

# EFFECTS OF INCLINE ON SPEED, ACCELERATION, BODY POSTURE AND HINDLIMB KINEMATICS IN TWO SPECIES OF LIZARD *CALLISAURUS DRACONOIDES* AND *UMA SCOPARIA*

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## Summary

We examined the effects of incline on locomotor performance and kinematics in two closely related species of iguanian lizards that co-occur in sandy desert habitats. *Callisaurus draconoides* differs from *Uma scoparia* of equal snout–vent length by being less massive and having greater limb and tail lengths. We analyzed high-speed video tapes of lizards sprinting from a standstill on a sand-covered racetrack which was level or inclined 30° uphill. *C. draconoides* sprinted significantly faster than *U. scoparia* on both level and uphill sand surfaces, although *U. scoparia* is considered to be more specialized for sandy habitats. Initial accelerations (over the first 50 ms) did not differ significantly either between species or between

inclines within species. Overall, the effects of incline were more pronounced for *C. draconoides* than for *U. scoparia*. For example, the incline caused a significant decrease in the maximum stride length of *C. draconoides* but not in that of *U. scoparia*. For *C. draconoides*, uphill stride durations were significantly shorter than on the level surface, and this partially compensated for the effects of shorter uphill stride lengths on velocity. *C. draconoides* ran bipedally more often than did *U. scoparia* on both the level and uphill surfaces.

Key words: locomotor performance, lizard, kinematics, incline, acceleration, *Callisaurus draconoides*, *Uma scoparia*.

## Introduction

The ability of organisms to sprint quickly may be critically important for effectively capturing prey, escaping predators and defending territories, and lizards have served as a model group for documenting the sprinting capacities of terrestrial vertebrates (Bennett and Huey, 1990; Garland and Losos, 1994; Hertz *et al.* 1988). Several studies have documented the effects of certain environmental variables such as temperature on the sprinting ability of lizards (Bennett, 1982; Marsh and Bennett, 1986). However, one environmental variable that has received relatively little attention, but which may have profound effects on sprinting performance, is incline.

Lizards and other terrestrial limbed organisms live in habitats that vary spatially in incline, but the effects of incline on locomotor performance in tetrapods are poorly understood. Incline and substratum can affect maximal velocity, acceleration and the net cost of transport, but the magnitudes of these effects are often size-dependent (Carothers, 1986; Farley and Emshwiller, 1996; Huey and Hertz, 1982, 1984; Taylor *et al.* 1972). For example, Huey and Hertz (1982) found that inclines caused significant decreases in maximal velocity in large (>40 g) lizards, but that maximal velocity in small lizards was virtually unaffected by incline. Consequently, Huey and Hertz (1984) suggested that small lizards might gain an advantage if they escaped larger predators by sprinting directly up steep inclines.

Explaining the ability of lizards to sprint with equal speeds on level and uphill surfaces poses a challenge. Whether animals alter their limb movements on varying inclines may depend both on the factors that constrain maximal speed and whether the animals run at physiologically maximal speeds. Although several studies have examined correlations between muscle physiology and the maximal running speeds of lizards on level surfaces (Marsh and Bennett, 1985; Swoap *et al.* 1993), the physiological constraints on the sprinting speeds of lizards are still not well understood. Farley and Emshwiller (1996) determined experimentally that the net cost of transport of small lizards moving up a 50° incline nearly doubled compared with values for locomotion on a level surface (see also Taylor *et al.* 1972). Consequently, if a lizard travels with the same average forward velocity and stride length on both inclined and level surfaces, then the energetic cost per stride on the incline must be greater than that on the level surface. If the mechanical work (and energetic cost) per stride constrains maximal speed, then a lizard would have to decrease its stride length in order to attain a maximal speed on an incline identical to that on a level surface. Similarly, if the power (work/time) per stride constrains speed, then modulating stride duration might be a mechanism for compensating for the additional work required to move uphill. Alternatively, if the stride length, stride frequency and forward velocity of lizards

sprinting uphill and on level surfaces are equal, the lizard may not be running at a physiological maximum, or some other factor may constrain speed. For accelerating locomotion, similar logic can be applied, but one must also account for the additional mechanical work required to accelerate the mass of the entire animal forwards. Thus, simultaneously determining kinematics and maximal velocities for lizards sprinting on different inclines provides a test for the hypothesis that lizards can attain equal maximal speeds on inclined and level surfaces by modulating stride length and duration. However, no study of lizards to date has determined whether incline affects limb kinematics.

Although acceleration is potentially important for ectotherms such as lizards that rely on bursts of sprinting to escape predators or capture prey, only Huey and Hertz (1984) have systematically studied acceleration in lizards. Huey and Hertz (1984) found that incline did not greatly affect initial acceleration in either large or small lizards, but they examined only one species. In the light of the morphological diversity among different species of lizards, the generality of Huey and Hertz's (1984) conclusions is unclear.

We examined the effects of incline on maximal velocity, acceleration, body posture and hindlimb kinematics in two lizard species, *Callisaurus draconoides* and *Uma scoparia*. For several reasons, these lizard species provide an excellent opportunity for testing the effects of incline on locomotor performance. First, both species co-occur on sand dunes where the footprints of lizards provide evidence of locomotion on inclines as steep as 30° (Jayne and Ellis, 1998). Second, these two species are closely related (De Queiroz, 1992) and are of similar size, but differ in such aspects of shape as the relative lengths of the limbs and tail (Fig. 1). Finally, the long hindlimbs of *C. draconoides* resemble those of lizard species that frequently run bipedally (Snyder, 1962). Hence, comparing these two species of lizards provides a unique opportunity for understanding whether incline differentially

affects locomotion for species with varying degrees of specializations for bipedality.

For *Callisaurus draconoides* and *Uma scoparia*, we address the following questions. (1) Does incline affect measures of whole-trial performance such as maximum velocity and maximum stride length? (2) How do kinematic variables change as a function of both incline and the successive strides that lizards take as they accelerate from a standstill? Moreover, are similar relationships between incline, stride number and kinematic variables observed in the two species? (3) How is bipedality related to both acceleration and velocity?

### Materials and methods

All data for *Callisaurus draconoides* (Blainville) and all statistical analyses presented are novel. However, to permit interspecific comparisons in the present study, we analyzed some *Uma scoparia* kinematic data (stride length, stride duration, velocity and acceleration) from Jayne and Ellis (1998). Additional kinematic data (stride width, step length and duration, trunk and tail angle, duty factor, occurrence of bipedal strides) and morphometric quantities for *U. scoparia* were determined in the present study.

### Study animals

We collected lizards during September 1996 from the Kelso dune system of the Mojave desert, located approximately 13 km southwest of Kelso in San Bernadino County, California, USA. Lizards were maintained individually in 72 cm × 72 cm (length × width) cages and provided with food (crickets and mealworms dusted with vitamin powder) 3–4 times weekly and water *ad libitum*. Incandescent light bulbs in the cages allowed the lizards to thermoregulate. After sprinting trials were completed, we analyzed data for seven lizards from each species that ran well on both level and uphill surfaces, and for which the first five strides of uphill and level trials were visible in the video tapes, as was necessary for a balanced experimental design. Values of snout–vent length (SVL) for *C. draconoides* and *U. scoparia* varied from 5.8 to 8.0 cm (mean ± s.d., 7.1 ± 0.86 cm) and from 6.3 to 7.9 cm (7.3 ± 0.08 cm), respectively. Because the two species do not differ significantly in SVL (unpaired *t*-test, *t* = 0.60, 12 d.f., *P* > 0.2), we did not adjust for effects of body size in statistical analyses. The masses of *C. draconoides* and *U. scoparia* varied from 4.3 to 10.7 g (7.8 ± 2.45 g) and from 8.4 to 21.1 g (13.1 ± 4.20 g), respectively.

### Laboratory performance trials

We elicited sprinting of lizards from a standstill on a 3 m long and 25 cm wide racetrack covered with a 1 cm layer of fine sand (passed through a 0.5 mm sieve), which was similar to sand observed in the natural habitat of both lizard species. The sides of the track were 25 cm high. The wall facing the video cameras was clear acrylic, and the back wall was painted with 10 cm reference lines. Four 500 W lights, approximately 1 m above the track, provided illumination. The far end of the

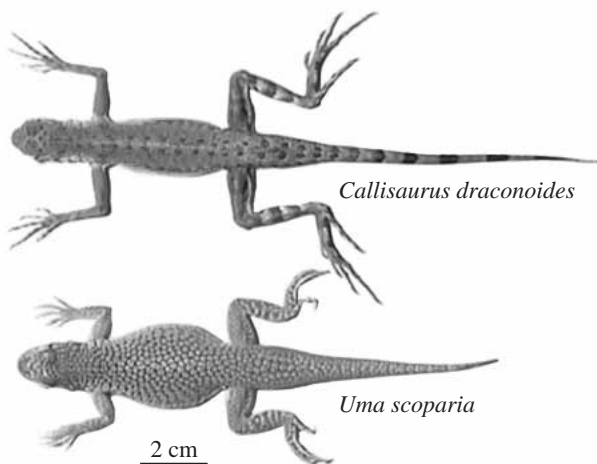


Fig. 1. Anesthetized adult specimens of *Callisaurus draconoides* (SVL 7.1 cm, mass 7.9 g) and *Uma scoparia* (SVL 7.0 cm, mass 10.7 g).

track contained a shelter constructed from black paper which resembled burrows used by the lizards in nature. We used two high-speed NAC HSV-500 video cameras to obtain lateral views (at 250 images s<sup>-1</sup>) of the lizards. The width of the view of each camera was 80 cm with a 10 cm region of overlap between the two images, giving a cumulative length of 150 cm in the middle of the track that was video-taped. After each trial, we used a 35 mm still camera mounted directly above the middle 1.5 m portion of the track to obtain photographs of footprints in the sand.

