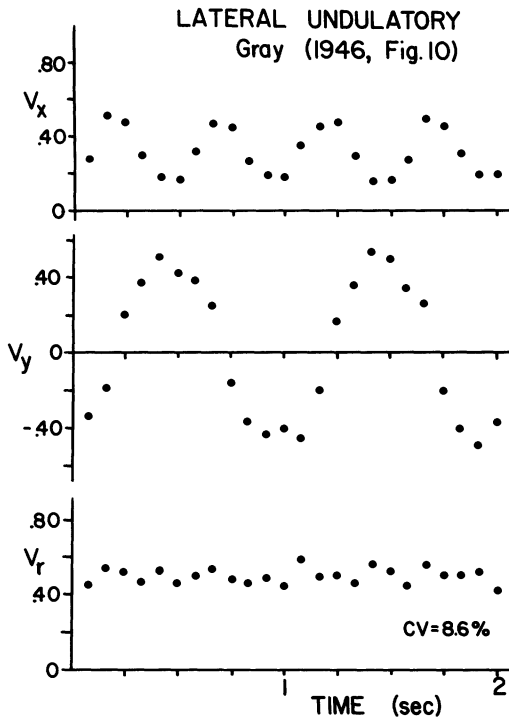


Fig. 3. Velocities vs time for Gray's model of lateral undulation. All velocities are in total lengths/sec, assuming a frequency of one cycle per sec. CV = coefficient of variation of  $V_r$ .

a species, the velocity profiles were compared for two or more different points along the body of the snake. With the exception of concertina locomotion, differences between body points

were attributable to the phase lag one would expect for a periodic pattern of movement travelling from anterior to posterior within the snake. For concertina locomotion, the patterns of left and right movement varied along the length of the snake. However, all such points along the snake still displayed patterns characteristic of concertina locomotion. No instances were observed where different regions of the snake were performing different modes. Hence, in this paper all reference to the simultaneous use of locomotor modes indicates that the entire body of the snake displayed velocity profiles with characteristics of more than one discrete locomotor mode.

In summary, the graphical approach for analyzing snake locomotion used three key steps to determine locomotor mode. First, if variation in  $V_r$  was low ( $CV < 37\%$ ) during one cycle of activity, then the mode was designated lateral undulation and  $V_y$  was used to determine the period of motion for this mode. Second, if  $V_r$  periodically equalled zero (and  $CV$  of  $V_r > 37\%$ ), then the locomotor mode was concertina or sidewinding. Third, these two modes were distinguished from each other by patterns of lateral movement. During concertina locomotion the pattern was either L, R, stop or L, stop, R, stop. For sidewinding, there was always an L, R, L pattern of movement between times of static contact. The periods of either  $V_x$ ,  $V_y$  or  $V_r$  could be used to determine one cycle of activity of sidewinding. If a sequence of locomotion did not meet these operational criteria for single locomotor modes, then I presumed that

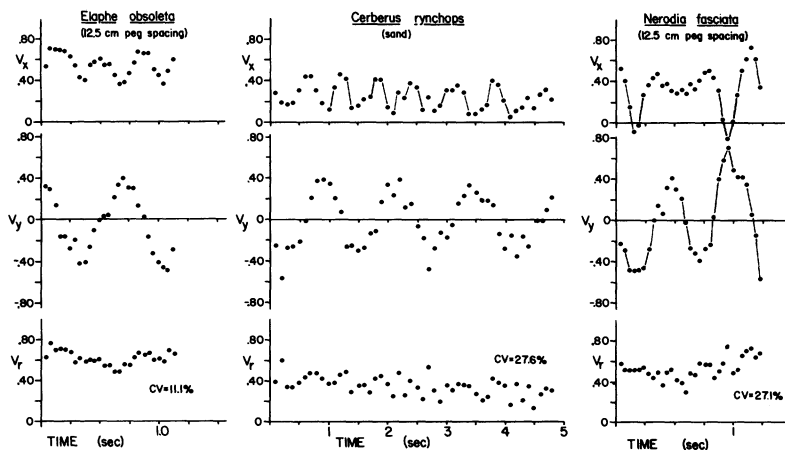


Fig. 4. Velocities vs time for lateral undulation for three species of snakes moving across various substrates. The oblique lines are to facilitate recognition of sequential points in time.

