KINEMATICS AND PERFORMANCE CAPACITY FOR THE CONCERTINA LOCOMOTION OF A SNAKE (*COLUBER CONSTRICTOR*)

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Summary

We used a motorized treadmill to determine the endurance (from 4.2 to 5.6 cm s^{-1}) and burst speed of five *Coluber constrictor* Linnaeus performing concertina locomotion in tunnels 3, 5 and 7 cm wide. The snakes had greatest average endurance at 4.2 cm s^{-1} within the 5 cm wide tunnel (80 min), and the average endurance of snakes moving in the 3 cm tunnel (24 min) was significantly lower than that observed for either the 5 or 7 cm tunnel at the same speed. In contrast to endurance capacity, there was no statistically significant effect of tunnel width on burst speed, and mean values ranged from 13.5 to 16.8 cm s^{-1}. The fastest burst speed observed was 20.8 cm s^{-1} in a 7 cm tunnel. Analysis of variance on kinematic variables measured from videotapes made of the endurance trials revealed highly significant effects of both speed and tunnel width on kinematics. As the tread speed increased among different endurance trials, the snakes primarily increased the frequency of movements and increased the average forward speed during the moving phase. However, the snakes did not significantly alter either the distance moved per cycle or the proportion of time spent moving in response to different tread speeds used in the endurance trials. Decreased tunnel width caused snakes (1) to move a smaller distance per cycle, (2) to use more regions of static contact with the sides of the tunnel, and (3) to orient the convoluted portions of the body at a smaller angle relative to the sides of the tunnel. Decreased tunnel width did not affect the average forward speed during the moving phase. Hence, tread speed and tunnel width affected different kinematic variables. Significant changes in kinematics did not always cause significant changes in locomotor performance capacity.

Introduction

A topic of central interest to studies of animal locomotion is the extent to which physiological and behavioral capacities allow animals to modulate their speed of movement. For example, numerous studies have tested locomotor performance

for the purposes of determining the maximum (burst) speeds that animals can attain, the capacity for sustaining locomotor activity (endurance) and the energetic demands of locomotion (e.g. Beamish, 1978; Taylor *et al.* 1982; Bennett, 1985; Full, 1989). Across a wide variety of vertebrate taxa and modes of locomotion, kinematic studies have shown that animals modulate their locomotor speed by some combination of increases in the frequency and/or the amplitude of their movements (Gray, 1968). The conspicuous changes in movement associated with changing locomotor speed have also been a convenient system for workers interested in modelling the neural control underlying the coordinated rhythmic movements of locomotion (Cohen *et al.* 1988). However, many studies that have determined locomotor performance lack kinematic data, and few kinematic studies have simultaneously documented maximum speeds and endurance. Consequently, it is unclear for many types of vertebrate locomotion the extent to which changes in kinematics are associated with changes in locomotor perform-ance.

A well-documented feature of the locomotion of limbless vertebrates is the change in mode of locomotion with both speed and surface contact (Gray, 1946; Gans, 1974; Jayne, 1986). Commonly, when limbless vertebrates encounter tunnels substantially wider than their bodies, they perform the concertina mode of locomotion, and this locomotor mode has been observed in many snake species as well as other lineages of vertebrates that have independently evolved a limbless condition (Gray, 1946; Gans, 1974; Jayne, 1986; Gans and Gasc, 1990). During concertina locomotion in tunnels, animals flex their bodies to wedge themselves against the sides of the tunnel, forming a region of static contact from which they then extend themselves forward. Hence, animals progress in this mode using periodic starts and stops. Recent work has found that the concertina mode of progression is particularly interesting because it is energetically very costly compared to other types of limbless and limbed locomotion on land, and this high energetic cost is associated with decreased endurance of concertina locomotion compared to lateral undulatory locomotion performed by the same snakes (Walton *et al.* 1990). The body of limbless animals must conform to the spacing of the walls of tunnels during concertina locomotion, and changing tunnel width predictably affects the kinematics of snakes performing this type of locomotion (Jayne, 1988). Hence, the movement of snakes within tunnels is amenable to experimental manipulation.

In this study, we manipulated both the width of tunnels and the speed of the tunnel treadmill used by snakes performing concertina locomotion, in order to accomplish three goals. First, we determined whether tunnel width affected either the burst speed or endurance of snakes and whether a single tunnel width optimized both these measures of locomotor performance. Second, we quantified the effects of tunnel width and speed on the kinematics of concertina locomotion particularly to examine the extent of frequency *versus* amplitude modulation of movement. Third, we examined whether significant changes in locomotor per-formance were accompanied by significant change in kinematic variables.

Materials and methods

Experimental animals

Five individuals of the species *Coluber constrictor* (black racer) were obtained from commercial suppliers. This species is characterized by a rather high aerobic capacity for activity for a snake (Ruben, 1976). However, the numbers of body vertebrae in *C. constrictor* ($N=5$, mean 181, range 177–189) and aspects of its axial musculature are not unusual for a non-constricting terrestrial colubrid snake (Jayne, 1982), and black racers readily perform the concertina mode of loco- motion within tunnels (Walton *et al.* 1990).

To minimize the effects of size on locomotor performance, we selected snakes with similar linear dimensions (mean snout–vent length=73 cm, range 70–77 cm; mean total length 94 cm, range 88–101 cm; mean width at mid-body 1.6 cm, range 1.4–1.7 cm) and mass (mean=118 g, range 101–132 g). The snakes were kept in cages with a daytime photothermal gradient of approximately 25–35 °C and an ambient night temperature of approximately 22 °C. The snakes were fed a maintenance diet of lizards and they were fasted for 5–7 days prior to a test.

Apparatus

We elicited concertina locomotion from snakes by using a motorized treadmill with a circular parallel-sided tunnel (2 m outside diameter), which rotated about its center in the horizontal plane. The floor of the tunnel was 7 cm wide and consisted of smooth plywood. Friction tape (3M medium-grade safety walk 7739) affixed to the vertical sides provided the surface with a high coefficient of friction, which effectively elicited the concertina mode of locomotion from the snakes. Strips of dense plastic foam covered with friction tape were used to reduce the tunnel width to 5 and 3 cm. The speed of the treadmill was controlled by a variable-speed electric motor. Portions of all trials were videotaped (at 30 frames s^{-1}) with a video camera (Panasonic PK-958) mounted directly above the treadmill, and a video timer (For A VTG-33) was used to dub time (±0.01 s) onto the videotape. Frame-by-frame analysis of the videotapes allowed us to verify treadmill speed and locomotor mode and to measure kinematic variables.