Prior to each trial, lizards were placed into standard-sized (5 gallon) containers with overhanging lights that raised their body temperature to 38–42 °C, which is a similar range to field active body temperatures measured while collecting the specimens (*C. draconoides*:  $N=5$ , mean  $\pm$  S.D., 38.8 $\pm$ 2.2 °C; range 36–42 °C; *U. scoparia*,  $N=22$ , mean  $\pm$  S.D., 39.7 $\pm$ 2.8 °C; range, 34.3–45.1 °C; *U. scoparia* data taken from Jayne and Ellis, 1998). For both level and uphill trials, we induced each lizard to run two or three times in rapid succession on each of two consecutive days by rapidly attempting to tap their hindquarters, and the horizontal and uphill trials began 2 and 6 days, respectively, after lizards were captured in the field. Thus, each lizard ran a total of 4–6 times on both the level and uphill surfaces.

Time is potentially a confounding factor in our experimental design, but at least the time between the level and uphill trials was minimal (4 days). Randomizing trials with regard to time would have extended the numbers of days required to finish the tests because of the logistics of, for instance, realigning the racetrack and cameras and heating the lizards. We were most concerned with minimizing the total time between the capture of the lizard and the last trial. Only healthy lizards (i.e. none with a shrunken tail base) were used in sprinting trials, and only lizards that ran well at least once on both level and uphill surfaces were included in analyses. For inclusion in the final statistical analyses, a trial needed to have the first five strides visible in the video tapes to give a balanced experimental design, and we analyzed only the best trial for each individual (longest stride length) on the level and uphill surfaces. We excluded trials from analyses if lizards brushed against the walls, or ran from side to side, as these situations could alter limb kinematics and complicate the determination of forward displacement from a lateral view.

#### Measurements

To elucidate morphological differences between *C. draconoides* and *U. scoparia*, we measured the following morphological variables on a series of preserved and/or anesthetized male and female specimens, some of which were used in performance trials: SVL, body mass, lengths of the tail, femur, tibia, hindfoot (from the heel to the distal end of the fourth metatarsal), fourth toe of the hindfoot, humerus, ulna and forefoot. The length of the forefoot was measured from the wrist to the base of the claw on the fourth toe. We also measured the distance between the right and left sides of the pelvis where the ilia protrude dorsally and most superficially.

Morphological measurements of the limbs were made on the right side of each lizard from the ventral view using calipers accurate to 0.1 mm.

We analyzed video images using custom-designed computer software. For each trial, we digitized the  $x$  and  $y$  coordinates of the snout at the starting time [one video image (4 ms) before the first perceptible movement] and at each successive time of the beginning and end of contact of the right hindfoot. From the  $x$  coordinates (the  $x$  axis was parallel to the long axis of the track) and the times of foot contact, we calculated the following variables: (1) stride length (distance traveled between successive footfalls), (2) stride duration, (3) step length (distance traveled while the foot contacts the ground), (4) step duration, and (5) duty factor (step duration/stride duration). At the start and at subsequent times of each right hind footfall, we determined the angles of the trunk and tail relative to the locomotor surface. We calculated angles from the digitized  $x$  and  $y$  coordinates of three points along the mid-dorsal line: near the right shoulder, near the right ilium, and on the tail approximately one snout–vent length from the base of the tail. Trunk angle was the angle between the locomotor surface and the line joining the shoulder and ilium points (positive values mean that the anterior trunk is oriented upwards); tail angle was the angle between the locomotor surface and the line joining the tail and pelvic points (positive values mean that the posterior tail is oriented upwards). We categorized a stride as quadrupedal when either forelimb touched the ground at any time during a stride, or as bipedal when neither forelimb touched the ground during a stride. Finally, we traced images from footprints in the sand from 35 mm photographs that we projected to 75–100% of life size. On each tracing, we measured the perpendicular distance (stride width) between the centroid of the left hind footprint and the line connecting the centroids of successive right hind footprints. We also expressed stride width as a percentage of stride length.

To calculate the acceleration for each trial, we first digitized the  $x$  coordinate of the snout at the starting point, then at 8 ms intervals for the first 80 ms, and then at 16 ms intervals for the remainder of the images in each trial. We then standardized forward displacements and times so that initial values were zero. The resulting values were fitted to equation 1 of Huey and Hertz (1984):

$$s = V_m[t - 1/k + (1/k)e^{-kt}], \quad (1)$$

where  $s$  is forward displacement (m),  $V_m$  is maximum forward velocity (m s<sup>-1</sup>),  $t$  is time (s) and  $k$  is a constant. The first and second derivatives of this function provide functions for forward velocity and acceleration, respectively.

#### Statistical analyses

For all analyses, we used SYSTAT 5.0 (Wilkinson, 1992), and  $P < 0.05$  was the primary criterion for statistical significance for all analyses. In tabular summaries of statistics, we provide relevant details such as degrees of freedom and exact values of statistical variables to clarify the magnitude of statistical differences and the potential effects of multiple comparisons.

All morphological measurements were  $\log_{10}$ -transformed before calculating least-squares regressions. We calculated least-squares regressions separately for each species to describe the scaling relationships of morphology. For the combined morphological data of both species, we also calculated least-squares regressions (using  $\log_{10}SVL$  as the independent variable) to generate residual values, which were then tested for interspecific differences using one-way analyses of variance (ANOVAs).

Because performance trials involved acceleration from a standstill, we were interested in how kinematics varied with each successive stride. Consequently, we used stride number as a fixed, crossed factor in the following analyses of variance (with the exception of the two-way ANOVA). To avoid missing cells in our experimental design, we restricted ANOVAs involving stride number ( $N=5$ ) to the first five strides of each trial. The first stride within a trial was designated as stride number one. Additional factors in our ANOVAs were incline ( $N=2$ ) and species ( $N=2$ ), which were both treated as fixed crossed factors. Our experimental design also involved repeated observations within each of the seven individuals per species, and we accounted for this by including individual as a random factor in the ANOVAs. Because of the difficulty of interpreting a four-way ANOVA involving species, incline, stride number and individuals, we first performed separate three-way ANOVAs within each of the two species to clarify whether incline and stride number had significant effects on kinematics and whether some of the effects on kinematics were interactive. To provide an overall test of whether the kinematics of each stride varied between species, we performed four-way ANOVAs with species, incline, stride number and individuals nested within species as the independent categorical variables. Finally, to elucidate incline and species effects on whole-trial performance traits (e.g. the maximum stride length *within* a trial), we performed ANOVAs with species and incline as fixed crossed factors and individual as a nested factor within species.

For these mixed-model three- and four-way ANOVAs, we used Scheffe (1959) to determine the appropriate ratios of mean square values needed to perform the appropriate  $F$ -test. Because of the lack of replication within each cell of our experimental design, we could not test the statistical significance of every effect, especially those terms involving the individual factor. However, we were primarily interested in controlling for individual variation while testing for other main effects and key interaction terms.

## Results

### Morphology

The scaling relationships in Table 1 confirm that *U. scoparia* is stocky compared with *C. draconoides* (Fig. 1). ANOVAs of residual values indicated that *C. draconoides* had lower mass ( $P=0.003$ ), narrower pelvic width ( $P=0.043$ ) and longer tarsal length ( $P=0.004$ ) than *U. scoparia*; for the remainder of the morphological variables listed in Table 1, residual values of *C. draconoides* exceeded those of *U. scoparia* by highly significant amounts ( $P<0.001$ ). On the basis of scaling equations, compared with *U. scoparia* with an  $SVL$  of 7.5 cm, *C. draconoides* has 23% less mass, 27% longer hindlimbs, 19% longer forelimbs, a 23% longer tail and a 43% longer fourth toe.

### Whole-trial performance

There was a significant interactive effect of species and incline on maximum stride length (Table 2), indicating that maximum stride length of *C. draconoides* decreased on the uphill surface, whereas that of *U. scoparia* was unaffected by incline. Similarly, mean stride duration of *C. draconoides* but not that of *U. scoparia* decreased when running uphill compared with the level surface (Table 2). *C. draconoides* had significantly greater maximum velocities than *U. scoparia* (Table 2) on both level and uphill surfaces. Initial accelerations (at 0.05 s) did not differ significantly between species on either

Table 1. Least-squares regression statistics relating  $\log_{10}$ -transformed body size variables to  $\log_{10}SVL$  in *Uma scoparia* ( $N=17$ ) and *Callisaurus draconoides* ( $N=15$ )

Variable	<i>C. draconoides</i>			<i>U. scoparia</i>		
	Slope	y-intercept	$r^2$	Slope	y-intercept	$r^2$
Body mass (g)	3.27±0.61	-1.91±0.52	0.78	3.26±0.12	-1.79±0.10	0.98
Tail length (cm)	0.63±0.14	0.42±0.11	0.73	0.91±0.05	0.09±0.04	0.97
Pelvic width (cm)	1.60±0.24	-1.51±0.20	0.77	1.32±0.10	-1.23±0.09	0.92
Femur length (cm)	1.08±0.12	-0.67±0.10	0.86	1.10±0.04	-0.76±0.04	0.98
Tibia length (cm)	0.88±0.10	-0.44±0.08	0.86	0.96±0.04	-0.62±0.04	0.97
Tarsal length (cm)	0.88±0.26	-0.72±0.22	0.47	0.92±0.07	-0.83±0.06	0.92
Fourth toe length (cm)	0.78±0.21	-0.40±0.18	0.52	0.57±0.04	-0.37±0.04	0.93
Humerus length (cm)	1.05±0.09	-0.76±0.08	0.91	0.93±0.04	-0.72±0.03	0.98
Ulna length (cm)	1.09±0.11	-0.85±0.09	0.88	1.16±0.05	-0.97±0.04	0.98
Forefoot length (cm)	0.63±0.11	-0.38±0.09	0.71	0.86±0.11	-0.68±0.10	0.80

Values are means  $\pm$  1 S.E.M.  
For all regressions,  $P<0.005$ .