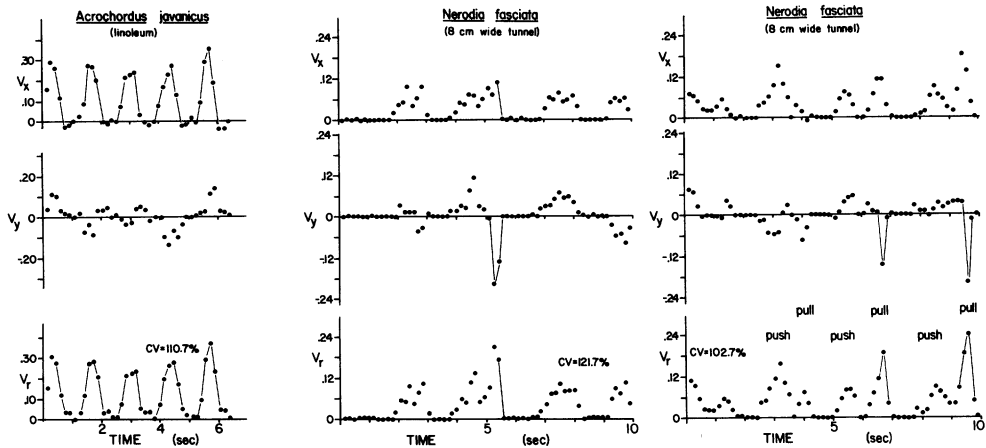


Fig. 5. Velocities vs time for concertina locomotion.

the snake was simultaneously combining two or more locomotor modes.

Figure 8 illustrates the velocities for a *Cerberus rynchops* combining locomotor modes while moving on sand. This snake made a series of parallel tracks (impressions in the sand) grossly resembling the shape and orientation of those produced during sidwinding (Fig. 1). During one cycle of activity (from 1.5–3.0 sec), the snake displayed R, L, R movement which normally indicates sidwinding. Yet, this snake never established static contact with the substrate (see  $V_r$ , Fig. 8) and hence was combining aspects of sidwinding with lateral undulation. Rather than the snake stopping as it touched the sand, the snake slid within each track (parallel to the length of the track).

The rotating glass pegs and pegboard were a very effective substrate for eliciting true lateral undulation over a wide range of speeds. Table 2 lists maxima of mean  $V_x$ , which was affected by the space between pegs. All *Nerodia* and *Elaphe* that used the 12.5 cm spacing attained their fastest speeds with this substrate. An 87 cm long *Nerodia* had the fastest mean absolute speed (164.1 cm/sec) and the second fastest mean specific speed (1.89 TL/sec). For *Elaphe*, the longest snake recorded the fastest mean absolute (110.0 cm/sec) and specific (0.75 TL/sec) forward velocities. For most slow sequences (mean  $V_x < 0.20$  TL/sec) of *Nerodia* on the glass peg apparatus,  $V_r$  was quite variable (CV > 40%) and R, L movements were made each cycle suggesting that *Nerodia* was combining lateral undulation with concertina locomotion.

In contrast to the snakes, *R. floridana* used

concertina locomotion when moving on the pegboard and wooden pegs (without the glass sheaths). Its ranges in mean  $V_x$  were 0.17–0.28 and 0.13–0.20 TL/sec for 2.5 and 5.0 cm peg spacing, respectively. Even though wooden pegs were used to minimize slippage, some backward slipping was still evident in nearly every cycle of activity and was greatest for the 5 cm peg spacing. After converting all of the negative  $V_x$ 's to zero, estimated mean  $V_x$  without slip-

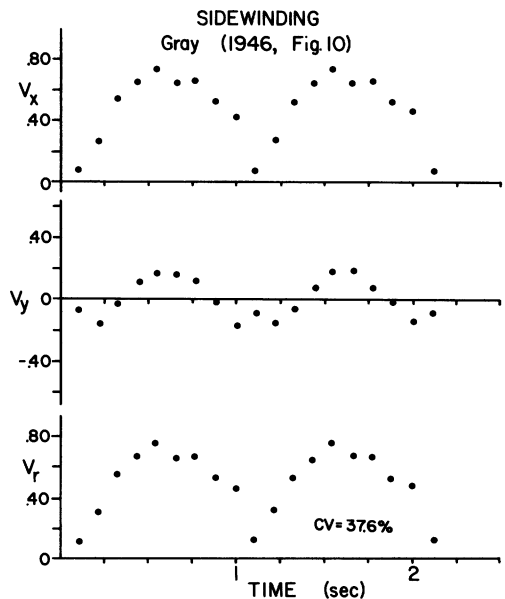


Fig. 6. Velocities vs time for Gray's model of sidwinding. Symbols are as in Fig. 3.



