

SPATIO-TEMPORAL GAIT CHARACTERISTICS OF LEVEL AND VERTICAL LOCOMOTION IN A GROUND-DWELLING AND A CLIMBING GECKO

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Summary

The effects of incline (vertical *versus* horizontal) on spatio-temporal gait characteristics (stride and step length, frequency, duty factor, degree of sprawling) were measured over a range of speeds in a ground-dwelling (*Eublepharis macularius*) and a climbing (*Gekko gekko*) species of gecko. Surprisingly, the climbing species also performs very well when moving on the horizontal substratum. In the present experiments, climbing speeds ranged from 0.6 to 1.2 ms⁻¹, whereas speeds for level locomotion were between 0.6 and 1.8 ms⁻¹. In contrast, the vertical climbing capacities of the ground-dweller are limited (speeds below 0.1 ms⁻¹ *versus* level speeds between 0.2 and 1.1 ms⁻¹). In general, we demonstrate that very little adjustment in gait characteristics is made by either species when they are forced to move on their non-habitual

substratum. Moreover, gait characteristics differ little between the species despite the clear differences in ecological niche. Higher level or climbing speeds are realized mainly (or exclusively in the case of level locomotion in *G. gekko*) by increasing stride frequency. Stride lengths and duty factors vary with speed in the ground-dweller, but not in the climbing species. Step length and the degree of sprawling are speed-independent (except for hind-limb sprawling in *G. gekko* on the level). It is argued that this common strategy suits climbing (fixed spatial variables, no floating phases) rather than level locomotion.

Key words: *Gekko gekko*, *Eublepharis macularius*, kinematics, locomotion, climbing, level locomotion, gait.

Introduction

Many studies of locomotion have documented the importance of trade-offs in evolutionary adaptation. Different environments place different, often conflicting, demands on the locomotor apparatus of animals, and species are predicted to evolve morphologies and physiologies that allow a high performance capability in their preferred micro-habitat (Moermond, 1979; Losos, 1990). This may come at the expense of performance capability in other contexts. For instance, bats foraging in densely vegetated areas tend to have short, broad wings designed for high manoeuvrability, while bats foraging in open spaces have long, narrow wings to reduce power requirements (Norberg, 1994).

For terrestrial tetrapods, the degree of inclination of the substratum may constitute an important environmental design factor: an animal moving on a steep or vertical substratum must generate propulsive forces, not only to overcome inertia (in the case of unsteady motion) and environmental resistance (from the air and the substratum), but also to counter gravity (e.g. Cartmill, 1985; ZAAF et al., 1999). On a very steep or vertical incline, the front legs must pull on the substratum to avoid backwards tumbling when the hind legs push to provide propulsion (e.g. Alexander, 1992; Cartmill, 1985), and the placement of the centre of mass close to the substratum is

presumably beneficial for similar reasons. Claws, adhesive pads, suction cups, a sculptured skin and a flattened body shape are obvious examples of morphological adaptations that allow a scansorial life-style.

Besides such obvious morphological adaptations, natural selection might also adjust locomotor behaviour (posture and gait) to meet the altered demands imposed by climbing. This can occur through subtle design changes (e.g. in joint morphology, musculo-skeletal mechanics, muscle physiology) and/or through alterations in motor patterns. For instance, arborealism in chameleons is reflected in their muscle architecture and composition (Peterson, 1984; Abu-Ghalyun, 1995) together with a highly specialised pattern of limb movement (Peterson, 1984; Losos et al., 1993). To achieve insight into adaptations and potential trade-offs at this level, one can carry out in-depth morphological, kinesiological and mechanical analyses in an effort to reveal all the mechanistic aspects of the behaviour (e.g. climbing). Alternatively, one can approach the problem from another perspective. Apart from an essential descending higher-level control and peripheral feedback, locomotor patterns and behaviour are moulded to a large extent by the intrinsic (physical) properties of the entire locomotor system (electrophysiological dynamics of the