Testing protocol

All tests were conducted in a temperature-controlled room that allowed us to regulate the snake's body temperature at 30 °C (±1 °C), which is near the preferred body temperature and within the range of active field body temperatures reported for this species (Fitch, 1963: Hirth and King, 1969; Vitt, 1974). Only one endurance or burst speed testing procedure per individual per day was conducted, and the order of trials was randomized with respect to treadmill speed and tunnel width.

We determined endurance of the snakes for three different tunnel widths (3, 5 and 7 cm) at treadmill speeds of 4.2, 4.9 and 5.6 cm s^{-1}. During the endurance trials the snakes were lightly tapped on the tail with either our fingers or a soft

brush to encourage continuous movement. When the snakes failed to match
treadmill speed three times in rapid succession the endurance trial was ended and
the time of the trial was recorded to the nearest 0.1 min. For one individual within
the 5 cm tunnel moving at $4.2\,\mathrm{cm\,s^{-1}}$ the endurance trial was terminated at 2 h.

Burst speeds were determined for the same three tunnel widths as for the
endurance trials. Beginning with a tread speed greater than $5.6\,\mathrm{cm\,s^{-1}}$, a snake was
allowed to crawl for about five cycles of movement, where a cycle equals the time
interval spanning successive initiations of static contact between a point on the
snake and the tunnel. The tread speed was then quickly increased in stepwise
increments of about $2\,\mathrm{cm\,s^{-1}}$ until the snake could no longer match speed; this first
part of the burst speed test usually lasted less than 1 min. After about 4 h of rest,
the snake was tested again for about 10 s at the fastest tread speed used previously.
Burst speed was then calculated as the maximum value of mean forward velocity
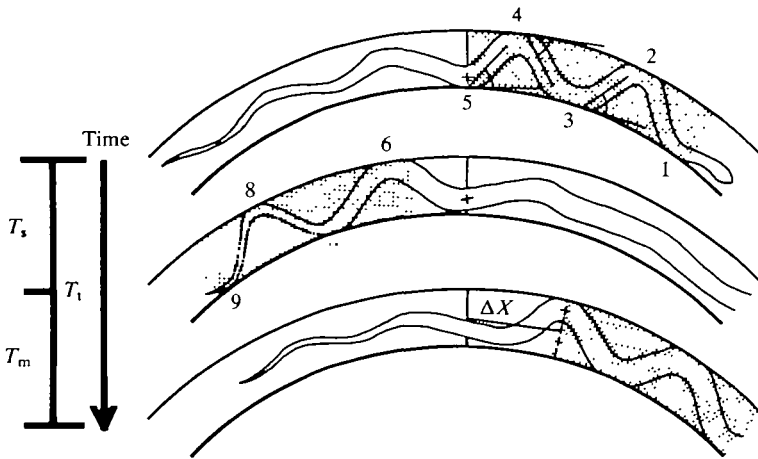ever observed for a single cycle of movement ($\bar{V}_X$, Fig. 1).

Fig. 1. Schematic diagram showing the method of measuring kinematic variables for
concertina locomotion in a tunnel. From top to bottom the three images represent the
times when static contact begins, ends and begins again for the paint mark (+) on the
back of the snake near mid-body. The stippled areas indicate zones of static contact
between the snake and the tunnel, and the solid line perpendicular to the sides of the
tunnel is a reference mark painted on the floor of the treadmill. The total time of a
cycle of movement (T_t) is divided into static and movement phases (T_s, T_m). The
numbers indicate successive regions of static contact with the sides of the tunnel and,
for this example, the maximum number of simultaneous regions of static contact with
the sides of the tunnel (N_{static}) is 5, whereas the total number of such regions along the
entire snake during one cycle (N_{total}) is 9. The mean angle between the three portions
of the snake's body (near mid-body as shown at top) and tangents through the sides of
the tunnel is $\bar{\alpha}$. The forward distance traveled per cycle is ΔX. The mean forward
velocities for the entire cycle and the movement phase are $\bar{V}_X = \Delta X / T_t$ and
$\bar{V}_m = \Delta X / T_m$, respectively. Frequency of movement, $f = 1/T_t$, and the proportion of
time in static contact, $PSTAT = T_s / T_t$, were also calculated for each cycle.

Kinematics

Using frame-by-frame playback of the videotape, we measured eleven kinematic variables for 3–5 cycles of movement from each endurance trial (Fig. 1). By following a paintmark on a mid-dorsal scale, near mid-body, we determined for each cycle of movement the following: (1) the duration of static contact ($T_s \pm 0.03$ s), (2) the duration of time spent moving ($T_m \pm 0.03$ s), (3) the total time (period) of one cycle ($T_t \pm 0.03$ s), (4) the distance traveled forwards ($\Delta X \pm 0.1$ cm), (5) the mean forward speed ($\bar{V}_X = \Delta X / T_t$) and (6) the mean forward speed while moving ($\bar{V}_m = \Delta X / T_m$). In addition, we determined (7) the maximum number of simultaneous regions of static contact with the sides of the tunnel (N_{static}), (8) the total number of different regions of static contact with the sides of the tunnel along the entire length of the snake (N_{total}), and (9) the mean angle between the snake's body and a tangent through the side of the tunnel at the region of static contact ($\bar{\alpha}$). (10) The frequency of movement (f in Hz) was calculated as the inverse of T_t, and (11) the proportion of a cycle spent in static contact (PSTAT) was calculated as T_s / T_t.

Statistical analysis

To detect effects of tread speed and tunnel width on individual kinematic variables, we used univariate analyses of variance (ANOVA) as the statistical method most easily interpreted and most appropriate for the small sample sizes within the cells of our experimental design (Bray and Maxwell, 1985). All ANOVAs were performed using unique sums of squares that were calculated with a microcomputer version (PC+ 2.0) of SPSS. For each snake and combination of tunnel width and treadmill speed, we chose 3–5 cycles of movement during which mean forward speeds were closely matched, so that the effects of tunnel width and individuals could be assessed without a confounding influence of speed. Tunnel width and speed were considered as fixed effects in these three-way ANOVAs, whereas individuals were treated as random effects. Following guidelines given in Zar (1984), we assessed the significance of speed and tunnel width by dividing the mean squares of these main effects by the appropriate two-way interaction involving the random effect (see Table 1), whereas the F-test of significance for individuals used the mean squares of the error term in the denominator.