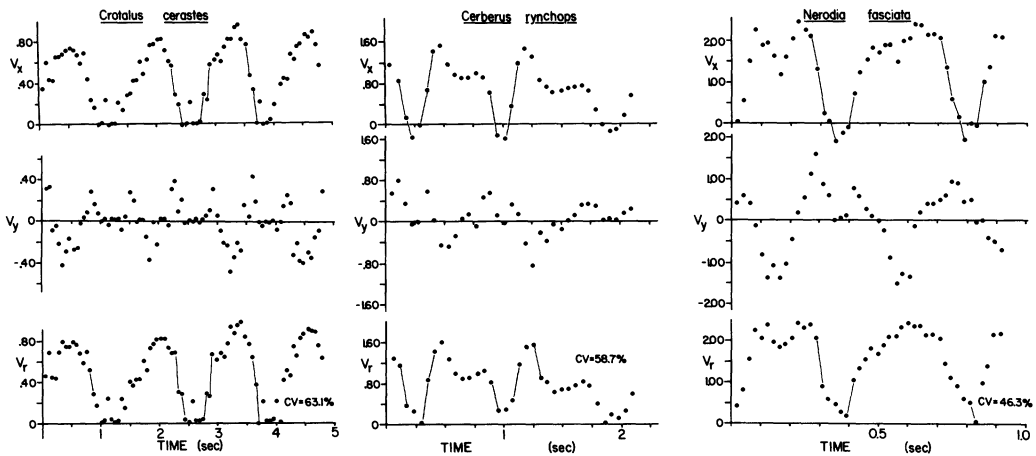


Fig. 7. Velocities vs time for snakes sidewinding on sand.

page ranged from 0.18–0.29 and 0.19–0.31 TL/sec for 2.5 and 5 cm peg spacing, respectively.

*A. javanicus* used concertina locomotion on a linoleum floor and the mean  $V_x$  for this snake ranged from 0.04–0.11 TL/sec. During the first (and fastest) filmed sequence of *Acrochordus*, practically no backward slippage was observed; however, as the ventral surface of the snake gathered dust, backward slipping became apparent.

When *Nerodia* were placed in tunnels with rubber sides, concertina locomotion was readily performed and backward slipping was rare. *Nerodia* 84–110 cm long attained mean  $V_x$  from 0.03–0.05 TL/sec in the 8 cm wide tunnel. For a large individual (110 cm), the tunnel with a 10 cm width and wooden sides was not very satisfactory for eliciting pure concertina locomotion. In this apparatus, mean  $V_x$  varied from 0.02–0.04 TL/sec and the snake usually did not stop, but continued to glide forward even while contacting the sides of the tunnel. The large coefficients of variation of  $V_r$  for these trials suggest use of some combination of concertina and lateral undulation.

When *Crotalus cerastes*, *Cerberus rynchops* and small *N. f. pictiventris* (Table 3) were placed on fine sand, sidewinding locomotion often resulted. The ranges in mean  $V_x$  for the sidewinding of these three species were 0.26–1.70, 0.39–1.20 and 0.42–1.36 TL/sec, respectively. Table 3 summarizes the maximum mean  $V_x$  and size of each snake that performed sidewinding on sand. Fig. 1 illustrates the determination of the angle between the track and the direction of travel ( $\beta$ ) and the distance between tracks

along the direction of travel (D), using the notation of Gans (1974). For *Crotalus*, *Cerberus* and *Nerodia*, the mean  $\beta$  (range) and mean D (range) were 26.5° (16–42), 0.60 TL (.56–.67); 38.2° (28–47), 0.57 TL (.50–.66); and 48.3° (34–55), 0.50 TL (.46–.60), respectively. Using a two-tailed  $t$  test, all mean  $\beta$ 's were significantly different from each other ( $P$  always  $< .01$ ). When the mean  $\beta$ 's (21.8° and 30.0°) of the two smallest *Crotalus cerastes* were compared over a comparable range of mean  $V_x$  (0.29–0.76 and 0.35–0.75 TL/sec), a two-tailed  $t$  test showed they were significantly different ( $t = 5.01$ ,  $P < .01$ ). Mean D of *Nerodia* was significantly smaller than that of either *Cerberus* ( $t = 2.67$ ,  $P < .05$ ) or *Crotalus* ( $t = 2.11$ ,  $P < .05$ ).

*C. cerastes* always performed sidewinding on a smooth, unobstructed sand surface. However, occasionally when individuals encountered the sides of the sandbox, rectilinear locomotion resulted. As the surface of the sand became more convoluted, all three species were likely to shift to lateral undulation. This was extremely rare for *Crotalus* and no films of this presumed lateral undulation were obtained. Analysis of velocity plots (Fig. 8) revealed that *Cerberus* and *Nerodia* readily combined sidewinding and lateral undulation while moving on the sand. The range in mean  $V_x$  of *Cerberus* performing lateral undulation on sand (0.15–0.29 TL/sec) did not overlap with the range in mean  $V_x$  for sidewinding, whereas the range in  $V_x$  for combined lateral undulation and sidewinding on sand (0.23–0.67 TL/sec) overlapped with the ranges in  $V_x$  both for sidewinding and lateral undulation on sand.