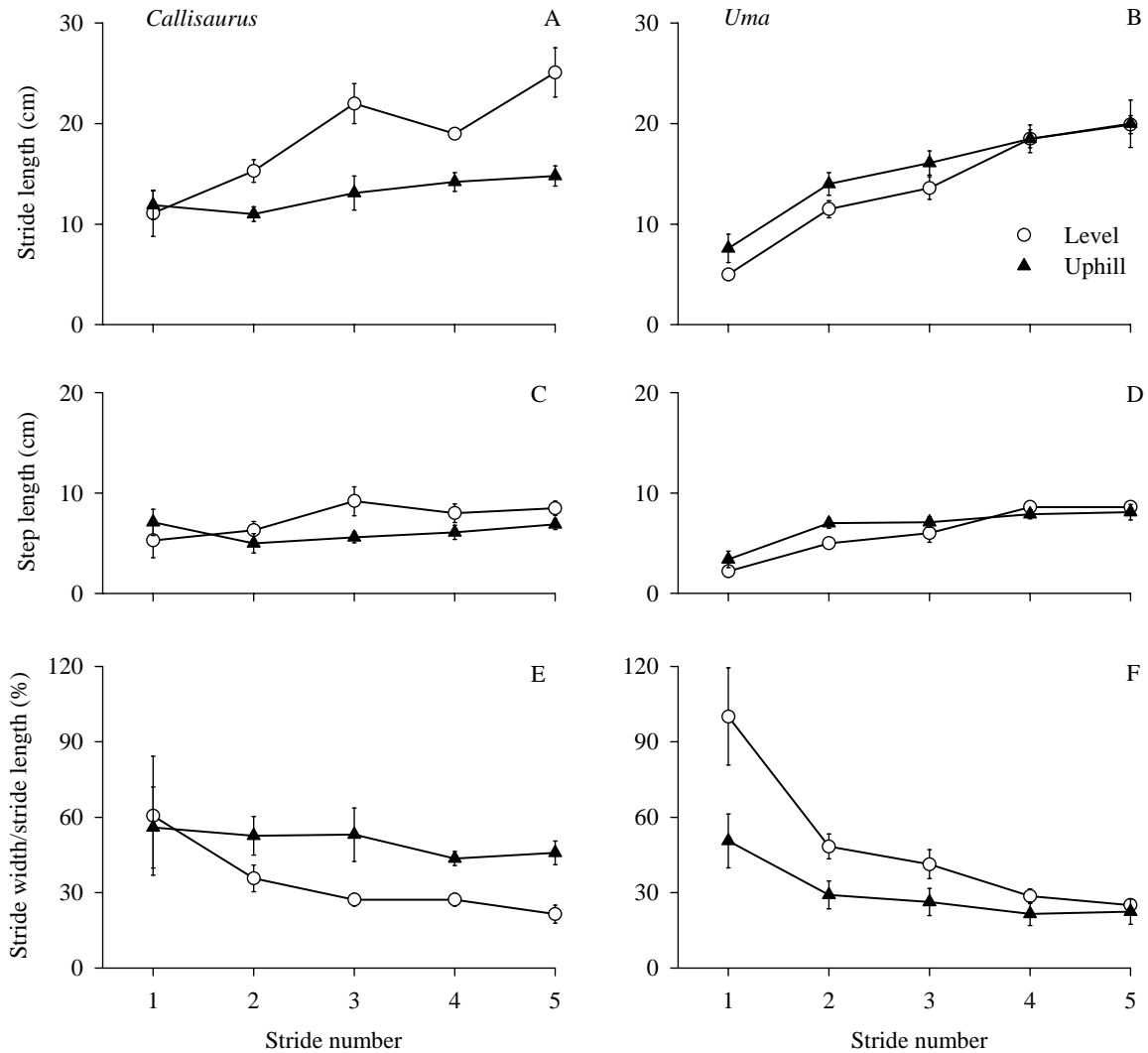


Fig. 2. Mean stride length (A,B), step length (C,D) and stride width/stride length (%) (E,F) versus stride number for *Callisaurus draconoides* (A,C,E) and *Uma scoparia* (B,D,F) during level (open circles) and uphill (filled triangles) locomotion. Lines connect mean ( $\pm$  S.E.M.) values.  $N=7$  for each species.

the level or uphill surfaces, but the acceleration of *C. draconoides* at 0.20 s was significantly greater than that of *U. scoparia*. The significant difference between species in the constant  $k$  (see equation 1) of the displacement function (Table 2) indicates that, compared with *U. scoparia*, the acceleration of *C. draconoides* declined less quickly with time on both the level and uphill surfaces.

#### Changes in stride patterns

As both species accelerated from a standstill, the average length of each successive stride increased significantly (Table 3; Fig. 2A,B). For both species on the level surface, the fifth stride was usually more than twice as long as the first stride (Fig. 2A,B). Stride number, incline and species interacted in a complex way. For example, in *C. draconoides*, the lengths of the first five strides on the incline were generally substantially shorter than those on the level surface (Table 3; Fig. 2A). However, the difference between stride lengths on

level and uphill surfaces also increased with each successive stride (Table 3, incline  $\times$  stride number interaction term). In *U. scoparia*, neither incline nor the incline  $\times$  stride number interaction term significantly affected stride length. A four-way ANOVA revealed no overall difference in stride length between the two species (Table 4), but both the species  $\times$  incline and species  $\times$  stride number interaction terms were significant. Step length increased significantly with stride number for *U. scoparia* but not for *C. draconoides* (Table 3; Fig. 2C,D), and this resulted in a significant species  $\times$  stride number effect in the four-way ANOVA (Table 4).

Stride width was effectively constant within each species regardless of stride number and incline. Because of the increase in stride length with successive strides, stride width expressed as a percentage of stride length decreased significantly with each successive stride within both species (Table 3; Fig. 2E,F). Within *U. scoparia*, the decrease in this variable was more rapid on the level surface than on the uphill surface (Fig. 2F).

Table 2. Mean values of whole-trial performance for *Callisaurus draconoides* running on a level and a 30° uphill surface

	<i>C. draconoides</i>		F-values		
			Species	Incline	Species× incline
	Level	30°	1,12 d.f.	1,12 d.f.	1,12 d.f.
Maximum stride length (cm)	30.4±1.1 (24.7–33.0)	22.5±1.3 (18.4–27.8)	3.5	24.6**	15.9*
Mean stride duration (ms)	88±4.4 (78–107)	71±2.8 (60–79)	0.6	5.2*	19.7**
Maximum velocity (m s <sup>-1</sup> )	3.54±0.17 (3.05–4.35)	3.17±0.16 (2.64–3.65)	13.1*	1.7	1.1
V <sub>m</sub> (m s <sup>-1</sup> )	3.15±0.08 (2.87–3.46)	3.19±0.42 (2.46–5.43)	2.3	1.1	0.7
k	8.60±1.25 (4.59–12.4)	7.28±1.38 (1.73–13.2)	6.9*	0.3	0.0
V at 0.05 s (m s <sup>-1</sup> )	1.08±0.14 (0.67–1.48)	0.84±0.10 (0.45–1.28)	1.2	2.5	0.0
V at 0.20 s (m s <sup>-1</sup> )	2.49±0.18 (1.95–3.09)	2.07±0.10 (1.59–2.46)	0.2	4.0	0.2
V at 0.40 s (m s <sup>-1</sup> )	2.97±0.11 (2.73–3.42)	2.63±0.10 (2.38–3.15)	1.3	4.4	0.0
a at 0.05 s (m s <sup>-2</sup> )	17.0±1.7 (11.9–22.1)	13.6±1.1 (8.6–18.1)	0.1	2.4	0.2
a at 0.20 s (m s <sup>-2</sup> )	4.7±0.4 (3.3–6.0)	4.7±0.6 (2.5–7.0)	5.5*	0.0	0.0
a at 0.40 s (m s <sup>-2</sup> )	1.1±0.3 (0.3–2.4)	1.6±0.6 (0.2–4.7)	3.1	0.0	0.8

Values are means ± 1 S.E.M. Range is given in parentheses.

For *C. draconoides*,  $N=6$  for all values resulting from curve-fitting ( $a$  and  $V$  values) for the level trials, and  $N=7$  for all remaining variables. Data analyzed for *U. scoparia* were from seven of the eight animals in Jayne and Ellis (1998).

\* $P<0.05$ , \*\* $P<0.001$ .

Maximum velocity and maximum stride length were single values per trial, whereas mean stride duration was calculated from all visible strides within each trial.

$a$  at 0.05 s,  $a$  at 0.20 s,  $a$  at 0.40 s, accelerations measured over 0.05 s, 0.20 s and 0.40 s, respectively;  $k$ , constant in equation 1;  $V$  at 0.05 s,  $V$  at 0.20 s,  $V$  at 0.40 s, velocities measured over 0.05 s, 0.20 s and 0.40 s, respectively;  $V_m$ , maximum forward velocity parameter in equation 1.