Because of individual differences in burst speeds and the difficulty in obtaining several cycles of high-speed concertina locomotion, the kinematic data for fast locomotion across all individuals could not be pooled easily or analyzed with a simple balanced design including reasonable replication at a single speed. Hence, to determine whether the effects of speed on kinematics observed over the limited range of speeds (during endurance trials) used in the ANOVA were generally valid, we relied primarily on supplemental kinematic measurements of high-speed movement obtained from a single individual during its burst speed trials. The observations for this single snake (used in Figs 3–6) appeared qualitatively similar to the more limited high-speed kinematic data from other individuals.

Results

Performance

Fig. 2 summarizes the effects of treadmill speed and tunnel width on performance. A three-way ANOVA (with width, speed and individuals as factors) on the endurance measurements detected highly significant effects of both tunnel width ($F_{2,8}=36.8$, $P<0.001$) and treadmill speed ($F_{2,8}=31.8$, $P<0.001$) on endurance (significance of individuals and interaction terms could not be tested because there was only one observation per individual). Endurance decreased sharply as tread speed was increased above $4.2\,\mathrm{cm\,s^{-1}}$, with mean endurance at $4.9\,\mathrm{cm\,s^{-1}}$ ranging from 17 to 37 % of those values observed at $4.2\,\mathrm{cm\,s^{-1}}$ (Fig. 2A). The greatest average endurance observed for the five animals was 80 min for snakes moving at $4.2\,\mathrm{cm\,s^{-1}}$ within the 5 cm wide tunnels. Snakes moving at $4.2\,\mathrm{cm\,s^{-1}}$ had a mean endurance within the 3 cm (24 min) tunnel that was significantly less than that in both the 5 cm ($t=-3.32$, $P<0.02$) and 7 cm ($t=-3.58$, $P<0.02$) tunnels, but endurance did not vary significantly between the 7 cm and 5 cm tunnels ($t=-1.76$, $P>0.10$) (two-tailed, paired t-tests). In contrast to the analysis of the measures of endurance, ANOVA (two-way, with width and individuals as factors) did not detect a significant effect of tunnel width on burst speed ($F_{2,8}=2.6$, $P>0.13$; Fig. 2B). Average burst speeds ranged from 13.5 to $16.8\,\mathrm{cm\,s^{-1}}$, with $20.8\,\mathrm{cm\,s^{-1}}$ being the single fastest burst speed observed for an individual.

Kinematics

The fact that the ANOVA on $\bar{V}_X$ (Table 1) only detected significant effects attributable to tread speed indicates that we successfully chose sequences in which all animals closely matched the treadmill speed, thereby simplifying the detection
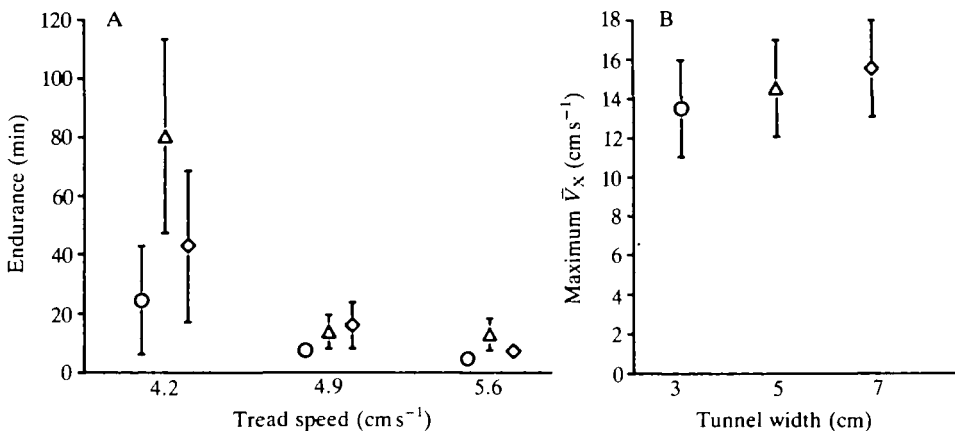

Fig. 2. Mean measures ($\pm$s.d.) of locomotor performance for the concertina movement of *Coluber constrictor* ($N=5$) in tunnels 3, 5 and 7 cm wide (O, $\triangle$ and $\diamondsuit$, respectively). (A) Endurance was the time that snakes were able to match treadmill speed. (B) Burst speed was the single greatest value of $\bar{V}_X$ observed for each individual.

Table 1. *Summary of F-values from three-way ANOVAs performed separately for each kinematic variable*

Kinematic variable	Main effects			Interaction terms			
	Speed (S) (2,8)	Width (W) (2,8)	Indiv (I) (4,144)	$S \times W$ (4,16)	$S \times I$ (8,144)	$W \times I$ (8,144)	$S \times W \times I$ (16,144)
T_s	12.5**	29.6***	3.0*	1.3	0.7	1.0	1.1
T_m	2.0	19.7***	6.9***	0.6	3.3**	1.8	1.6
T_t	4.0	42.9***	7.2***	0.7	3.3**	1.3	1.5
ΔX	3.7	87.6***	7.8***	1.6	2.5*	0.8	1.6
$\bar{V}_X$	88.0***	0.4	0.6	0.9	0.7	0.6	0.8
$\bar{V}_m$	41.4***	0.2	0.6	1.2	0.9	2.1*	1.4
N_{static}	1.3	37.3***	13.0***	1.4	3.1**	9.4***	5.1***
N_{total}	1.6	176.8***	10.5***	0.8	3.2**	5.7***	3.0***
$\bar{\alpha}$	3.0	680.6***	3.7*	1.7	1.6	2.0	1.7
f	8.6*	118.9***	8.9***	4.0*	3.0**	0.9	2.1*
PSTAT	0.7	0.3	2.8*	0.8	0.8	2.0	1.5

See List of abbreviations for definitions of kinematic variables.

*, ** and *** indicate $P<0.05$, $P<0.005$ (approximates Bonferroni correction for multiple comparisons) and $P<0.001$, respectively.

Degrees of freedom are shown in parentheses beneath each effect.

of genuine effects of tunnel width. Analyses of variance summarized in Table 1 show that there were widespread significant effects of both treadmill speed and tunnel width on the kinematics of concertina movement over the range of speeds used for the endurance trials, with 3 of 10 variables (excluding $\bar{V}_X$) affected by speed and 8 variables affected by tunnel width. The kinematic variables can be grouped into three broad categories: (1) time variables (T_s, T_m, T_t, f and PSTAT), (2) postural variables (ΔX N_{static}, N_{total}, $\bar{\alpha}$) and (3) speed ($\bar{V}_X$, $\bar{V}_m$), which is a combination of time and postural variables. We consider time and postural variables to be the primary indicators of frequency and amplitude modulation, respectively.