neuromuscular components; mechanical dynamics of the musculoskeletal components, etc.) and its interactions with the environment (see also, for instance, Diedrich and Warren, 1995; Diedrich and Warren, 1998a; Diedrich and Warren, 1998b; Full and Kubow, 1998; Holt et al., 1990; Holt et al., 1991; Kugler and Turvey, 1987; Latash, 1998; Schöner et al., 1990; Stewart, 1995; Stewart and Golubitsky, 1992; Thelen and Smith, 1994). The spatio-temporal characteristics and patterns of the locomotor cycles can therefore be considered as the collective result of these intrinsic properties (design) and the dynamics of the locomotor system (e.g. Aerts et al., 2000; Latash, 1998; McFadyen and Bélanger, 1997; Peck and Turvey, 1997; Van Damme et al., 1998; Verstappen and Aerts, 2000; Zernicke and Smith, 1996). Studying and comparing spatio-temporal gait characteristics (stride frequency, stride and step length, duty factor, relative phase, etc.) of species with widely different locomotor habits (ground-dwelling *versus* climbing) can thus reveal whether specific differences in 'design' and/or control strategies are present without requiring an examination of all the intricate details of the morphology or the dynamics and laws of all the underlying processes.

Lizards of the Gekkota group present ideal opportunities for the study of potential trade-offs between a cursorial (ground-dwelling) and a scansorial (climbing) lifestyle. The Eublepharidae represent the ancestral condition for gekkotans and are almost exclusively ground-dwelling (Grismer, 1988; Russell, 1976; Russell, 1979). Many Gekkonidae, in contrast, are specialised climbers, living almost exclusively on vertical structures. We have studied two species that differ widely in microhabitat use: the ground-dwelling *Eublepharis macularius* and the scansorial *Gekko gecko*. These two species clearly differ in general body shape and posture in relation to their preferred habitat. Whereas *G. gecko* has the typical dorso-ventrally flattened shape of climbers, *E. macularius* has a more cylindrical body shape (Fig. 1). Moreover, *G. gecko* keeps its body close to the substratum while *E. macularius*, when moving, shows a more erect posture (Fig. 1). Furthermore, previous analyses have identified a number of functional differences in appendicular musculature that were interpreted as adaptations to their respective microhabitats (Zaaf et al., 1999).

The present study focuses on the spatio-temporal gait characteristics (stride length, step length, stride frequency, duty factor, relative phase) to investigate whether the extreme differences in lifestyle between the two species are reflected in these characteristics. The following features are examined. (i) Does the manner in which the specialist climber modulates its locomotor speed differ from the ancestral strategy displayed by the ground-dwelling species? When climbing vertically, the consequences of an erratic step are likely to be severe, and climbing might thus require more precision in terms of leg positioning compared with level locomotion. Therefore, it would appear to be advantageous to control speed by altering the temporal aspects (frequency, duty factor) only, keeping the spatial variables (stride and step length) constant. A floating phase (no legs in contact with the substratum) should be

avoided, and front leg patterns might differ from those of the hind legs, given their different action in vertical climbing (see above). A ground-dwelling species can safely modulate its speed by changing both the spatial and temporal variables of its gait. (ii) If the climbing strategy is an expression of the intrinsic properties of the system of the climbing species, then we hypothesise that the latter will retain this style of speed modulation when moving on a level surface. This potentially constrains its performance on the level. (iii) Given the higher flexibility in speed modulation strategy, the ground-dwelling species has the opportunity to adjust its locomotor strategy when climbing. In this case, gravity might affect its performance drastically if modulation of the behaviour is insufficient.

To evaluate these hypotheses, we will test how the spatio-temporal gait characteristics of *Eublepharis macularius* and *Gekko gecko* change with speed, whether they differ between species, between substratum gradients (vertical *versus* horizontal) and (given the difference in possible role while climbing) between the fore and hind legs.

Materials and methods

Three *Gekko gecko* (L.) and three *Eublepharis macularius* (Blyth) were used in this study. All individuals had similar snout-vent lengths (Table 1). The animals were obtained from a commercial dealer and housed in pairs in separate terraria (60 cm×100 cm×40 cm) on a 12 h:12 h light:dark photoperiod. Ambient temperature varied from 26 °C during the day to 20 °C at night. A heating lamp provided a basking place at a higher temperature (40 °C). The animals were provided with food (crickets, mealworms and grasshoppers) and water *ad libitum*.

Spatio-temporal gait variables of climbing and level locomotion were compared for the specimens. For the experiments, a track was constructed consisting of two removable wooden boxes at each end of a glass tunnel

Table 1. Morphometric data for the specimens used in this study

	Snout-vent length (cm)	Mass (g)	Fore-limb length (cm)	Hind-limb length (cm)
<i>Gekko gecko</i>				
Specimen 1	13.03	57.92	2.97	3.91
Specimen 2	13.29	61.78	3.45	4.52
Specimen 3	12.36	40.01	3.30	3.90
Mean ± s.d.	12.89±0.48	53.24±11.62	3.24±0.25	4.11±0.36
<i>Eublepharis macularius</i>				
Specimen 1	13.33	60.11	3.31	4.05
Specimen 2	12.39	45.31	3.10	3.57
Specimen 3	12.72	43.11	3.25	3.89
Mean ± s.d.	12.81±0.48	49.51±9.25	3.22±0.11	3.84±0.24

Further morphometric data for these species can be found in Zaaf et al., 1999.