F-values are from an ANOVA (factors: species, incline, individual nested within species) comparing level and uphill performance of *C. draconoides* and *U. scoparia*.

Table 3. F-values from three-way ANOVAs performed separately for *Callisaurus draconoides* and *Uma scoparia* for each variable

Variable	<i>C. draconoides</i>			<i>U. scoparia</i>		
	Incline (1,6)	Incline× stride		Incline (1,6)	Incline× stride	
		Stride (4,24)	stride (4,24)		Stride (4,24)	stride (4,24)
Stride length	25.8*	15.1**	3.5*	2.2	33.7**	2.3
Step length	2.2	1.4	1.5	2.4	30.4**	5.2*
Stride width/ stride length	4.3	3.2*	0.5	11.6*	12.1**	4.4*
Stride width	3.9	1.7	1.7	0.5	1.3	0.5
Stride duration	6.2*	9.4**	0.7	8.3*	0.9	0.8
Step duration	0.3	20.4**	0.7	0.7	2.4	1.7
Duty factor	1.4	9.3**	0.4	1.1	5.4*	0.9
V <sub>stride</sub>	5.1	67.2**	4.7*	0.3	56.2**	1.3
Trunk angle	3.5	8.2**	5.8*	2.8	4.2*	1.0
Tail angle	7.3*	0.8	1.7	0.0	1.4	1.2
Predicted acceleration	0.5	127.0**	1.2	4.6	41.7**	1.9

\* $P<0.05$ , \*\* $P<0.001$ .

Predicted accelerations were calculated from force-displacement curves (see equation 1).

V<sub>stride</sub>, stride length/stride duration.

Main effects and interaction terms are listed above each column.

Degrees of freedom are given in parentheses.

Table 4. F-values from four-way ANOVAs performed separately on each variable

Variable	Incline (1,12)	Stride (4,48)	Species (1,12)	Species× Species× incline× stride		
				incline (1,12)	stride (4,48)	stride (4,48)
Stride length	7.5*	45.1**	2.2	22.6**	4.5*	2.5
Step length	0.4	14.0**	0.8	4.2	6.0**	1.4
Stride width/ stride length	0.5	13.9**	0.2	9.8*	1.3	0.1
Stride width	2.1	2.7*	1.4	5.0*	0.2	0.7
Stride duration	0.2	3.7*	0.1	13.4*	7.2**	0.1
Step duration	0.1	19.7**	0.3	0.9	7.5**	0.5
Duty factor	0.0	14.0**	0.6	2.6	1.1	0.5
V <sub>stride</sub>	5.2*	122.2**	3.5	3.1	1.3	2.3
Trunk angle	0.0	10.4**	0.2	6.2*	1.4	5.2*
Tail angle	4.3	1.7	0.9	3.9	0.8	2.4
Predicted acceleration	1.7	90.2**	0.1	3.3	1.0	0.1

\* $P<0.05$ , \*\* $P<0.001$ .

Predicted accelerations were calculated from force-displacement curves (see equation 1).

V<sub>stride</sub>, stride length/stride duration.

Main effects and interaction terms are listed above each column.

Degrees of freedom are given in parentheses.

The four-way ANOVA confirmed that the effects of incline on stride width/stride length were species-dependent (Table 4).

In *C. draconoides*, stride durations decreased significantly with stride number on both level and uphill surfaces, and stride duration also decreased significantly on the uphill surface (Table 3; Fig. 3A). For *U. scoparia*, stride durations were constant for each surface (Table 3; Fig. 3B), although stride duration increased significantly on the uphill relative to the level surface. Consequently, the effects of both incline and stride number on stride duration were species-dependent (Table 4). Variation in step duration was generally similar to that observed for stride duration, but step duration was unaffected by incline for each species (Table 3; Fig. 3C,D). Both species showed similar patterns of variation in duty factor, which decreased significantly with stride number, but was unaffected by incline (Table 3; Fig. 3E,F).

*Velocity and acceleration*

$V_{\text{stride}}$  (stride length/stride duration) showed a significant

positive relationship with stride length during both uphill and level locomotion in *C. draconoides* (Fig. 4). However, the correlation between  $V_{\text{stride}}$  and stride length was much higher during level trials than during uphill trials, probably as a result of a greater range of stride lengths obtained during level trials. Analysis of covariance showed that neither regression slopes ( $F_{1,93}=0.04, P>0.75$ ) nor y-intercepts ( $F_{1,94}=0.003, P>0.75$ ) were significantly different between *U. scoparia* and *C. draconoides* on the level surface. On the uphill surface, regression slopes did not differ between *U. scoparia* and *C. draconoides* ( $F_{1,95}=0.88, P>0.25$ ), but the y-intercept for *C. draconoides* was significantly greater than that for *U. scoparia* ( $F_{1,96}=21.35, P<0.001$ ).

For both species, there was a highly significant, nearly threefold increase in  $V_{\text{stride}}$  from the first to the fifth stride (Table 3; Fig. 5). Within *C. draconoides*, the increase in  $V_{\text{stride}}$  with increased stride number depended on incline (Table 3; Fig. 5); initial values of  $V_{\text{stride}}$  on the level and uphill surfaces were similar but the later strides on the incline were slower.

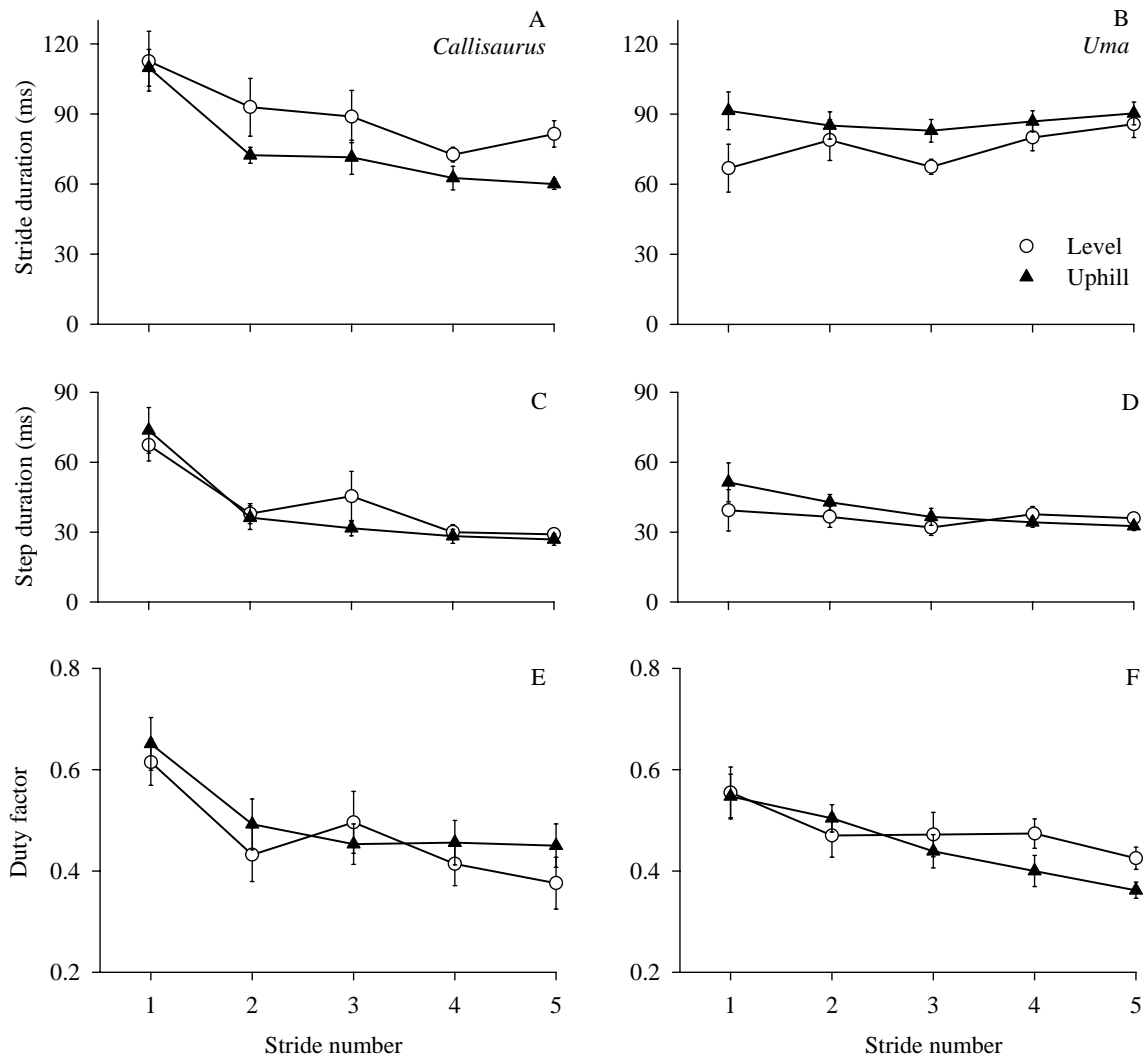


Fig. 3. Mean stride duration (A,B), step duration (C,D) and duty factor (E,F) versus stride number for *Callisaurus draconoides* and *Uma scoparia* during level (open circles) and uphill (filled triangles) locomotion. Lines connect mean ( $\pm$  S.E.M.) values.  $N=7$  for each species.