Time variables

The durations of a cycle of movement (T_t) and of the moving and static phases (T_m, T_s) decreased with decreased tunnel width (Tables 1, 2). Plots of T_t *versus* speed revealed a large variance within each of the three tread speeds used for the ANOVA; hence, no significant effect of speed on T_t was observed for the limited range of speeds used in the ANOVA. However, plots of T_t *versus* speed over a wider range of speeds (2–21 cm s^{-1}) for a single snake revealed a clear curvilinear decrease with increased speed, despite the variable nature of the data. Such curvilinear decreases in period commonly occur with increased locomotor speed, whereas transforming period into frequency (f) often reveals linear relationships between f and speed.

Table 2. *Means of kinematic variables measured during endurance trials pooling observations for all (5) individuals at each combination of tunnel width and tread speed*

	3 cm width Tread speed $(cm\,s^{-1})$			5 cm width Tread speed $(cm\,s^{-1})$			7 cm width Tread speed $(cm\,s^{-1})$		
Kinematic variable	4.2 (24)	4.9 (19)	5.6 (19)	4.2 (22)	4.9 (22)	5.6 (22)	4.2 (21)	4.9 (22)	5.6 (18)
T_s	0.64	0.52	0.42	0.82	0.68	0.64	0.85	0.78	0.82
T_m	0.86	0.75	0.60	1.22	0.96	1.09	1.34	1.25	1.15
T_t	1.51	1.27	1.03	2.04	1.64	1.72	2.19	2.02	1.97
ΔX	6.00	6.01	6.03	8.15	7.81	9.38	9.02	9.41	11.44
$\bar{V}_X$	4.02	4.78	5.92	4.14	4.91	5.49	4.18	4.77	5.81
$\bar{V}_m$	7.08	8.26	10.26	7.47	8.31	9.04	7.18	8.03	10.26
N_{static}	11.2	10.5	12.6	7.5	7.5	7.1	5.7	5.6	5.9
N_{total}	14.9	14.1	15.1	9.6	8.8	9.2	6.6	6.6	6.6
$\bar{\alpha}$	38	40	38	59	59	61	84	85	90
f	0.68	0.80	1.00	0.54	0.66	0.60	0.48	0.55	0.54
PSTAT	0.42	0.41	0.41	0.42	0.40	0.38	0.40	0.39	0.42

See List of abbreviations for definitions of kinematic variables.
T_s, T_m and T_t are in s; ΔX is in cm, $\bar{V}_X$ and $\bar{V}_m$ are in $cm\,s^{-1}$ and f is in Hz.
Sample sizes are shown in parentheses beneath each combination of tread speed and tunnel width.

The ANOVA on the frequencies obtained during the endurance trials (Table 1: f) revealed that this variable significantly increased with both decreased tunnel width and increased tread speed (Table 2). Similarly, frequency data obtained over a wider range of $\bar{V}_X$ for a single individual (Fig. 3) showed highly significant ($P<0.001$) linear increases with increased $\bar{V}_X$ for each of the three tunnel widths. An analysis of covariance on the data shown in Figs 3A,C,E revealed significant ($P=0.002$) differences among the three slopes of the regressions relating f to $\bar{V}_X$ for each tunnel width. Inspection of the values predicted by the regressions (Fig. 3) shows that the relationship of f to $\bar{V}_X$ was similar for the 5 and 7 cm tunnels, whereas for a given $\bar{V}_X$ in the 3 cm tunnel the snake used a higher frequency of movement than that in either the 5 or 7 cm tunnels.

In addition to significant decreases in the durations of the static (T_s) and moving (T_m) phases of concertina locomotion with decreased tunnel width, T_s decreased significantly with increased speed. The values of T_s and T_m, like the T_t values, were quite variable at slow speeds and decreased curvilinearly with increased tread speed. T_s and T_m changed with speed and tunnel width during the endurance trials such that the proportion of a cycle spent in the static phase (PSTAT) did not change significantly (grand mean 0.41, range 0.17–0.62) among any of the three speeds and tunnel widths used during the endurance trials (Tables 1, 2). As shown in Fig. 4, for two of the three tunnel widths there were significant positive

correlations between PSTAT and $\bar{V}_X$ (3 cm tunnel, $r=0.57$, $P=0.009$; 5 cm, $r=0.15$, $P=0.94$; 7 cm, $r=0.46$, $P=0.03$). Considering that $\bar{V}_X$ in Fig. 4 ranged from slow to burst speed, the effect of $\bar{V}_X$ on PSTAT seemed minimal even for the significant correlations. For example, when $\bar{V}_X$ is 3 or 15 cm s^{-1}, values of PSTAT predicted for the 3 cm tunnel are 0.387 and 0.521 and for the 5 cm tunnel 0.393 and 0.513, respectively.
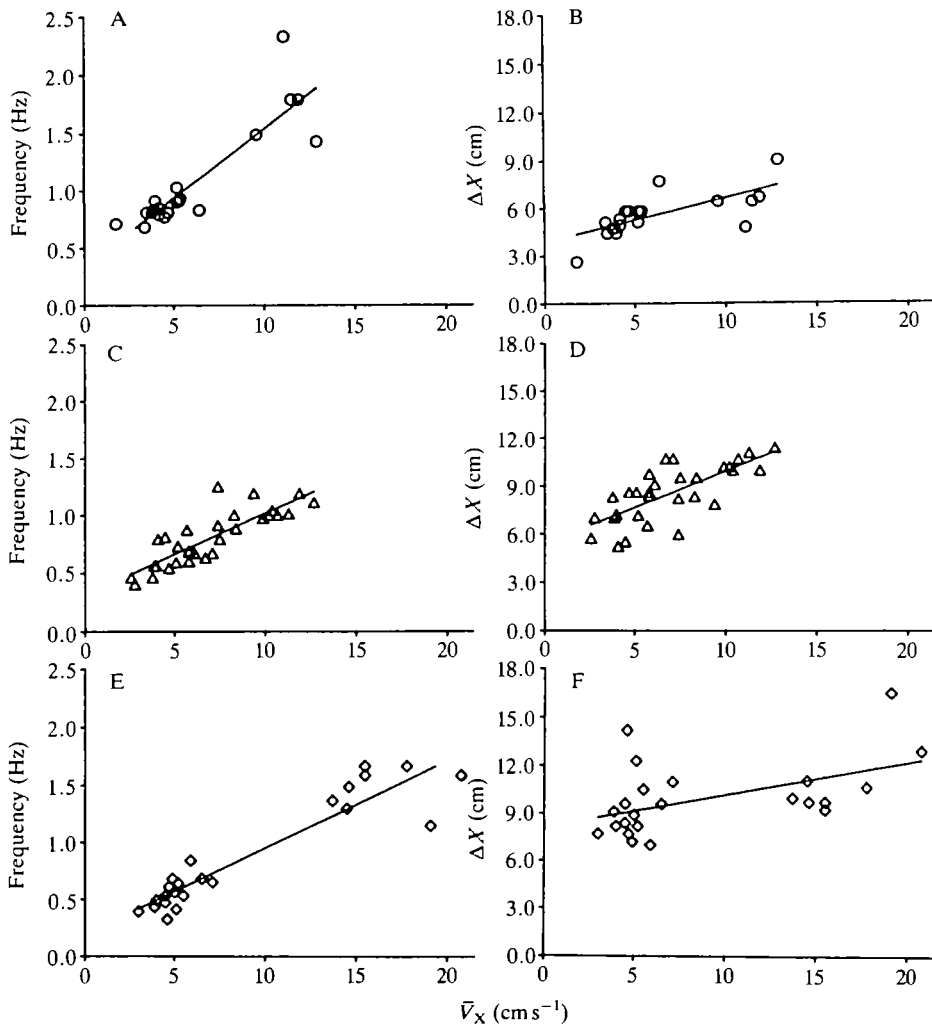