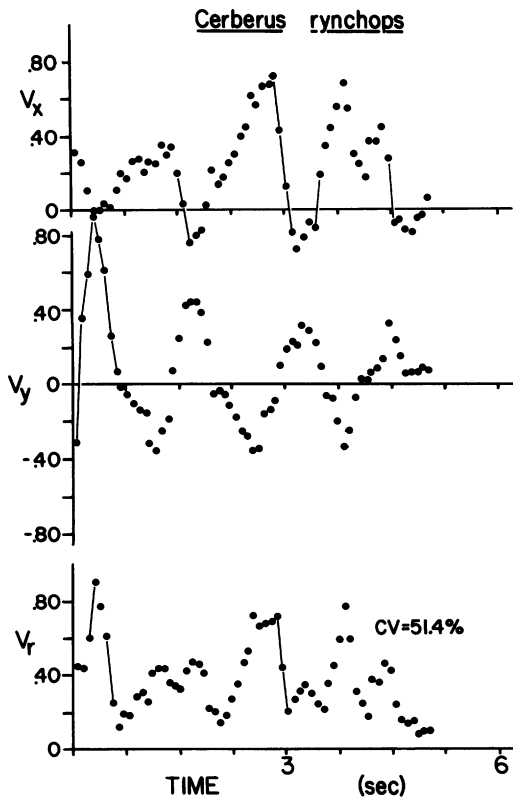


Fig. 8. Velocities vs time for *Cerberus rynchops* combining lateral undulation and sidewinding while moving on sand.

Table 4 summarizes the regressions of  $V_x$  as a function of  $f$  for snakes performing lateral undulation and sidewinding. To compare the predicted values ( $V_x$ ), pairs of regressions were superimposed and regions with non-overlapping 95% confidence limits were considered significantly different. Snakes moved faster for a given frequency as the distance between pegs increased. For *Nerodia* with the 12.5 cm spacing, a greater  $V_x$  is predicted than with either the 10.0 cm (for  $f > 1.4$  Hz) or the 7.5 cm spacing (for  $f > 1.2$  Hz). Similarly, for *Elaphe* with the 12.5 cm peg spacing, a greater  $V_x$  is predicted compared to the 7.5 cm spacing (for  $f > 1.3$  Hz). The predicted  $V_x$ 's for *Nerodia* were greater than those of *Elaphe* for both the 7.5 and 12.5 cm peg spacings (for  $f > 1.3$  Hz). There were no significant differences in predicted  $V_x$  among any of the three species when sidewinding was used. For *Nerodia*, there were no significant differences predicted for sidewinding vs 12.5 cm peg spacing vs swimming (Jayne,

TABLE 2. MAXIMUM MEAN FORWARD VELOCITIES FOR SNAKES PERFORMING LATERAL UNDULATION ON PEGBOARD WITH ROTATING GLASS PEGS. \* indicates gravid snake. # indicates snake with incomplete tail.

Species	Total length (cm)	Mass (gm)	Maximum mean $V_x$ (TL/sec)		
			Peg spacing		
			7.5 cm	10.0 cm	12.5 cm
<i>Nerodia fasciata</i>	91	218	—	0.47	—
<i>pictiventris</i>	88#	643*	—	0.53	1.19
	87	183	—	0.46	1.89
	84	218	—	0.22	—
	81	278*	—	—	1.03
	80#	238	0.36	0.97	1.89
	73#	235*	0.97	1.51	—
	70#	154	0.51	0.22	0.76
<i>Elaphe obsoleta</i>	147	454	0.62	—	0.75
<i>quadrivittata</i>	123#	627	0.32	—	0.61
	120#	517	0.39	—	0.56

1985). For the swimming of *E. guttata* (Jayne, 1985) compared to the closely related *E. obsoleta* using the 12.5 cm peg spacing, a greater  $V_x$  was predicted over all common values of  $f$ . These differences in the relation of  $V_x$  to  $f$  imply differences in waveform. For example, as interpeg distance increases for both *Nerodia* and *Elaphe*, the waves of undulation appear to become larger (in wavelength and amplitude) and approach the size of undulations used during swimming.

Because of the variable patterns of lateral movement during concertina locomotion, determining  $f$  is problematic for this mode. In some sequences of *Rhineura* and *Acrochordus*, slippage created especially complicated patterns of  $V_y$  compared to  $V_x$  (and  $V_r$ ). Consequently, the values of  $f$  were calculated as  $1/(\text{period of})$

TABLE 3. MAXIMUM MEAN  $V_x$  FOR SNAKES SIDEWINDING ON SAND.