(140 cm×20 cm×15 cm) fixed on a wooden support. The tunnel was large enough to permit free limb and body movements, and its floor was covered with a layer of cork. To study climbing, the tunnel was mounted vertically. The animals were placed in the box at the bottom of the tunnel and induced to climb through it towards the other box fixed at the top. When an animal entered the top box, the boxes were switched and the procedure was repeated. To study level locomotion, the same arrangement was used, but with the tunnel in a horizontal position. To increase the speed range, *E. macularius* were also placed on an adjustable-speed treadmill. For each condition, animals were trained for 1 week before filming. For the experiments, all lizards were marked with white non-toxic paint dots on the tip of the snout, on the centre of the pectoral and pelvic girdles and on the mid-forefoot and mid-hindfoot. In *G. gecko*, the mid-forefoot and mid-hindfoot are the first limb segments that contact the substratum and the last to leave it (before and after the digits touch and leave the substratum,

respectively; see Russell, 1975). We therefore decided to place markers at the level of the metatarsus and metacarpus (needed to determine step length and stride length; see below).

Level locomotion and climbing sequences were recorded in dorsal view using a NAC-1000 high-speed video system set at 500 frames s⁻¹. Animals were given at least 15 min rest between successive trials. One of the *E. macularius* specimens was also videotaped while moving along the treadmill with the belt at zero speed. This experiment allowed us to test whether the treadmill affects gait variables in these lizards.

Only sequences in which the animals moved straight and at a constant speed were retained for further analysis. From the positions of the marker on the snout tip early and late in these sequences, an approximate estimate of speed was obtained. On the basis of these estimates, nine climbing sequences were selected for two specimens of *G. gecko*, representing a velocity range as wide as possible. Inducing horizontal locomotion was more difficult in this species because the animals often