Fig. 3. Plots of frequency of movement (f) and forward movement per cycle (ΔX) *versus* $\bar{V}_X$ for a single individual moving at speeds ranging from slow to burst speed within tunnels 3 cm (○, $N=20$), 5 cm (△, $N=30$) and 7 cm (◇, $N=23$) wide. Least-squares regressions are shown for each figure and are as follows (±s.E. of slope). (A) $f=0.121(\pm0.015)\bar{V}_X+0.332$.   (B) $\Delta X=0.281(\pm0.069)\bar{V}_X+3.837$.   (C) $f=0.071(\pm0.009)\bar{V}_X+0.305$.   (D) $\Delta X=0.458(\pm0.081)\bar{V}_X+5.369$.   (E) $f=0.076(\pm0.006)\bar{V}_X+0.187$. (F) $\Delta X=0.207(\pm0.074)\bar{V}_X+8.134$.
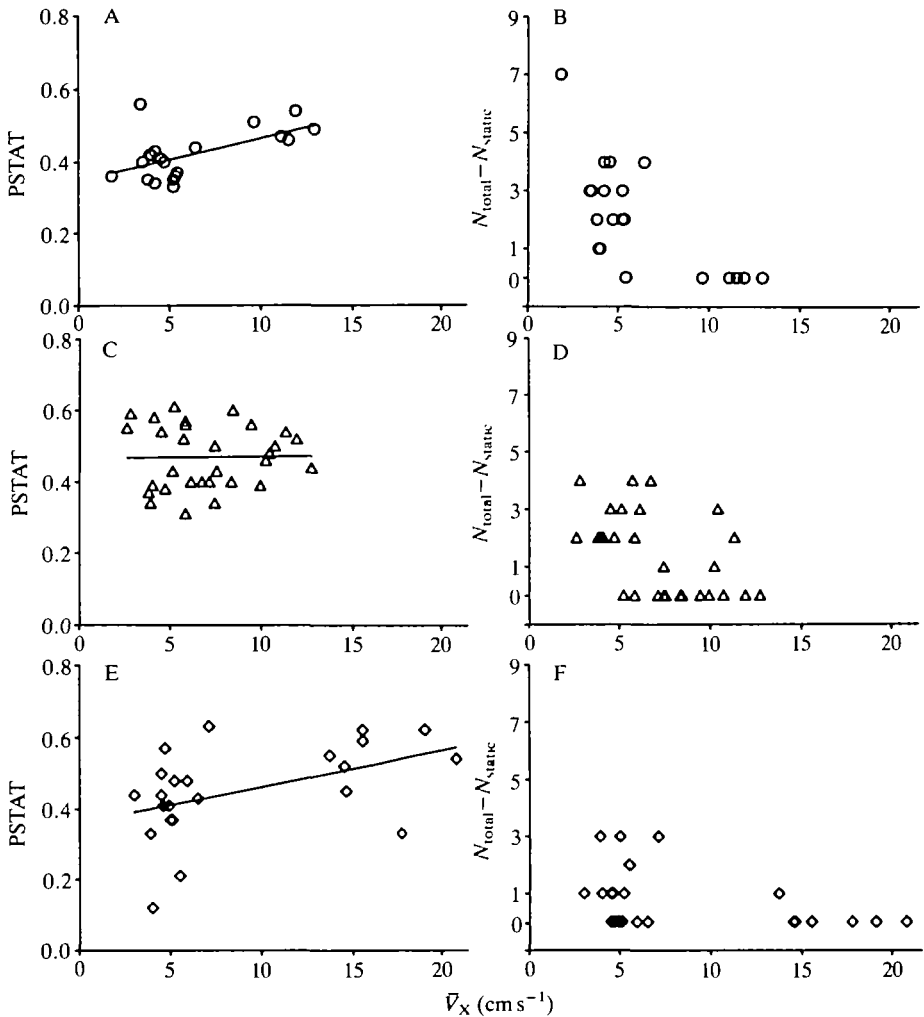
Fig. 4. Plots of kinematic variables *versus* $\bar{V}_X$ for a single snake (same one as in Fig. 3) moving at speeds ranging from slow to burst speed within 3 cm (O, $N=20$), 5 cm ($\triangle$, $N=30$) and 7 cm ($\Diamond$, $N=23$) tunnels. (A) PSTAT=0.012($\pm$0.004)$\bar{V}_X$+0.350. (C) The regression PSTAT=0.0005($\pm$0.006)$\bar{V}_X$+0.467 was not significant and mean PSTAT=0.47. (E) PSTAT=0.0102($\pm$0.004)$\bar{V}_X$+0.363. (B, D, F) The difference between the maximum number of simultaneous regions of lateral static contact and total number of such region *versus* $\bar{V}_X$.