Species	TL (cm)	Mass (gm)	Max mean $V_x$ (TL/sec)
<i>Crotalus cerastes</i>	30.1	27.0	0.75
	33.5	27.0	1.70
	35.7	41.0	0.76
<i>Cerberus rynchops</i>	46.0	28.0	0.73
	49.5	24.0	1.20
<i>Nerodia f. pictiventris</i>	30.0	9.9	1.36

TABLE 4. LEAST SQUARES REGRESSIONS FOR  $V_x = mf + b$ .  $V_x$  = mean forward velocity in TL/sec,  $f$  = frequency of undulation in Hertz,  $m$  = slope and  $b$  = Y-intercept. lu = lateral undulation, sw = sidewinding,  $r^2$  = coefficient of determination and  $N$  = sample size used for regression. \* = from Jayne (1985).

Species (range length)	Mode	Substrate	m	b	$r^2$	N
<i>N. f. pictiventris</i> (70–80 cm)	lu	7.5 cm pegs	.331	.022	.78	14
(70–88 cm)	lu	10.0 cm pegs	.369	-.054	.70	31
(70–88 cm)	lu	12.5 cm pegs	.721	-.282	.55	42
(71–99 cm)*	lu	water	.450	.056	.77	15
(30 cm)	sw	sand	.497	0	.92	8
(22–39 cm)*	lu	water	.459	-.087	.85	21
<i>E. o. quadrivittata</i> (120–147 cm)	lu	7.5 cm pegs	.117	.173	.24	19
(120–147 cm)	lu	12.5 cm pegs	.261	.072	.72	19
<i>E. g. guttata</i> (100–142 cm)*	lu	water	.329	.001	.92	17
<i>Cerberus rynchops</i> (46–50 cm)	sw	sand	.650	-.129	.98	8
<i>Crotalus cerastes</i> (33–36 cm)	sw	sand	.529	.053	.94	34

$V_x$ ). For *Rhineura*,  $f$  ranged from 1.1–3.1 Hz for 2.5 cm peg spacing and from 1.5–2.2 Hz for 5.0 cm peg spacing. For *Acrochordus*,  $f$  ranged from 0.31–0.48 Hz. For *Nerodia* performing concertina in an 8 cm wide tunnel,  $f$  ranged from 0.24–0.55 Hz.

Interestingly, at a given  $f$  the speeds attained by *Nerodia* using concertina locomotion in a 10 cm wide tunnel (e.g.,  $V_x = 0.05$  TL/sec where  $f = .31$  Hz) resemble  $V_x (=0.06$  TL/sec) predicted from the regression for lateral undulation with the 10 cm peg spacing. However, the snakes I filmed did not usually perform lateral undulation using frequencies of movement as low as those of concertina locomotion. *Rhineura* used much higher frequencies than snakes while performing concertina locomotion and the  $V_x$  attained for such  $f$  was generally much slower than the  $V_x$  that would be predicted for the lateral undulation of snakes (Table 4).

#### DISCUSSION

The tremendous difference between maximum  $V_x$  attained by *Nerodia* performing concertina (0.05 TL/sec) and terrestrial lateral undulation (1.88 TL/sec) illustrates the need to document the locomotor mode before comparing maximum speeds. Perhaps different locomotor modes partially account for the different maximum speeds reported by Mosauer (1935a) for *Lichanura* (10 cm/sec) compared to *Masticophis* (166 cm/sec). The relationships among substrate, locomotor mode and maximum speed are likely to further complicate comparisons of

maximum speeds among species. Gans and Mendelssohn (1972) described a hierarchy of locomotor modes used by snakes in response to the substrate. For lizards with reduced limbs, Gans (1985) suggested that the choice of locomotor mode depends on velocity. Similarly, for a given substrate, snakes may use a hierarchy of locomotor modes in attaining increased velocity. For example, as *Cerberus* increased its speed while moving on sand, pure lateral undulation, lateral undulation combined with sidewinding and then pure sidewinding were used. Interspecific comparisons of maximum speeds (attained with a given mode on comparable substrates) should help to determine whether the relationships among substrate, locomotor mode and speed differ among species.