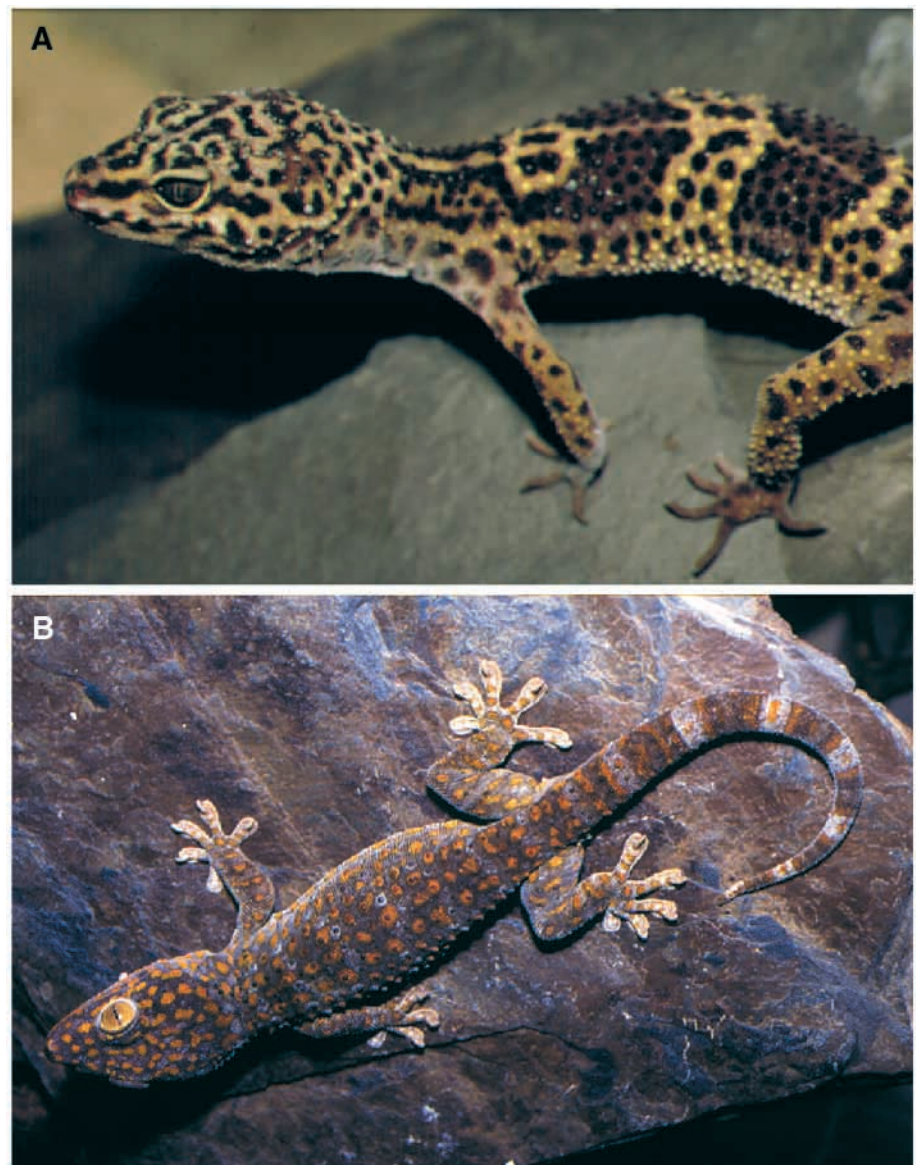


Fig. 1. (A) The ground-dweller *Eublepharis macularius* (snout–vent length 12.39 cm) and (B) the specialist climber *Gekko gecko* (snout–vent length 13.03 cm).

preferred to move on the side-walls of the corridor or simply sat on the side-walls enclosing the belt of the treadmill. We obtained useful results for five trials and two trials, respectively, for the two specimens used for climbing and eight from an additional individual. For the three *Eublepharis macularius* specimens, seven, five and five level locomotion sequences were used. One specimen refused to climb. For the other two specimens, four and six climbing sequences were selected.

For each of these sequences, the marked body points were digitised frame by frame over a complete locomotor cycle. A more precise estimate of speed was obtained from the slope of the forward displacement of the tip of the snout against time (linear regression; r^2 values were always well above 0.97, indicating that speed was fairly constant throughout the measured stride). Stride length (the distance travelled by the body during an entire cycle), step length (the distance travelled when a specific leg contacts the ground), stride frequency (the number of cycles per second) and duty factor (the fraction of the cycle that a particular foot is on the ground) were determined according to the methods of Van Damme et al. (Van Damme et al., 1998).

Limb angles at touch-down and at lift-off were calculated as the angle between a line connecting the foot/hand with the centre of the respective girdle and an axis through the girdle perpendicular to the mid-sagittal plane (straight posture). Limb angles in front of the perpendicular axis are considered positive; behind this axis, they are negative.

The degree of sprawling was determined by measuring the distance between the markers on the pelvic or pectoral girdle and the mid-hindfoot/forefoot in stance when the forefoot and the hindfoot are directly lateral to the shoulder and hip, respectively.

The relative phase was calculated for the fore-limb, using touch-down of the ipsilateral hind-limb as the reference time (relative phase 0°). The relative phase was expressed as the relative timing (within the cycle) of fore-limb touch-down multiplied by the stride frequency.

To analyse differences in limb kinematics between species and substrata, we first ran a multiple analysis of covariance (MANCOVA) with the gait characteristics as the dependent variables, species and substratum as the factors and speed as a covariate. Testing all characteristics simultaneously was not possible because of a lack of degrees of freedom. We therefore performed two MANCOVAs, one for each pair of limbs. Because we also wanted to estimate species and substratum differences in speed modulation strategies, we proceeded with univariate tests on each gait characteristic. Relationships between speed and spatio-temporal gait characteristics were established by means of least-squares linear regression analysis. When gait characteristics changed with velocity, analysis of covariance (ANCOVA, velocity entered as covariate) was used to assess inter-specific differences, differences between fore- and hind-limbs and the effect of inclination (horizontal versus vertical). Otherwise, differences were tested using t -tests.

Results

Effects of experimental arrangement and inter-individual differences

Preliminary analyses revealed no differences in gait characteristics between *E. macularius* moving on the treadmill or in the tunnel in the absence of the treadmill (ANOVA, all $P > 0.10$). As was to be expected from their similarity in overall size and limb dimensions (Table 1), differences among individuals within species were also not significant (ANOVA, all $P > 0.05$). Therefore, we combined data from different experimental arrangements and individuals for further analyses.