Postural variables

In contrast to the time variables, none of the four postural variables varied significantly among the three speeds used for the endurance trials, but all postural variables were affected strongly by changes in tunnel width (Tables 1, 2; Fig. 5). The forward distance moved per cycle (ΔX) is analogous to the stride length of limbed locomotion, and the means of this quantity averaged for all three

endurance trial speeds for the 3, 5 and 7 cm tunnel widths were 6.0 cm (N=62), 8.5 cm (N=66) and 9.9 cm (N=61), respectively. For a given speed, ΔX often varied considerably. For example, for a single individual (Fig. 3D) in the 5 cm tunnel, ΔX ranged from 6.5 to 9.8 cm for $\bar{V}_X$ between 5.7 and 5.8 cm s^{-1}. For the data obtained over the wide range of speeds (Fig. 3), ΔX showed a highly significant positive correlation with $\bar{V}_X$ for each of the tunnel widths. Values of ΔX from separate regressions for the 3, 5 and 7 cm wide tunnels predict that ΔX increases 72, 81 and 28 % from values at $\bar{V}_X$=3 cm s^{-1} to those for $\bar{V}_X$=15 cm s^{-1}, whereas the respective increases predicted from the slowest and fastest tread
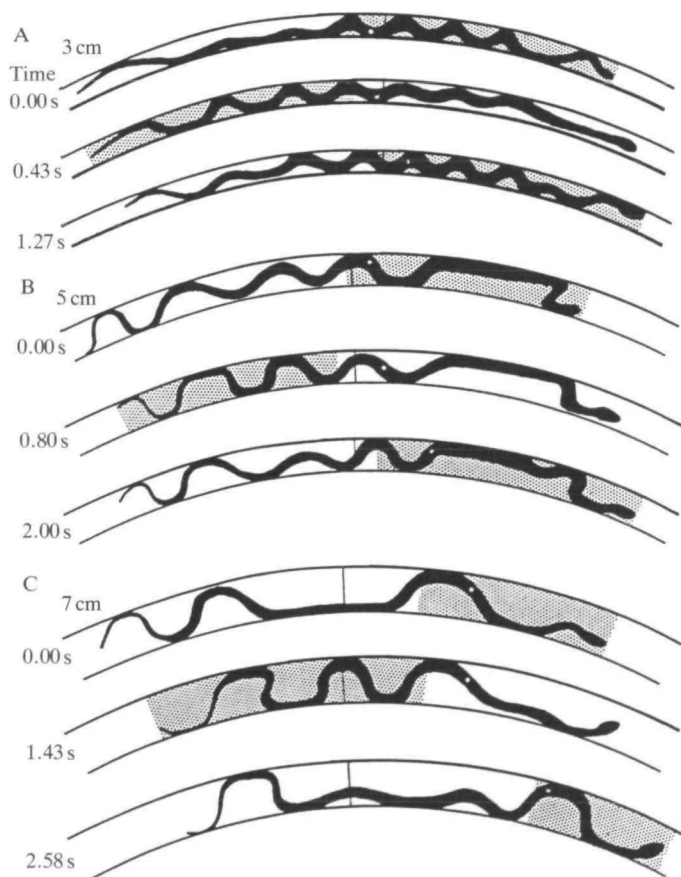

Fig. 5. Figures drawn from video images of a single snake (used for Figs 3 and 4) performing concertina locomotion during endurance trials for 3 cm (A) 5 cm (B) and 7 cm (C) wide tunnels. From top to bottom within each series of figures for a single tunnel width, images are at the time of the initiation of static contact, the beginning of movement and the re-establishment of static contact between the tunnel and the part of the snake marked by white paint. Note that the paint mark was not in the identical anatomical position on the snake in the three different trials. Stippled areas indicate static contact between the snake and the tunnel. (A) $\bar{V}_X$=4.5 cm s^{-1}. (B) $\bar{V}_X$=4.2 cm s^{-1}; (C) $\bar{V}_X$=3.8 cm s^{-1}.

speed used in the endurance tests were only 8, 9 and 3 %. Analysis of covariance on the data from a single snake shown in Fig. 3B,D,F revealed that the slopes of the regressions relating ΔX to $\bar{V}_X$ did not differ significantly ($F_{2,67}=2.53$), but the elevations of the regressions differed significantly ($F_{2,69}=32.4$) and agreed with the finding from the endurance trials that a greater distance was traveled per cycle in wider tunnels (Table 2).

The distance traveled per cycle depends on the number of regions of static contact with the sides of the tunnel, the angle of the body relative to the sides of the tunnel, and the extent of straightening that occurs during the moving phase of concertina locomotion. Fig. 5 illustrates how these measures of overall body posture vary with tunnel width.

The maximum number of regions simultaneously in static contact with the sides of the tunnel (N_{static}) and the total number of regions of static contact along the length of the snake (N_{total}) were both significantly affected by tunnel width (Table 1). Mean values of N_{static}, averaged for all of the endurance trial data, for each tunnel width were 11.4, 7.3 and 5.7 for the respective tunnel widths of 3, 5 and 7 cm. The equivalent mean values for N_{total} were 14.7, 9.2 and 6.6. Values of N_{total}, observed over the wider range of speed included in Fig. 3, did not show any significant correlation with $\bar{V}_X$ for any of the tunnel widths. Over the wide range of speeds, N_{static} had a significant correlation with $\bar{V}_X$ for two of the tunnel widths (3 cm, $r=0.55$, $P=0.012$; 5 cm, $r=0.31$, $P=0.095$; 7 cm, $r=0.55$, $P=0.007$). Analysis of covariance of the data shown in Fig. 6A revealed that the slopes of regressions relating N_{static} to $\bar{V}_X$ for the three tunnel widths were not significantly different ($F_{2,67}=1.4$), and that the elevations differed significantly among these regressions ($F_{2,69}=95.3$). As indicated by the difference between N_{total} and N_{static} (Fig. 4), for speeds greater than 60 % of burst speed N_{static} often equaled N_{total}.

The maximum distance that the snake can advance going from the fully flexed to the fully extended position depends partly on the angle between the snake's body and the side of the tunnel ($\bar{\alpha}$). Values of $\bar{\alpha}$ measured during the endurance trials were not affected by treadmill speed, but they were strongly affected by the width of the tunnel (Tables 1, 2). For example, mean values of $\bar{\alpha}$ from the endurance trials were 39°, 60° and 86° for respective tunnel widths of 3, 5 and 7 cm. Identical to the results from the endurance trials, values of $\bar{\alpha}$ determined over the wider range of speed (Fig. 6B) showed no indication ($P>0.2$) of significant correlations with $\bar{V}_X$.