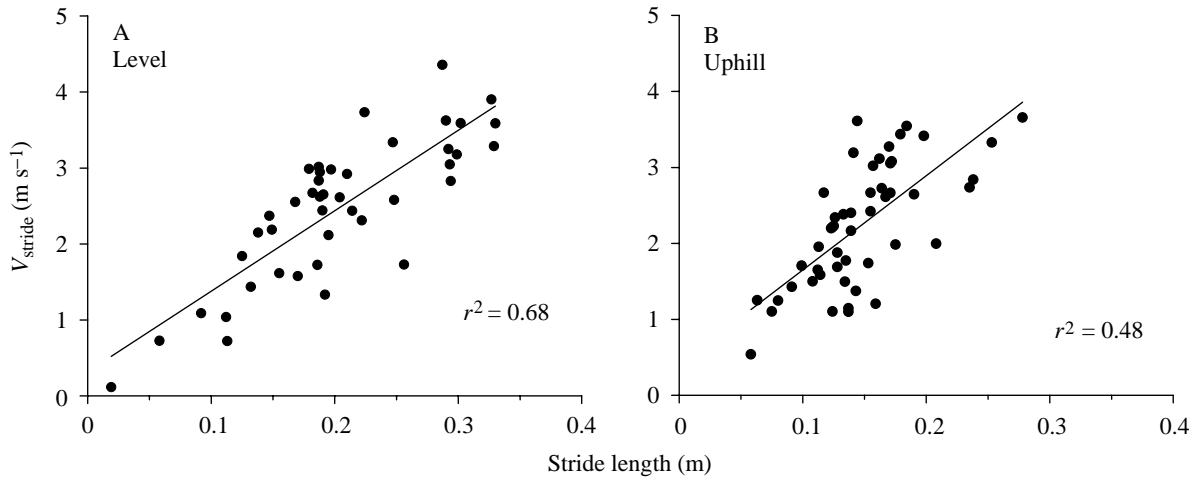


Fig. 4.  $V_{\text{stride}}$  (stride length/stride duration) versus stride length during (A) level ( $N=43$ ,  $y=10.58x+0.32$ ,  $r^2=0.68$ ,  $P<0.001$ ) and (B) uphill ( $N=50$ ,  $y=12.40x+0.41$ ,  $r^2=0.48$ ,  $P<0.001$ ) locomotion in *Callisaurus draconoides*. Least-squares regression lines are shown. See Jayne and Ellis (1998) for regression lines for *Uma scoparia*.

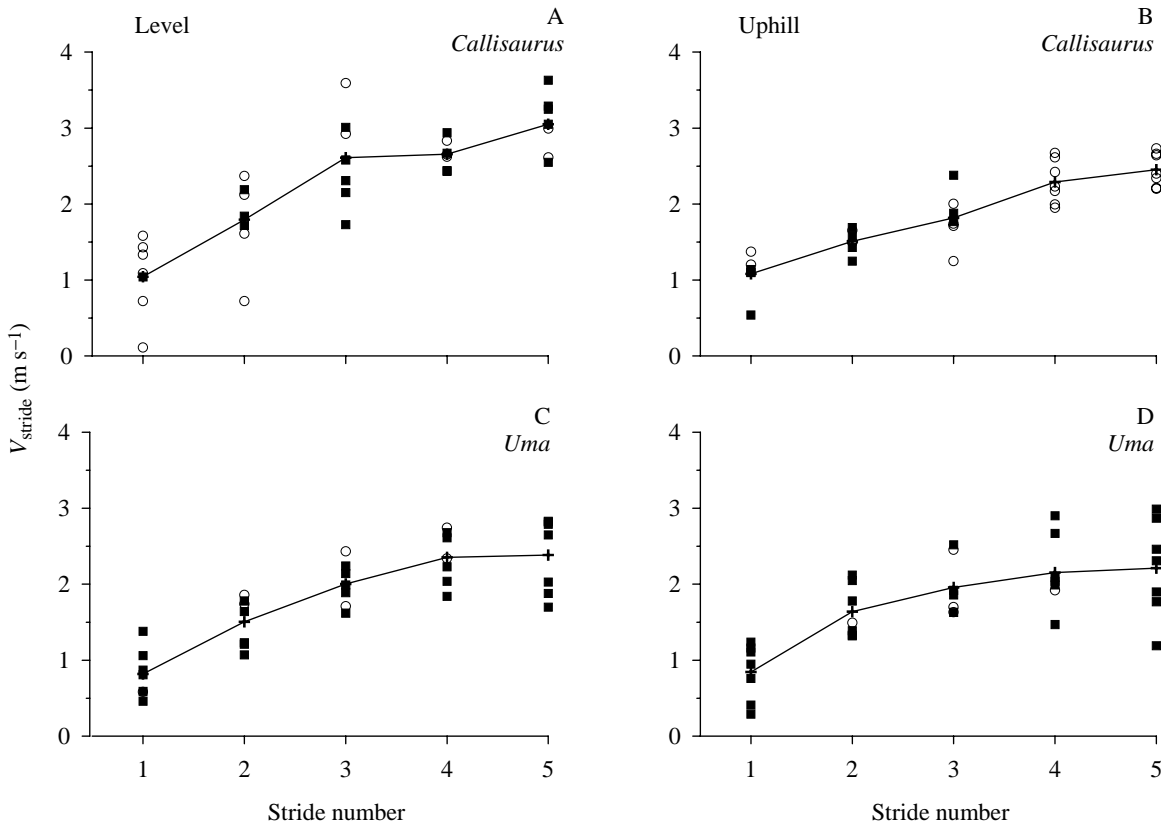


Fig. 5.  $V_{\text{stride}}$  (stride length/stride duration) versus stride number during level (A,C) and uphill (B,D) locomotion in *Callisaurus draconoides* (A,B) and *Uma scoparia* (C,D). Each point is a value for a single stride of one lizard. Lines connect mean values for each stride number. Open circles represent bipedal locomotion; filled squares represent quadrupedal locomotion.

Analysis of covariance revealed that the slopes of the relationships between  $V_{\text{stride}}$  (dependent variable) and stride length (independent variable) were not significantly different within *C. draconoides* between level and uphill surfaces ( $F_{1,89}=0.73$ ,  $P>0.30$ ), but that the uphill regression line had a

significantly greater y-intercept ( $F_{1,90}=9.0$ ,  $P<0.005$ ). Thus,  $V_{\text{stride}}$  tends to be greater for equivalent stride lengths on the uphill surface compared with the level surface in this species.

In general, the exponential model of displacement as a function of time (Huey and Hertz, 1984) fitted the actual



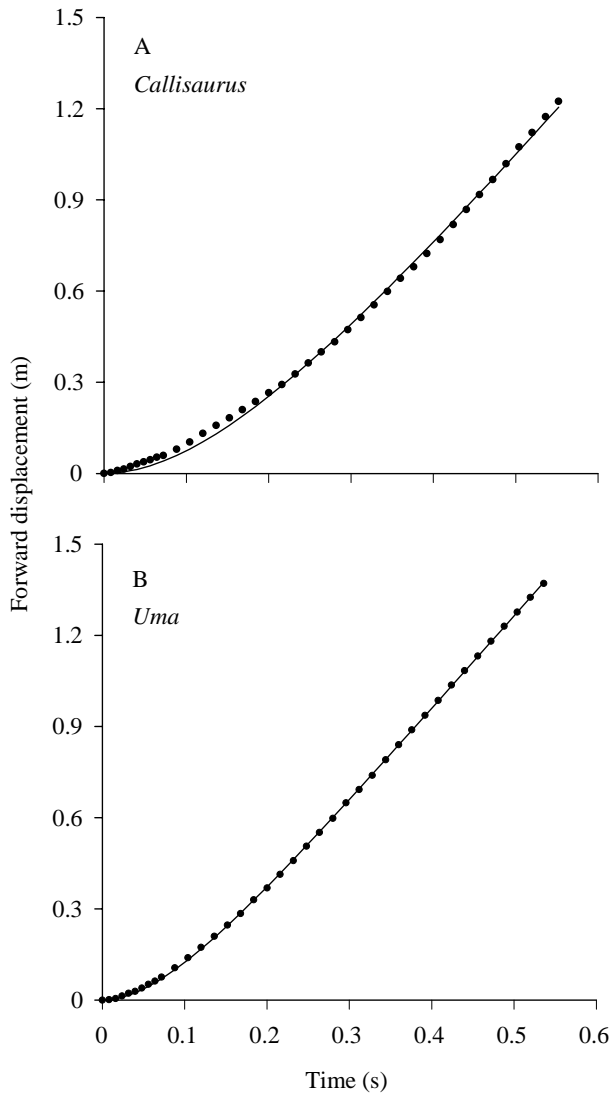


Fig. 6. Forward displacement *versus* time for level locomotion in *Callisaurus draconoides* (A) (maximum forward velocity,  $V_m=3.13\text{ m s}^{-1}$ ,  $k=5.74$ , see equation 1) and *Uma scoparia* (B) ( $V_m=3.06\text{ m s}^{-1}$ ,  $k=11.47$ ). Raw data are plotted with curves fitted to the data using equation 1.

forward displacement data well (Fig. 6). For both species, acceleration on both level and uphill surfaces decreased significantly with successive strides (Fig. 7; Tables 3, 4). The model that we used to calculate acceleration involves an exponential decay over time. Certain features of Fig. 7 are consistent with the significant variation found in stride duration between species and between inclines (Table 3). For example, *U. scoparia* had longer stride durations on the uphill than on the level surface; hence, the acceleration calculated at the end of the first stride on the uphill surface is for a greater elapsed time than that of the first stride on the level, giving a lower value of acceleration at this point.

