

QUANTITATIVE ANALYSIS OF THE SPEED OF SNAKES AS A FUNCTION OF PEG SPACING

By S. BENNET, T. McCONNELL AND S. L. TRUBATCH

*Department of Physics-Astronomy, California State University,
Long Beach, California 90840*

(Received 28 June 1973)

INTRODUCTION

Since biblical times the slithering motion (lateral undulation) of snakes has aroused man's curiosity. Several investigators (Mosauer, 1932; Gray, 1950; Gans, 1962) have shown that serpentine motion is produced by lateral reaction forces exerted on the snake as it pushes against local irregularities in the terrain along its path. Experiments with snakes in artificial environments (Gray, 1950) in which the bumps and depressions of the terrain are replaced by pegs, show that the net longitudinal force pushing the snake forward remains fairly constant as the number of pegs simultaneously pushed against increases, while the ratio of body length to peg spacing (henceforth referred to simply as the ratio) remains fixed. On the other hand a simultaneous increase of the ratio coupled with an increase in the number of simultaneously contacted pegs leads to an increase in longitudinal force. However, such experiments have not been performed over paths of continuous contact and thus give no information about speed as a function of peg spacing. Furthermore, earlier experiments were performed with only linear arrays of pegs and thus give no information about the snake's ability to maintain a desired speed as the relative orientations of peg contacts change.

It has been reported (Gans, 1970) that a snake requires at least three simultaneous contact points during times of continuous forward progress; and that these points should lie in particular (unspecified) spatial patterns. This implies that speed should be a sensitive function of peg spacing as the ratio drops below three - the shortest length which permits continuous contact with three pegs. Further reductions in the ratio should lead to dramatic changes in speed as the snake will be forced to supplement lateral undulation with either sidewinding or rectilinear motion. Also, as the peg spacing increases the number of suitably placed contact sites decreases, again diminishing speed.

In the experiments reported below the relation between speed and the ratio of body length to peg spacing was measured for three species of snakes. It is the first quantitative data of its kind published.

MATERIALS AND METHODS

The base of the race course was a 2.2 × 4.4 metre sheet of plywood. It was sanded smooth and painted with two coats of high gloss enamel to minimize the friction between it and the snake. The smoothness of the board was verified operationally by

Table 1. *Snakes used and their dimensions*

Species	Length (cm)	Width (cm)
<i>Elaphe subocularis</i> (rat snake)	46.1	1.0
<i>Arizona elegans</i> (glossy snake)	63.5	1.3
<i>Arizona elegans</i> (glossy snake)	106.0	1.9
<i>Crotalus scutulatus</i> (rattlesnake)	50.8	3.2

the snakes themselves; they could travel across it only by side-winding. By smoothing the board to this extent rectilinear motion was eliminated as a mode of travel.

Contact points for undulatory motion were provided by studding the board with pegs made from wooden dowelling 1.6 cm in diameter. Because inter-peg spacing is an essential parameter in this experiment, the race course was laid out in a pattern which establishes this distance as unambiguously as possible. Although preliminary experiments were performed with square arrays of pegs, as have been used in all previous experiments of this kind, this pattern was eventually abandoned because the distances between any peg and its surrounding immediate neighbours are not all equal. Clearly, pegs which are at diagonally opposite corners of a square are farther apart than those at adjacent corners.

The spacing problem was finally resolved by arranging the pegs in a hexagonal pattern on the final race course. Pegs were placed at the vertices and centres of all the hexagons. This is the only arrangement for which all the nearest-neighbour spacings are equal. However, this pattern still suffers from the inherent ambiguity of any peg arrangement in that two non-nearest-neighbour pegs can be connected by a straight line which is longer than the fundamental peg spacing.

The original 366 pegs were spaced apart by a distance of 8.8 cm from centre to centre. The larger peg spacing was 19.7 cm from centre to centre, and was obtained by selectively removing pegs so as to maintain the hexagonal pattern. These were the only two peg spacings used.

Several snakes were tested, and of the candidates four were chosen for their comparative level of cooperation and ability to maintain a speed that appeared relatively constant. Because snakes eat but once a week it is difficult to make them perform by the usual method of offering a food reward. Instead, they were chased across the board by tapping randomly on their posterior ends. Only snakes which consistently responded to this stimulus were used.

The four snakes used and their dimensions are listed in Table 1. The poisonous snakes were not defanged.

The average speed for any run was determined by measuring the distance between the initial and final positions of the head and by timing the trip with a hand-held stop-watch. All runs were made at an ambient temperature of 21 °C, and were performed at the same time of day – mid-morning.

RESULTS

The speeds attained by the various snakes as they traversed the race course are summarized in Table 2. Each entry is the average of six runs.