Speed variables

Snakes could change their mean forward speed either by altering their speed when moving ($\bar{V}_m$) or by varying the proportion of time spent moving. The ANOVA on values of $\bar{V}_m$ from the endurance trials indicated the $\bar{V}_m$ was significantly affected by treadmill speed but unaffected by tunnel width. Measurements of $\bar{V}_m$ from the wider range of speeds (Figs 6C, D) showed very high and significant positive correlations with $\bar{V}_X$ ($r>0.94$) for all tunnel widths, and analysis of covariance confirmed that there were no significant differences in either
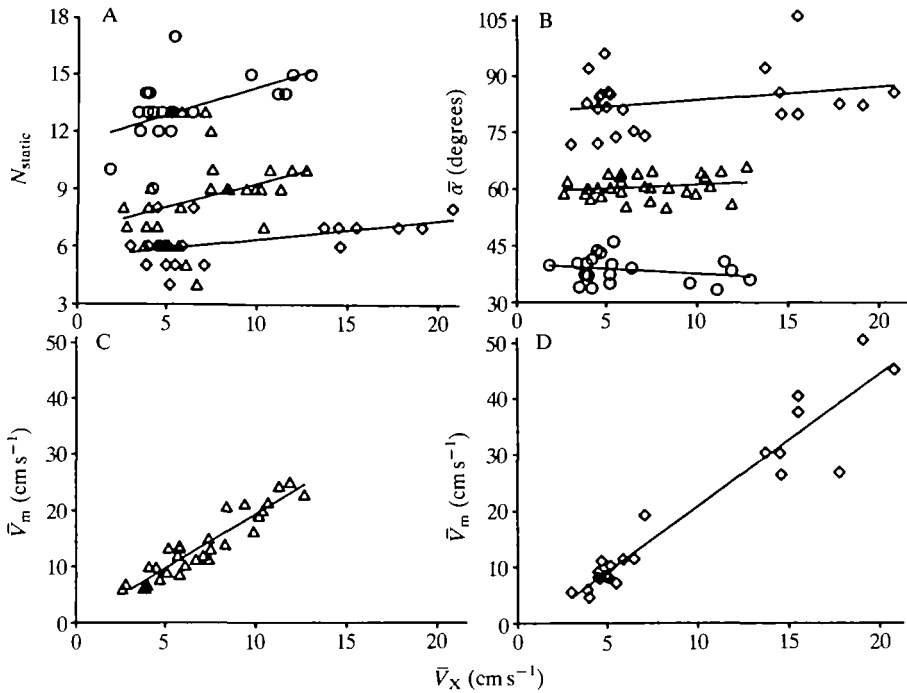
Fig. 6. Plots of kinematic variables *versus* $\bar{V}_X$ for a single snake (same one as in Fig. 3) moving at speeds ranging from slow to burst speed within 3 cm (O, $N=20$), 5 cm ($\triangle$, $N=30$) and 7 cm ($\diamond$, $N=23$) wide tunnels with least-squares regressions. (A) for 3 cm width $N_{static}=0.293(\pm0.105)\bar{V}_X+11.41$; for 5 cm width $N_{static}=0.253(\pm0.146)\bar{V}_X+6.77$ (slope not significant, mean $N_{static}=8.53$); for 7 cm width $N_{static}=0.099(\pm0.033)\bar{V}_X+5.37$. (B) None of the slopes for these regressions was significant and mean values of $\bar{\alpha}$ for 3, 5 and 7 cm widths were 39°, 61° and 83°, respectively. (C) $\bar{V}_m=1.95(\pm0.14)\bar{V}_X-0.08$. (D) $\bar{V}_m=2.36(\pm0.15)\bar{V}_X-2.74$.

the slopes ($F_{2,67}=2.23$) or the elevations ($F_{2,69}=1.17$) of the regressions relating $\bar{V}_m$ to $\bar{V}_X$. Hence, snakes performing concertina locomotion change $\bar{V}_X$ primarily by changing their speed while moving ($\bar{V}_m$) rather than by changing the proportion of time spent moving (as indicated by analysis of PSTAT).

Discussion

Comparative locomotor performance

One unexpected finding of this study was that the burst speed measure of performance for the concertina movement of *C. constrictor* was unaffected by tunnel width, whereas endurance of snakes was significantly affected by tunnel width (Fig. 2). One might predict that conditions favoring endurance (and by implication energetic cost) would also favor greater burst speed, because a comparison between locomotor modes of *C. constrictor* does reveal such an association. For the lateral undulation of *C. constrictor*, Walton *et al.* (1990)

reported an average burst speed of $153\,\mathrm{cm\,s^{-1}}$ (measured over 50 cm) and one snake moved at $250\,\mathrm{cm\,s^{-1}}$ over 25 cm, whereas the fastest average concertina burst speed in this study was only $16.8\,\mathrm{cm\,s^{-1}}$ and one individual moved at $20.8\,\mathrm{cm\,s^{-1}}$ in the 7 cm tunnel. Comparing lateral undulation with concertina locomotion in *C. constrictor* (Walton *et al.* 1990), the average endurance is much greater (33 min at $16.7\,\mathrm{cm\,s^{-1}}$ *vs* 7 min at $5.6\,\mathrm{cm\,s^{-1}}$) and the net cost of transport is much less (1.15 *vs* $8.49\,\mathrm{ml}\,O_2\,g^{-1}\,km^{-1}$) in lateral undulation. Thus, how generally endurance and sprinting performance are correlated either among different locomotor modes or among different environmental conditions remains an open question.

Comparisons with the limited data available for the speed [in total lengths (*TL*) per second] of concertina locomotion of limbless reptiles helps to clarify whether *C. constrictor* is unusual in its ability to perform this movement. For concertina locomotion performed by animals on a variety of surfaces Jayne (1986) reported $\bar{V}_X$ of $0.13\text{--}0.28\ TL\,\mathrm{s^{-1}}$ for the amphisbaenian *Rhineura floridana* (TL=29 cm; crawling past pegs spaced at 2.5 and 5 cm intervals) and $0.04\text{--}0.11\ TL\,\mathrm{s^{-1}}$ for the snake *Acrochordus javanicus* (*TL* 74 cm; crawling on linoleum). For the concertina movement of snakes in stationary parallel-sided tunnels 10 cm wide, Jayne (1988) found $\bar{V}_X$ varied from 0.06 to 0.11 $TL\,\mathrm{s^{-1}}$ for *Nerodia fasciata* (*TL* 100 cm) and from 0.04 to 0.11 $TL\,\mathrm{s^{-1}}$ for *Elaphe obsoleta* (*TL* 159 cm). Gans and Gasc (1990) found that the center of gravity of the legless lizard *Ophisaurus apodus* (*TL* 91–98 cm) traveled at forward speeds of $0.02\text{--}0.03\ TL\,\mathrm{s^{-1}}$ during concertina locomotion in a stationary tunnel 4 cm wide. Although not all of these previous studies attempted to elicit maximum speeds, it is clear the concertina mode of locomotion is very slow compared to most other modes of limbless locomotion (Jayne, 1986; Gans and Gasc, 1990), and there is no indication that *Coluber constrictor* is less effective at performing this type of movement than are other limbless reptiles.