#### Body and tail posture

Within both species, trunk angle varied significantly with

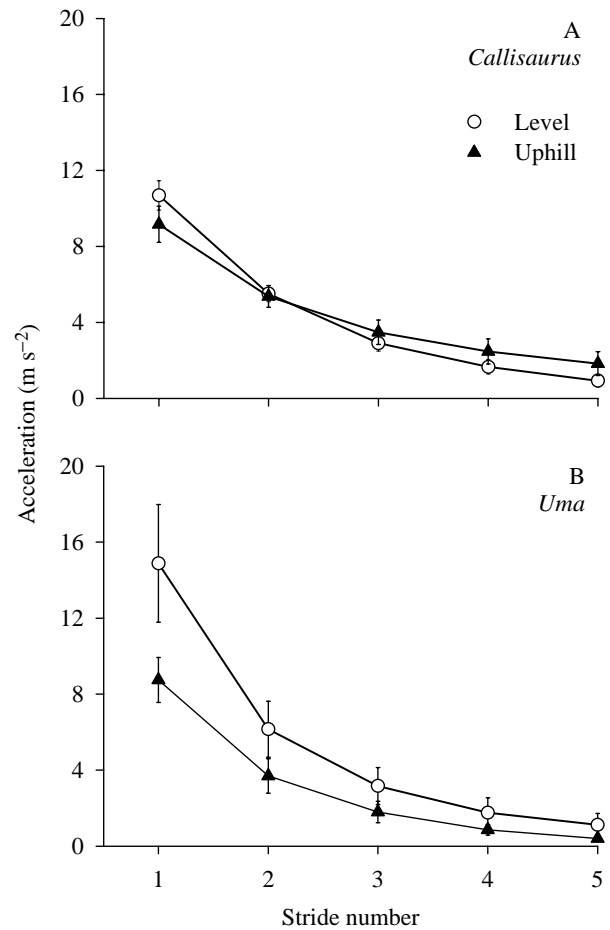


Fig. 7. Mean accelerations (predicted from fitting to equation 1) *versus* stride number in *Callisaurus draconoides* (A) and *Uma scoparia* (B) during level (open circles) and uphill (filled triangles) locomotion.

stride number (Table 3) such that the lowest values were consistently for the latest strides (Fig. 8). Within *C. draconoides*, changes in trunk angle with stride number were also incline-dependent (Table 3), with values showing a very regular pattern of decrease on the level but not on the uphill surface. Overall, trunk angle did not differ significantly between species in a simple fashion, but a significant interactive effect of species and incline on trunk angle existed (Table 4).

Tail angle within *C. draconoides* varied significantly with incline (Table 3) such that values in uphill trials were greater than those on the level surface (Fig. 9A,B). Despite the lack of a statistically significant effect of stride number on the tail angle of this species, the first strides on the level surface tended to have high values (Fig. 9A). In contrast, there were no statistically significant effects of either incline or stride number on tail angle in *U. scoparia* (Table 3).

#### Bipedality

For the total of 35 strides, five strides by each of seven individuals examined for *C. draconoides*, 49% and 66% were

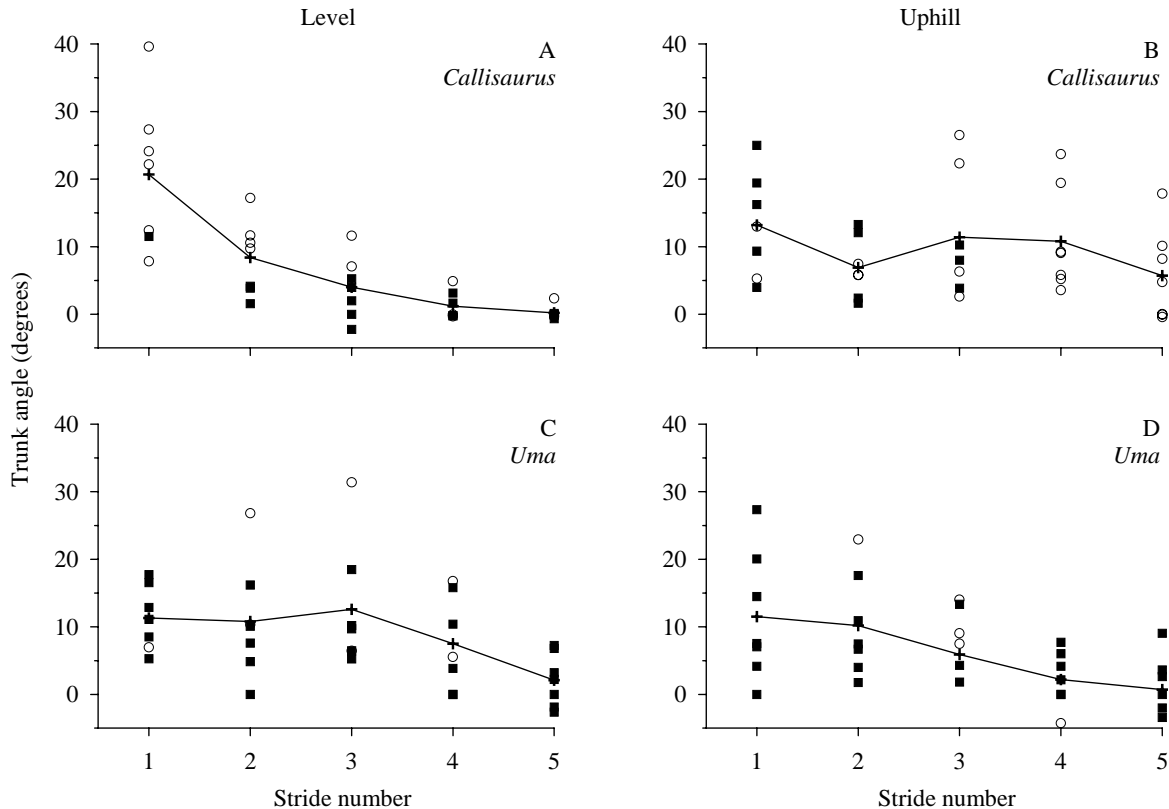


Fig. 8. Trunk angle *versus* stride number during level (A,C) and uphill (B,D) locomotion in *Callisaurus draconoides* (A,B) and *Uma scoparia* (C,D). Each point represents an individual stride of each lizard. Lines connect mean values for each stride number. Open circles represent bipedal locomotion; filled squares represent quadrupedal locomotion.

bipedal on the level and uphill surfaces, respectively, whereas for *U. scoparia*, these quantities were only 20% and 14%, respectively. For *C. draconoides* during level trials, bipedal running was most common in the first few strides. In contrast, for the uphill trials in *C. draconoides*, the occurrence of bipedal running increased with stride number to the point where all of the fourth and fifth strides were bipedal (Fig. 10A). The occurrence of bipedality in *U. scoparia* tended to increase initially and then decline with successive strides for both level and uphill surfaces (Fig. 10B).

Because many kinematic variables covaried with increasing stride number, we examined qualitatively whether the kinematics of bipedal and quadrupedal strides differed for a particular stride number. For a particular stride number, the speeds of bipedal and quadrupedal strides were similar within both species (Fig. 5). For trunk angle, the most apparent difference between bipedal and quadrupedal strides was that in *C. draconoides* on the level surface at a particular stride number, bipedal strides consistently had the greatest trunk angles (Fig. 8A). For *U. scoparia* on the level surface, the single greatest trunk angle within strides 2, 3 and 4 was for a bipedal stride; however, not all of the bipedal strides clustered together within each stride number (Fig. 8C). For the uphill trials of both species, trunk angle had no obvious association with bipedality at a particular stride number (Fig. 8B,D), and tail angle lacked any regular pattern of

variation for bipedality in any of the experimental conditions (Fig. 9).

A different approach is to ignore any confounding effects of stride number and determine whether a kinematic quantity was correlated with bipedality regardless of stride number. To do this we encoded bipedal strides as 1 and quadrupedal strides as 0, and then calculated Pearson product-moment correlation coefficients ( $r$ ) between this quantity and the kinematic variable of interest. For *C. draconoides* during level trials (Fig. 8A), there was a significant positive correlation ( $r=0.56$ , 33 d.f.,  $P<0.002$ ) between bipedality and trunk angle, whereas these quantities were not significantly correlated for the uphill trials ( $r=-0.08$ , 33 d.f.,  $P>0.70$ ). For *U. scoparia* during level locomotion, bipedality and trunk angle were significantly positively correlated ( $r=0.40$ , 33 d.f.,  $P<0.025$ ), whereas these two quantities were not significantly correlated during uphill locomotion ( $r=0.19$ , 33 d.f.,  $P>0.20$ ).