The maximum mean  $V_x$  of *N. f. pictiventris* and *E. o. quadrivittata* performing terrestrial lateral undulation can be compared to the maximum mean  $V_x$  during aquatic lateral undulation of *N. f. pictiventris* and *E. g. guttata* (Jayne, 1985). Both studies used similar temperatures and recorded maximum  $V_x$  over similar time intervals. Although sidewinding is often presumed to be a rapid locomotor mode, the maximum mean  $V_x$  of a 30 cm sidewinding *Nerodia* was only 1.34 TL/sec compared to 2.54 TL/sec attained by a 28 cm swimming *Nerodia*. While performing terrestrial lateral undulation, maximum mean  $V_x$  was 1.89 TL/sec for an 80 cm *Nerodia* and two others exceeded 1.50 TL/sec. A slightly slower maximum  $V_x$  of 1.47 TL/sec was recorded for a 77 cm swimming *Nerodia* (Jayne, 1985). *E. obsoleta* and *E. guttata* are very similar

in terms of their behavior, weight-length proportions, numbers of vertebrae and segmental lengths of major epaxial muscles. In this study, a 147 cm *E. o. quadrivittata* attained a maximum mean  $V_x$  of 0.75 TL/sec. Maximum mean  $V_x$  of 1.32 TL/sec was attained by a swimming *E. g. guttata* (142 cm, 803 gm) and adults of this species commonly attained swimming speeds greater than 0.75 TL/sec (Jayne, 1985).

The relative forward velocity of the terrestrial lateral undulation of *Nerodia* was consistently faster than that of *Elaphe* (Table 2). Scaling considerations, peg spacing and behavioral differences are three factors that could confound this result. An increase in mass should be the most important factor affecting scaling, but the heaviest snake was a gravid *Nerodia* (643 gm) which still managed to move 0.40 TL/sec faster than the fastest *Elaphe*. Bennet et al. (1974) and this study found that peg spacing affects maximum velocity of snakes. However, when the space between pegs was comparable (10% of total animal length), a 73 cm *Nerodia* still attained a maximum mean  $V_x$  of 0.97 TL/sec compared to values of only 0.56 and 0.61 TL/sec for the two shortest *Elaphe*. The number of attempts to bite handlers suggests that *Elaphe* were not more docile than *Nerodia*; therefore, habituation to the stimulus for eliciting fast locomotion does not appear likely. Thus, morphological or physiological differences between *Elaphe* and *Nerodia* probably cause the different maximum forward velocities.

After comparing *Lichanura roseofuscus* with *Masticophis flagellum*, Ruben (1977) suggested that musculo-skeletal adaptations for locomotor speed and constriction may be mutually exclusive. *Nerodia* and *Elaphe* share many qualitative similarities of musculature common to advanced snakes (Mosauer, 1935b; Gasc, 1974), but they have different numbers of vertebrae and segmental lengths of major epaxial muscles that are characteristic of non-constricting and constricting colubroid snakes, respectively (Jayne, 1982). During terrestrial lateral undulation, the maximum speeds of *Nerodia* and *Elaphe* support Ruben's (1977) suggestion. However, maximum relative  $V_x$ 's for the swimming of *Nerodia* and *Elaphe* were not significantly different (Jayne, 1985). This differential performance emphasizes the need to distinguish terrestrial from aquatic lateral undulation.

An enhanced ability to determine locomotor mode may have bearing on some of the more

general conclusions about snake locomotion. For example, Gray and Lissmann (1950) elegantly determined the ratio of lateral to longitudinal forces exerted by a snake crawling past different numbers of pegs and this ratio increased with the number of pivotal points. They illustrated postures of snakes crawling past one and two pegs and these appear to differ from those observed for *Nerodia* performing pure lateral undulation in this study (Fig. 1). Hence, comparing the ratios of force components might be complicated by changes in locomotor mode. Ruben (1977) used the number of lateral pivotal points to compare locomotor performance of snakes, but his comparison was incomplete because of the lack of additional kinematic data.

Data from previous studies of the sidewinding of *Crotalus cerastes* agree closely with this study. Mosauer (1935a) reported a maximum velocity of 91 cm/sec and a prowling velocity of 14 cm/sec for a *C. cerastes* of unknown size. Since a 55 cm long *C. cerastes* is considered a large individual (Klauber, 1972), this species can likely attain a maximum  $V_x$  greater than 2.0 TL/sec, compared to the 1.7 TL/sec I found. Gans and Mendelssohn (1972) reported a speed on sand of 45 cm/sec for a 38 cm *C. cerastes* at 39.5 C. With regard to the angle formed between the track and the overall direction of travel, Brain (1960) found  $\beta$  ranging from 17–40°, with a mean of 26° for a 30 cm *C. cerastes*. The minimum length of snake that must be lifted between tracks is equal to the perpendicular distance between tracks ( $= D \cdot \sin \beta$ ). Based on the mean  $\beta$  and  $D$  for *Crotalus*, *Cerberus* and *Nerodia*, these estimated lengths are 26.9, 35.1 and 37.3 %TL, respectively. An increase in this distance suggests less of the snake's body is available to establish static contact with the substrate.