Relating kinematics to performance

We found that frequency modulation was more important than amplitude modulation for altering forward speed of concertina movement of *C. constrictor*. Only timing variables (Table 1: T_s, and f) and $\bar{V}_m$ were affected significantly by the tread speeds used for the endurance trials; therefore, the significant decreases in endurance observed for all tunnel widths from 4.2 to $4.9\,\mathrm{cm\,s^{-1}}$ (Fig. 2) are associated with kinematic differences related to increased frequency of movement. Because the periodic movements involved in concertina locomotion include stopping, increased f necessarily increases the number of changes in momentum per unit time, and more changes in momentum would be expected to increase energetic requirements, thereby reducing endurance with increased tread speed. Although there are many differences between lateral undulatory locomotion and concertina locomotion, both modes do have significant frequency modulation with speed. Walton *et al.* (1990) found that f of concertina locomotion of *C. constrictor* was 2.4 times that of lateral undulation at the same speed ($\bar{V}_X$=5.6 cm s^{-1}) and

suggested that increased f contributed to the sevenfold increase in net cost of transport of concertina compared to lateral undulatory locomotion.

Besides an increased number of changes in momentum with increased speed, the close association between speed of movement ($\bar{V}_m$) and tread speed suggests that the magnitude of change in momentum within each cycle will also increase with increased $\bar{V}_X$, causing a further expected decrease in endurance. The zone of static contact between the tunnel and the convoluted region of the snake's body (Fig. 5) must generate a sum of lateral and ventral frictional forces sufficient for the snake to overcome the following: (1) an initial static frictional resistance; (2) sliding frictional resistance during movement; and (3) changes in the momentum of the portion of the snake that is being extended forward (Gans, 1974). There are two means of increasing the frictional forces needed in the anchored region: (1) increasing the amount of the snake's mass in static contact with the tunnel and (2) increasing the normal forces applied to the sides either by some combination of applying more force at individual regions of lateral contact with the tunnel or by increasing the number of regions contacting the sides of the tunnel. The latter mechanism would require active muscular effort, and hence would provide another factor contributing to decreased endurance with increased $\bar{V}_X$. The slight increase in N_{static} (Fig. 6A) and decrease in $N_{total} - N_{static}$ (Fig. 4) that occur for fast speeds may support the notion that snakes use the latter mechanism. Presently, no studies have quantified the lateral forces applied to the sides of the tunnel during concertina locomotion, but this would clearly be a productive area for future work.

Many of the mechanical and energetic consequences of decreasing tunnel width are similar to those of increasing tread speed because of the significant increased frequency of movement. However, unlike the effects of changing tread speed, changing tunnel width had highly significant effects on every variable that could be used to quantify the posture of the animals within the tunnels. Significant changes in postural variables (N_{static}, N_{total}, $\bar{\alpha}$, and ΔX) occurred among all three tunnel widths and the direction of change (increase or decrease) for each of these variables was the same going from the 3 to 5 cm and from the 5 to 7 cm tunnel widths. Because there was no significant difference between the endurance of snakes in the 5 and 7 cm tunnel widths, it is clear that changes in body position by themselves are not necessarily sufficient to cause a change in performance (either endurance or burst speed) during concertina locomotion. It was especially surprising to find that the mean endurance of snakes in the 7 cm tunnels was less (though not significantly) than that in 5 cm tunnels, despite the fact that ΔX was greater. Perhaps the theoretical advantages of greater ΔX and lower f are offset by some disadvantages of the 7 cm width. For example, the combination of vertebral length and lengths of axial muscles might be such in *C. constrictor* that considerable muscular effort is required to stiffen the body between successive regions of static contact on opposite sides of the tunnel in order to exert sufficient forces against the walls of the tunnel. It is also not obvious how differences in vertebral flexion and orientation ($\bar{\alpha}$) and lengths of body between successive regions of

lateral static contact might affect the mechanical advantage of the axial muscles both during application of pressure to the sides of the tunnel and during extension of the vertebral column. Jayne (1988) studied the concertina locomotion for snakes of two genera (*Nerodia* and *Elaphe*) that varied greatly in their axial musculature, shape (body width 3.4 cm, *TL* 100 cm *versus* body width 2.0, *TL* 159 cm) and number of body vertebrae (237 *versus* 127) and found that there were statistically significant differences in the postures of animals within tunnels of various widths. Although correlations between the axial anatomy of snakes and specialization in habitat have been described (Gasc, 1974; Jayne, 1982), determining the effects of variation in axial anatomy on performance in other modes of limbless locomotion can be surprisingly difficult (Jayne, 1985; Jayne and Bennett, 1989). The high energetic cost of concertina locomotion (Walton *et al.* 1990) makes it easier for us to detect significant effects of tunnel width on endurance in our study of a single species. Exploiting this fact in future interspecific comparisons of the performance and kinematics of this locomotor mode may greatly facilitate our understanding of the consequences of variation in axial anatomy and kinematics of limbless locomotion.

In a classic study, Gray and Lissmann (1950) measured the forces that a snake exerted against a series of pegs as it crawled (probably by lateral undulation). They found that the ratio of lateral forces to forward forces increased with increased numbers of pivotal points, suggesting that terrestrial lateral undulation with a greater number of waves is less efficient. Gray (1946) also observed that snakes increased the number of flexed regions used during concertina locomotion in tunnels of decreased width, and the present study indicates a clear decrement in endurance associated with the narrowest tunnel used. The extent to which this decreased performance is the consequence of an increased requirement for mechanical work or decreased efficiency remains an open issue. Furthermore, it remains unclear the extent to which one could generalize for diverse modes of limbless locomotion that decreased efficiency occurs with increased numbers of flexions along the animal's body.

List of abbreviations

f	frequency (Hz)
N_{static}	maximum number of simultaneous regions of static contact with the sides of the tunnel
N_{total}	total number of regions of static contact with the sides of the tunnel
PSTAT	proportion of a cycle spent in static contact
T_m	time spent moving (s)
T_s	duration of static contact (s)
T_t	total time for one cycle of movement (s)
TL	total length of snake (cm)

$\bar{V}_m$ mean forward speed for one cycle of movement (cm s^{-1})

$\bar{V}_X$ maximum mean forward velocity for one cycle of movement (cm s^{-1})

ΔX distance traveled forward per cycle of movement (cm)

$\bar{\alpha}$ mean angle between the snake's body and a tangent through the side of the tunnel at the region of static contact (degrees)

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