For the small peg-spacing trials all subjects travelled an average distance of one

Table 2. Snake speeds for different peg spacings

Species	Small spacing Speed (cm/sec)	Large spacing Speed (cm/sec)
<i>E. subocularis</i>	23.2 ± 0.8	9.4 ± 0.9
	18.3 ± 0.8	10.7 ± 0.8
	17.2 ± 0.8	—
<i>A. elegans</i> (106 cm)	35.2 ± 0.8	23.1 ± 0.8
<i>C. scutulatus</i>	13.4 ± 0.5	17.2 ± 0.5
	21.6 ± 0.5	—
	19.3 ± 0.3	18.1 ± 0.9
<i>A. elegans</i> (63.5 cm)	30.7 ± 0.8	17.5 ± 0.8
	35.0 ± 1.5	17.0 ± 0.5

metre per run, while the average distance travelled per run for the larger peg spacing was only two-thirds of a metre. This difference in distance travelled may be related to the energy required to maintain sufficient body rigidity for movement. Less energy is required to maintain rigidity over several closely spaced contact points than over fewer contact points more distantly spaced (Gans, 1970). These short running distances, which are much smaller than the dimensions of the board, reflect the reluctance of the snakes to perform even when chased.

Of the four snakes used the rat snake and the smaller of the two glossy snakes showed the greatest decrease in speed. In both cases their speeds were approximately halved. During runs on the larger peg-spacing course these snakes had difficulty in maintaining continuous contact with the pegs and would thrash about until their body loops could make another contact point.

The rattlesnake, however, showed no decrease in speed with increase in peg spacing although it is of intermediate length with respect to the two snakes discussed above. However, it did side-wind somewhat while traversing the larger peg-spacing course. It did not thrash about wildly as the thinner snakes did.

The longer of the two glossy snakes also showed a significant reduction of speed on the larger peg-spacing course, although it is long enough to maintain continuous contact with several pegs during both sets of runs. However, its speed was reduced by only one-third on the large peg-spacing course as compared to that obtained on the course with small peg spacing.

The two glossy snakes traversed the small peg-spacing course at approximately the same speed. On this course both could maintain continuous contact with several pegs. The shorter of the two glossy snakes and the rattlesnake also attained approximately the same speed on the larger peg-spacing course. However, this equality is believed to be accidental in view of the thrashing of the glossy snake and the side-winding of the rattlesnake while running this course.

DISCUSSION

The dependence of speed on the ratio of body length to peg spacing is clearly illustrated by the data in Table 3. As expected, some snakes travel at a reduced speed when the ratio decreases. Although a numerical correlation of the speed and the ratio is

Table 3. *Speeds of the various snakes compared with their ratios of body length to peg spacing*

Species	$\frac{\text{Body length}}{\text{Peg spacing}}$	Average speed (cm/sec)
<i>E. subocularis</i>	5.2	19.5
	2.3	10.5
<i>C. scutulatus</i>	5.8	18.1
	2.6	17.7
<i>A. elegans</i> (both together)	12.1	35.2
	7.2	32.8
	5.4	23.1
	3.2	17.3

Table 4. *Longitudinal forces developed by Tropidonotus natrix on linear peg arrays with various numbers of pegs and various length-to-spacing ratios. (After Gray)*

$\frac{\text{Body length}}{\text{Peg spacing}}$	No. of pegs	Longitudinal force (g)
10.6	9	22
5.3	4	18
5.3	3	17
5.3	2	17

difficult to ascertain, the critical value of three for the ratio is corroborated by the data.

The combined data for the two glossy snakes shows a monotone decrease in speed as the ratio decreases. For large values of the ratio, which differed by 40%, the corresponding values of the speed differed by only 10%. This slow rate of speed decrease at high values of the ratio is a result of the availability to both snakes of a large number of suitably oriented contact sites on the small peg-spacing race course. The substantial drop in speed experienced by the long glossy snake when placed on the large peg-spacing race course is due more to a reduction in the number of favourably oriented contact points than to a reduction in the number of simultaneous contact points, since the ratio is still fairly high for this run. The more drastic decrease in speed experienced by the short glossy snake on the large peg-spacing race course is undoubtedly due to the loss of contact sites and unfavourable orientation of these sites.

Further evidence of the importance of contact-site orientation can be obtained by comparing the results in Table 3 with those in Table 4. The data in Table 4 shows that for a fixed ratio the longitudinal force, which is presumably directly proportional to the longitudinal speed, is a very insensitive function of the number of linearly arranged contact sites. However, a 50% increase in the ratio coupled with a simultaneous decrease in the number of pegs leads to an 18% reduction of longitudinal force. The comparable situation in the present experiment is provided by the long glossy snake. A 55% decrease in ratio coupled with a simultaneous decrease in the number of peg contacts leads to a 34% decrease in speed. This more drastic decrease in speed is due to the unavailability of suitably oriented peg contacts because of the hexagonal pattern.

The rat snake also shows a 46% decrease in speed with a 56% decrease in peg spacing. Here again the change is drastic because the ratio goes from a value above three to one below this critical value.

Only the rattlesnake was unaffected by the ratio. This independence of the speed from external factors is caused by the snake's ability to combine lateral undulation with sidewinding in varying degrees as needed.

SUMMARY

1. The speed of snakes moving by lateral undulation was measured on a smooth board studded with equally spaced pegs arranged in a hexagonal pattern.
2. For some snakes speed was drastically reduced (by as much as 50%) as the ratio of body length to peg spacing was reduced from values as high as twelve to values near or below three.
3. Speed is also influenced by the relative orientation of the pegs contacted by the moving snake.
4. Snakes which can sidewind use this ability to maintain a constant speed when the number of contact points available is insufficient for continuous lateral undulation.

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