### Discussion

Compared with similarly sized *U. scoparia*, the longer-limbed *C. draconoides* attained faster maximal speeds both on the level and uphill. The stride lengths of *C. draconoides* decreased significantly when running uphill, whereas the stride lengths of *U. scoparia* were unaffected by incline. On the uphill surface, *C. draconoides* partially compensated for

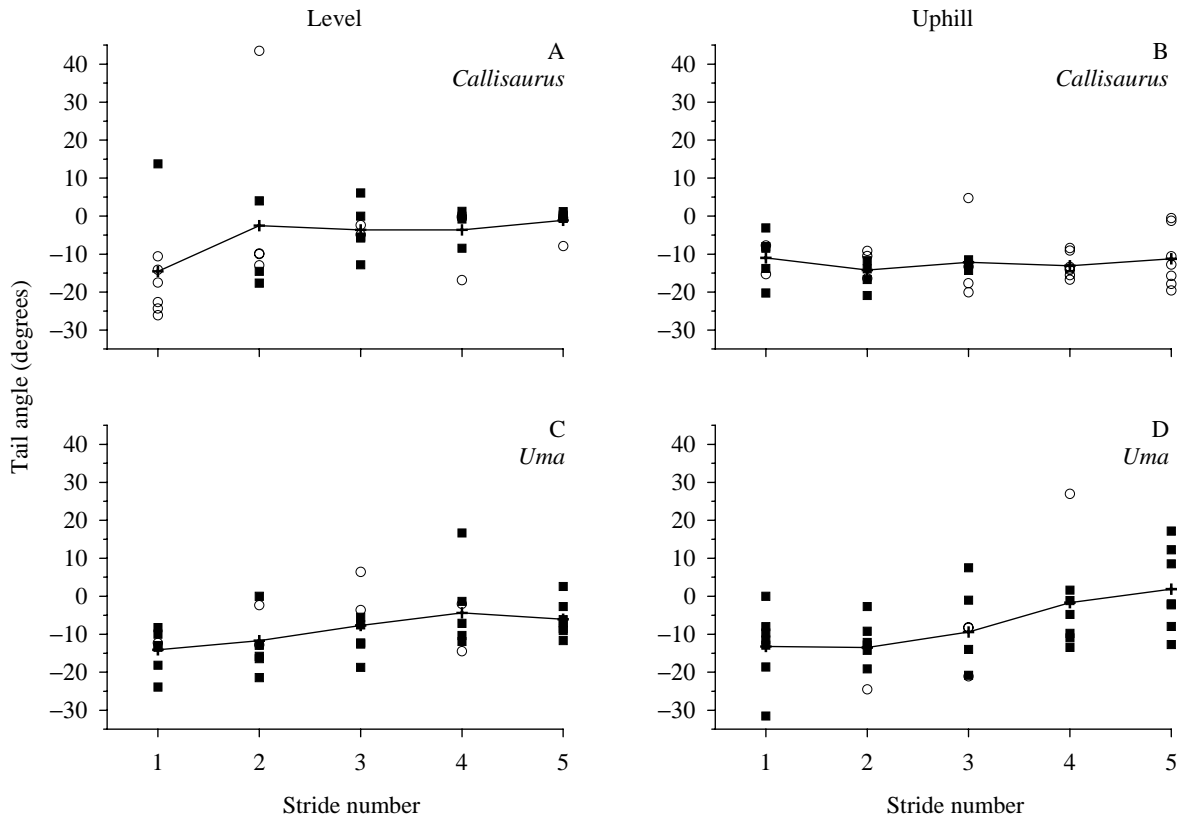
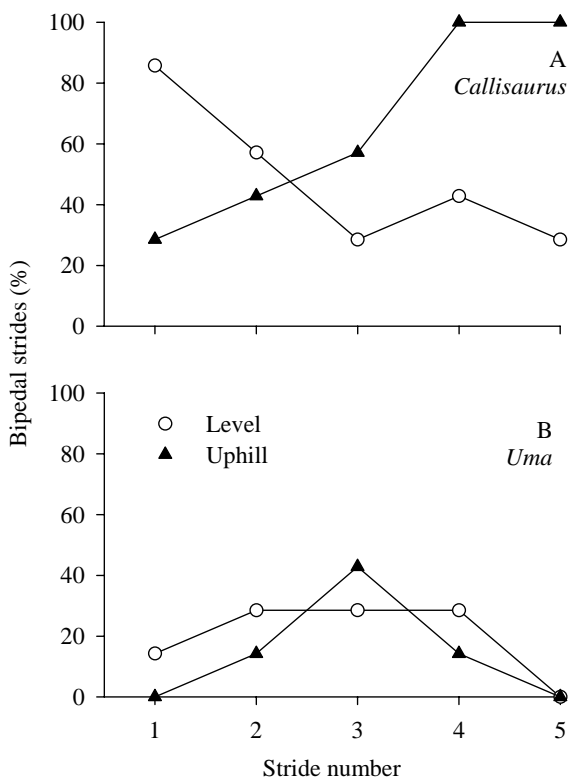


Fig. 9. Tail angle *versus* stride number during level (A,C) and uphill (B,D) locomotion in *Callisaurus draconoides* (A,B) and *Uma scoparia* (C,D). Each point represents an individual stride of each lizard. Lines connect mean values for each stride number. Open circles represent bipedal locomotion; filled squares represent quadrupedal locomotion.



decreased stride length by increasing stride frequency, but the forward velocities of later strides still decreased significantly compared with those on the level surface. Another striking result was how incline affected the use of bipedal locomotion by *C. draconoides*.

*Ecological relevance*

We used sand and a 30° incline for laboratory tests of locomotor performance because we have observed *C. draconoides* and *U. scoparia* co-occurring in a sand dune habitat where inclines range up to 30°. In our laboratory trials, inclines had more discernible effects on the locomotion of *C. draconoides* than *U. scoparia*, suggesting that these species may differ in their use of inclines in the natural environment. For example, to prevent a reduction in performance in a natural environment, lizards might simply avoid sprinting up steep inclines, but this appears not to be the case for *U. scoparia* in its natural habitat (Jayne and Ellis, 1998). In the future, we hope to investigate whether the sprinting of *C. draconoides* in its natural habitat differs from that of *U. scoparia* regarding the use of inclines.

Fig. 10. Percentage of strides that were bipedal *versus* stride number for *Callisaurus draconoides* (A) and *Uma scoparia* (B) during level (open circles) and uphill (filled triangles) locomotion. N=35 strides from seven animals in each species.

Although physiological ecologists have become increasingly aware of the need for field studies to determine whether organisms utilize their maximal capacities in nature (Garland and Losos, 1994; Hertz *et al.* 1988), few studies have examined how organisms perform in nature. Jayne and Ellis (1998) found that *U. scoparia* only utilize approximately 75% of their maximal sprint performance capabilities in the laboratory compared with field values, and they suggested that submaximal laboratory sprinting of this species contributed to the lack of a difference between the speeds recorded on level and uphill surfaces in the laboratory. Thus, the degree to which speed is affected by incline may depend on how closely lizards sprint to their physiological maximum. Below, we discuss further potential physiological constraints on sprinting performance.

Field studies of *C. draconoides* will also prove critical for determining whether this species is indeed faster than *U. scoparia* in nature, as it is in the laboratory. Jayne and Ellis (1998) used maximal stride lengths of *U. scoparia* to estimate its mean field escape velocities, which ranged from 3.6 to 3.9 m s<sup>-1</sup>; these field values are similar to the laboratory values measured for *C. draconoides* on the level surface (3.1–4.4 m s<sup>-1</sup>). That *C. draconoides* runs faster than *U. scoparia* on sand under controlled laboratory conditions is especially intriguing. *U. scoparia* lives exclusively on loose sand, whereas *C. draconoides* is often found on harder surfaces, such as rocky dry creek beds (Norris, 1951; Stebbins, 1944, 1985). The enlarged scales forming fringes on the toes of *U. scoparia* enhance running speed on sand, as shown by Carothers (1986), who removed these toe fringes and found that running speed on sand decreased significantly but that speed on hard surfaces was unchanged. The *C. draconoides* that we studied lack toe fringes; however, this trait has evolved independently several times within diverse lizard taxa that inhabit loose and shifting surfaces including a Baja population of *C. draconoides* (Luke, 1985).

When comparing *U. scoparia* with *C. draconoides*, one should consider aspects of locomotion other than speed that may be important. For example, *U. scoparia* can burrow rapidly into sand to avoid detection (Arnold, 1994; Stebbins, 1944), and morphological characteristics, such as its shovel-nosed head and robust axial musculature (Fig. 1), suggest that it is specialized for burrowing. Its tail is also relatively short and thick for a lizard (Fig. 1); short, thick tails have evolved repeatedly in snakes that are burrowing specialists (Jayne, 1982). Although *U. scoparia* lack the extremely short limbs often found in burrowing specialists, one should note that reduced limb length is commonly viewed as an adaptation for burrowing in squamate reptiles (Gans, 1975). Thus, certain aspects of the morphology of this species may represent a compromise between the conflicting functional requirements of proficient burrowing and rapid running on the surface, whereas *C. draconoides* appears to be more specialized for attaining rapid speeds during surface locomotion.

#### *Limits to locomotor performance*

One important goal in studies of locomotion is to understand

the factors that affect maximal performance. Two crude categories of morphological variation widely considered to affect locomotor performance of squamate reptiles are size and shape (Garland, 1984; Losos, 1990; Miles, 1994). Previous studies deliberately utilized a wide range of animal sizes to clarify the effects of size on locomotion up inclines (Huey and Hertz, 1982; Taylor *et al.* 1972). The present study compared two closely related species of lizards with very similar masses primarily to clarify how differences in shape influence sprinting ability on inclines.

Many studies of lizards have focused on whole-limb dimensions as the primary morphological variable underlying differences in maximal sprinting speeds among species (see Garland and Losos, 1994) on the assumption that elongate limbs enhance speed by increasing stride length. The length of the hindlimb from the hip to the tip of the fourth toe of *C. draconoides* is approximately 27% greater than that of a *U. scoparia* of equal SVL. Furthermore, on the level surface, maximal speed and stride length of *C. draconoides* were significantly greater than those of *U. scoparia* by 41% and 33%, respectively. However, on the incline, maximal speeds of *C. draconoides* also were significantly (23%) faster than those of *U. scoparia* even though mean maximal stride lengths (22.5 versus 22.2 cm) did not differ significantly between the two species. These effects of incline clearly demonstrate the pitfalls of assuming that longer legs enhance sprinting speed by increasing stride length.