The three species of snakes that performed sidewinding in this study do not appear to be equally proficient sidewinders. *Nerodia* was the least proficient. The combination of lateral undulation and sidewinding was easily elicited from small *Nerodia* on sand, but they usually had to be frightened in order to perform pure sidewinding. In contrast, *Cerberus* readily performed pure sidewinding and pure lateral undulation as well as simultaneously combining these two modes. During field work, I frequently observed sidewinding by undisturbed *Cerberus* on tidal mud flats in Malaysia. *Crotalus cerastes*, a desert viperid, is an extremely proficient sidewinder (Gans and Mendelssohn, 1972). My observations suggest that *Cerberus* belongs to

another distinct group of proficient sidewinders and Wall's (1919) observation of its sidewinding is supported.

The relationship of sidewinding to other modes of locomotion is not well understood. Based on observations of *Tropidonotus natrix*, Gray (1946) emphasized the similarity of sidewinding to lateral undulation. He suggested that superimposing a wave of vertical vertebral flexion on a wave of lateral flexion, characteristic of lateral undulation, would generate a pattern of external resistive forces that predicts sidewinding motion. Using similar reasoning, Brain (1960) also considered sidewinding to be derived from lateral undulation.

Gans (1962, 1974) suggested that sidewinding more closely resembles concertina locomotion because of the use of static contact. Gans (1974) stated that at a given instant during either of these modes, there are generally two regions of the snake's body that are in static contact with the substrate. Hence, the other portions of the snake are being accelerated forward either by being pushed away from a more posterior point of static contact or by being pulled toward a more anterior point of static contact.

In my study, the pattern of sidewinding shown by *Nerodia* (Fig. 7), the least proficient sidewinder, is very similar to that predicted by Gray (1946) (Fig. 6). The observed transition from lateral undulation to sidewinding for *Cerberus* and *Nerodia* moving on sand supports evolutionary speculation of Gray (1946) and Brain (1960). If the muscular mechanisms of sidewinding and lateral undulation are fundamentally similar, then one might expect to see the combined use of lateral undulation that was commonly displayed by these species. Gray (1946) did not film any of the specialized sidewinders studied by Gans and Mendelssohn (1972). In fact the sidewinding of *Crotalus cerastes* (Fig. 7) differs slightly from the model of Gray (Fig. 6) by having a longer time of static contact between the snake and the substrate. The sidewinding of *Cerberus* (Fig. 7) was different from *C. cerastes* and the model of Gray because of the second acceleration within each cycle of activity. This second acceleration strongly resembles the pushing and pulling phases that were evident in three cycles of activity of a sequence of concertina locomotion of *Nerodia* (Fig. 5). Hence, for each cycle, a point on *Cerberus* may be pushed from a posterior track and then pulled to the next successive region of static contact (track). Therefore, the

sidewinding of *Cerberus* supports the evolutionary suggestion of Gans. Furthermore, if the pulling phase immediately followed or overlapped with the pushing phase, the patterns of sidewinding shown by *Crotalus* and *Nerodia* could be predicted. Fig. 7 emphasizes that all sidewinding is not alike and the study of different taxa may have complicated the resolution of the relationships of major locomotor modes. Electromyographic studies of the different modes of snake locomotion should help resolve this question.

#### ACKNOWLEDGMENTS

This work was completed as part of a PhD dissertation submitted to the Department of Zoology at Michigan State University, East Lansing, Michigan. Financial support was provided by National Science Foundation Dissertation Improvement Grant No. BSR-8401874 and grants from the Michigan State University and national chapters of the Sigma Xi, the Research Society, as well as from NIH grant NS16270 to J. Edwards. J. Edwards, my advisor, provided much encouragement and support throughout my dissertation work and offered many insightful criticisms of an earlier draft of this manuscript. P. Ocello cheerfully assisted with digitizing data, animal keeping chores and many filming sessions. C. Gans generously provided prepublication copies of manuscripts on limbless locomotion. D. Straney provided additional comments on an earlier draft of this manuscript.

#### LITERATURE CITED

- BENNET, S., T. MCCONNELL AND S. L. TRUBATCH. 1974. Quantitative analysis of the speed of snakes as a function of peg spacing. *J. Exp. Biol.* 60:161-165.
- BRAIN, C. K. 1960. Observations on the locomotion of the Southwest African adder, *Bitis peringueyi* (Boulenger), with speculations on the origin of sidewinding. *Ann. Transvaal Mus.* 24:19-24.
- GANS, C. 1962. Terrestrial locomotion without limbs. *Amer. Zool.* 2:167-182.
- . 1974. Biomechanics an approach to vertebrate biology. University of Michigan Press, Ann Arbor, Michigan.
- . 1985. Limbless locomotion—a current overview, pp. 13-22. *In: Proceedings international symposium on vertebrate morphology. Fortschritte der Zoologie, Gustav Fischer Verlag, Stuttgart and New York.*
- , AND H. MENDELSSOHN. 1972. Sidewinding

- and jumping progression of vipers, p. 17–38. In: *Toxins of animal and plant origin*, Vol. 1. A. de Vries and E. Kochva (eds.). Gordon and Breach, London, England.
- GASC, J. P. 1974. L'interpretation fonctionnelle de l'appareil musculosquelettique de l'axe vertebraal chez serpents (Reptilia). *Mem. Mus. Natl. Hist. Nat. ser. a, Zool.* 83.
- GRAY, J. 1946. The mechanism of locomotion in snakes. *J. Exp. Biol.* 23:101–120.
- , AND H. W. LISSMANN. 1950. The kinetics of locomotion of the grass snake. *Ibid.* 26:354–367.
- HECKROTE, C. 1967. Relations of body temperature, size, and crawling speed of the common garter snake, *Thamnophis s. sirtalis*. *Copeia* 1965:759–763.
- JAYNE, B. C. 1982. Comparative morphology of the semispinalis-spinalis muscle of snakes and correlations with locomotion and constriction. *J. Morph.* 172:83–96.
- . 1985. Swimming in constricting (*Elaphe g. guttata*) and nonconstricting (*Nerodia fasciata pictiventris*) colubrid snakes. *Copeia* 1985:195–208.
- KLAUBER, L. M. 1972. *Rattlesnakes*. University of California Press, Berkeley, California.
- MOSAUEER, W. 1932. On the locomotion of snakes. *Science* 76:583–585.
- . 1935a. How fast can snakes travel? *Copeia* 1935:6–9.
- . 1935b. The myology of the trunk region of snakes and its significance for ophidian taxonomy and phylogeny. *Publ. Univ. Cal. Los Angeles Biol. Sci.* 1:81–121.
- RUBEN, J. A. 1977. Morphological correlates of predatory modes in the coachwhip (*Masticophis flagellum*) and rosy boa (*Lichanura roseofusca*). *Herpetologica* 33:1–6.
- WALL, F. 1919. A popular treatise on the common Indian snakes. *J. Bombay Natl. Hist. Soc.* 26:88–93.
- DEVELOPMENTAL AND CELL BIOLOGY, UNIVERSITY OF CALIFORNIA AT IRVINE, IRVINE, CALIFORNIA 92717. Accepted 22 Nov. 1985.

*Copeia*, 1986(4), pp. 927–936

## Vocal Sac Variation among Frogs of the Genus *Rana* from Western North America

MARC P. HAYES AND DANA M. KREMPFELS

Vocal sac condition of 460 frogs was examined by dissection for five western North American *Rana* (*Rana boylei* group sensu Case, 1978): *R. aurora* (N = 280), *R. boylei* (N = 24), *R. cascadae* (N = 113), *R. muscosa* (N = 22) and *R. pretiosa* (N = 21). *R. boylei* consistently exhibits small, paired subgular sacs, whereas *R. muscosa* and *R. pretiosa* lack vocal sacs. *R. cascadae* typically lacks vocal sacs, whereas *R. aurora* may have no vocal sacs, a single asymmetric vocal sac, paired sac rudiments or paired vocal sacs. *R. aurora* exhibits a striking step-cline in vocal sac condition: northern populations lack vocal sacs, southern populations have small, paired subgular sacs and frogs with intermediate vocal sac conditions occur mostly in the 480 km between these northern and southern population assemblages. The two most common vocal sac variants within *R. aurora* (an absence of vocal sacs and paired subgular sacs) are congruent with available data that suggest trenchant morphological and behavioral differences between the two previously defined subspecies, *R. a. aurora* and *R. a. draytonii*. *R. aurora*, as currently defined, may actually be two species in secondary contact. Reduced vocal sac apparatus among members of the *R. boylei* group is correlated with their weak vocalizations.

VOCAL sac characteristics are important in anuran systematics because they can exhibit significant variation between related species (Boulenger, 1886; Tyler, 1971), but rarely vary intraspecifically (Liu, 1935). Although descrip-

tions exist (Table 1), vocal sacs among *Rana* species endemic to western North America (*R. boylei* group sensu Case, 1978; *R. aurora*, *R. boylei*, *R. cascadae*, *R. muscosa* and *R. pretiosa*) have not been studied comprehensively. Boulenger