Differences in the length of the hindfoot between *C. draconoides* and *U. scoparia* were even more pronounced than those for total length of the hindlimb (Fig. 1), and this limb dimension may be particularly important for relating limb morphology to maximal locomotor performance. For steady-speed locomotion in the lizard *Dipsosaurus dorsalis*, Fielers and Jayne (1998) found that, in contrast to low speeds, the heel often did not touch the ground during high-speed running. Similarly, as indicated by footprints in the sand, the heels of both *C. draconoides* and *U. scoparia* generally did not touch the substratum during rapid accelerations from a standstill. Thus, the importance of the foot dimensions in contributing to step and stride length may be speed-dependent. Furthermore, variable use of different portions of the limb also provides a cautionary note for analyses that use only whole-limb length to correlate morphology with variation in maximal speeds of locomotion.

Studying only high-speed steady locomotion on level surfaces could result in misleading interpretations regarding the functional consequences of structural variation between species because a large part of the locomotor repertoire of lizards involves both unsteady locomotion and movement up and down inclines. In contrast to the highly significant differences between *C. draconoides* and *U. scoparia* in maximal sprinting velocities, mean values of initial (first 0.05 s) acceleration for these two species were extremely similar both for both level (17.0 versus 16.3 m s<sup>-2</sup>) and uphill (13.6 versus 13.3 m s<sup>-2</sup>) trials. Like Huey and Hertz (1982), we found that acceleration generally declined exponentially after

an initial rapid acceleration. Furthermore, *C. draconoides* attained higher maximal speeds than *U. scoparia* on both the level and uphill surfaces because the rate of exponential decay in its acceleration ( $k$  in Table 2) was less rapid than that of *U. scoparia*. For *Laudackia stellio* similar in size to those in the present study (10 g), scaling equations for a level and 30° uphill surface predict initial accelerations of 8.1 and 6.7 m s<sup>-2</sup> and maximal velocities of 1.62 and 1.51 m s<sup>-1</sup>, respectively (Huey and Hertz, 1982, 1984). These are lower than those determined in the present study; the 6°C lower body temperatures of *L. stellio* may have contributed to these interspecific differences in performance.

Although running uphill did not affect the initial accelerations of all sizes of *L. stellio*, the maximum speeds of large individuals decreased significantly when running uphill (Huey and Hertz, 1982, 1984). Thus, the size-dependent decline in maximum speeds of *L. stellio* running up inclines and the interspecific differences in speed found between *C. draconoides* and *U. scoparia* in the present study may be better explained by differences in the exponential rate of decrease in acceleration rather than by differences in initial acceleration. Comparison of values of acceleration calculated later in the sequences (0.05–0.20 s) illustrates how relatively small differences in these accelerations can cause substantial differences in the final maximal speeds. Lever systems best suited for high output velocities are generally least suited for high output forces (Hildebrand, 1985). To attain faster speed, increasing the initial acceleration will require increased amounts of force, whereas accelerating for a longer period may be an alternative that requires less increase in force. Thus, compared with *U. scoparia*, the elongated limbs of *C. draconoides* may constitute a lever system that is well-suited to attaining maximal velocities on a level surface but results in a greater reduction in performance in situations that require high forces, such as accelerating uphill. More comparative data are needed to assess which morphological traits correlate with rapid acceleration, particularly on different inclines or substrata (e.g. sand).

Whether the shape differences between *C. draconoides* and *U. scoparia* caused the observed differences in sprinting performance is unclear because the size and/or physiology of their locomotor muscles may also differ. How muscle physiology limits locomotor performance is still not well understood and is an active area of research. Earlier work with the limb muscles of the lizard *Dipsosaurus dorsalis* (Marsh and Bennett, 1985) found that the time course of twitch tension was only likely to limit limb cycling frequencies at body temperatures below the normal range for activity of this lizard. More recently Swoap *et al.* (1993) used the work-loop method to determine the *in vitro* power output of a *D. dorsalis* limb muscle and quantified the effects of both temperature and the frequency of sinusoidal length changes on power output. However, the aspects of muscle contraction that limit limb cycling frequency and locomotor speed *in vivo* are still not clear. Swoap *et al.* (1993) showed that the maximal limb cycling frequency of the intact lizards was less

than the frequency that optimized the power output of the *in vitro* muscle preparation at high temperatures. Thus, an increase in stride frequency as recorded in the present study for *C. draconoides* on the inclined surface could be a mechanism for increasing the power output of the muscles. Another interesting finding in the present study was the extent to which running speed increased with successive strides while stride frequency remained relatively constant (strides 2–5). In contrast, previous studies of steady-speed locomotion in lizards have shown that stride frequency increases significantly with increased running speed (Jayne *et al.* 1990; Fieler and Jayne, 1994; Reilly and Delancey, 1997). This decoupling of speed and stride frequency during accelerating locomotion, combined with the effects of an incline, may represent variation that can be exploited experimentally in future studies seeking to clarify how muscle physiology may limit locomotor performance.

#### Bipedality

Although bipedal locomotion has evolved several times within vertebrates, the advantages of this mode of limbed locomotion are still debated and not well understood (Djawdan and Garland, 1988; Gatesy and Biewener, 1991; Snyder, 1949, 1952, 1962). Lizards are the only extant group of reptiles known to move using bipedal locomotion, and bipedal locomotion has been observed in a wide variety of lizard taxa. Snyder (1962) suggested that bipedal locomotion in lizards is advantageous for attaining high speeds; however, few quantitative data are available to support this claim.

In *C. draconoides*, we attempted to clarify which kinematic variables were most responsible for variation in  $V_{\text{stride}}$  and acceleration, and also to determine whether the incidence of bipedal running had significant predictive value for either of these measures of performance. To do this, we used different multiple regression models with  $V_{\text{stride}}$  and acceleration as dependent variables, and bipedal running (bipedal strides=1, quadrupedal strides=0), incline, stride number and the bipedal  $\times$  incline interaction as the potential independent variables. We found that incline and stride number explained a very large percentage of the variation in  $V_{\text{stride}}$  (71%), and the inclusion of bipedal running or the bipedal  $\times$  incline interaction explained little additional variation (<2%). Similarly, for acceleration, we found that stride number alone explained 70% of the variation in acceleration, and that incline, bipedal running and the bipedal  $\times$  incline interaction explained little additional variation (<2%). Thus, in contrast to Snyder's (1962) suggestion, we found that bipedality in *C. draconoides* had little predictive power for either velocity or acceleration, regardless of incline.

If bipedality is not predictive for velocity and acceleration, then why does bipedal running occur in so many species of lizards? For certain species such as the frilled dragon *Chlamydosaurus kingii*, the initial bipedal stance may be part of a defensive display unrelated to sprinting performance. Similarly, prior to escaping, *C. draconoides* curls its tail dorsally as a pursuit-deterrent signal to potential predators

(Hasson *et al.* 1989). Thus, some of the large and positive tail angles we measured for *C. draconoides* (Fig. 9) may be unrelated to speed; however, the negative values of most tail angles indicate an orientation opposite to that involved in the display. Another possibility is that bipedal locomotion, at least during level trials, is simply a consequence of high torque about the hip joint during an initial rapid acceleration that causes lizards to elevate their trunk. In this latter case, high trunk angles and bipedal running during initial strides would be *consequences*, not *causes*, of rapid accelerations.

The use of the tail as a counterweight is also considered to be important for bipedal running in lizards, and most lizard species that frequently use bipedal locomotion have very long tails (Snyder, 1949, 1952, 1962). Furthermore, partial tail loss in species of lizards with bipedal tendencies adversely affects stability (Snyder, 1949) and maximal velocity (Ballinger *et al.* 1979; Punzo, 1982). We found no obvious relationship between tail angle and bipedal running, regardless of incline. Compared with other bipedal specialists such as the lizard genera *Crotaphytus* and *Basiliscus*, in which tail lengths range from two to three times the body length (Snyder, 1962), *C. draconoides* has a relatively short tail. However, relative to *U. scoparia*, *C. draconoides* has both a longer tail and a greater incidence of bipedal running. It is worth noting that *C. draconoides* falls within a clade of primarily sand-dwelling lizards (*Uma*, *Holbrookia*, *Cophosaurus* and *Phrynosoma*), all of whom have relatively short tails (De Queiroz, 1992). It would be interesting to determine whether the long tail of *C. draconoides* is a derived character from a short-tailed ancestor.

The degree to which bipedal locomotion of lizards is associated with high trunk angles is also unclear. Photographs of lizards running bipedally commonly show high (>30°) trunk angles, but quantitative data are lacking. We found that high trunk angles were positively correlated with bipedal locomotion during sprinting on the level surface in both species, but the relationship between bipedality and trunk angle became decoupled on the uphill surface. The reason why the relationship between bipedal locomotion and trunk angle changed with incline is unclear. Perhaps during uphill locomotion, high positive trunk angles decrease stability or increase the tendency to fall backwards. Finally, the ability of *C. draconoides* to run bipedally at very high speeds (>3 m s<sup>-1</sup>) and shallow trunk angles (<10°) indicates that substantial elevation of the trunk is not a necessary condition for high-speed bipedal locomotion in lizards.

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