The mean body sizes and limbs dimensions of all individuals used here are very similar (Table 1), so inter-specific comparisons of spatio-temporal gait variables can be performed without normalisation (i.e. dynamic similarity conditions apply; e.g. Alexander, 1992).

Multivariate analyses

Multivariate analysis of covariance revealed a highly

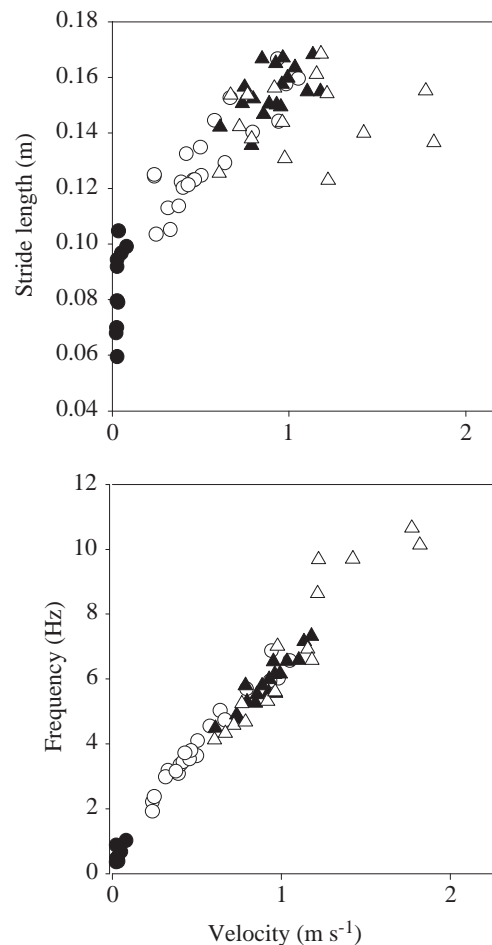


Fig. 2. Stride lengths and stride frequencies for *Gekko gecko* (triangles) and *Eublepharis macularius* (circles) moving at different velocities on vertical (filled symbols) and horizontal (open symbols) substrata.

significant species \times substratum interaction effect in both hind-limb (Wilk's $\lambda=0.34$, d.f.=7,53, $P<0.0001$) and fore-limb (Wilk's $\lambda=0.18$, d.f.=7, 53, $P<0.0001$) gait characteristics. This suggests that the effect of inclination on the kinematics of locomotion differed between the two species.

The significant species \times substratum interaction effect could be a statistical artefact of the extremely low velocities attained by *E. macularius* on the vertical substratum. We therefore present the results of univariate tests for each species below.

Gait characteristics and speed

We were able to measure the gait characteristics of *G. gecko* moving at velocities on the level between 0.6 and 1.8 m s⁻¹ and for climbing between 0.6 and 1.2 m s⁻¹. For *E. macularius*, we obtained level data velocities between 0.24 and 1.05 m s⁻¹. *Eublepharis macularius* proved to be a poor climber, and we were therefore able to assess climbing gait characteristics for a small range of low velocities (0.025–0.085 m s⁻¹) only.

On the level, *G. gecko* increased its velocity by increasing its stride frequency. Stride length, step length, limb angle at lift-off and at touch-down and duty factor did not change with speed (Table 2; Figs 2–4). The hind-limbs were placed more sagittally at higher speeds (i.e. a reduction in the degree of sprawling), but this was not the case for the fore-limbs

(Table 2; Fig. 5). The relative phase of the fore-limb did not change with speed and equalled 0.5 (i.e. diagonal pairs move in synchrony; Table 2; Fig. 6).

On the vertical substratum, both stride length and stride frequency increased with increased velocity (Table 2; Fig. 2), but the change in stride length was relatively small in comparison with the change in stride frequency. For instance, as calculated from the regression equations in Table 2, the stride frequency of climbing *G. gecko* changed by 75% as speed increased from 0.5 to 1.0 m s⁻¹. Over the same velocity interval, stride length increased by 13%. As for level locomotion, step length, limb angle at lift-off and touch-down and duty factor were independent of speed in climbing *G. gecko* (Table 2; Figs 3, 4). The hind-limbs were placed more laterally at higher speeds (i.e. increased sprawling), but this was not the case for the fore-limbs (Table 2; Fig. 5). The relative fore-limb phase (0.5) was independent of speed (Table 2; Fig. 6).

Ground-dwelling *E. macularius* increased both stride frequency and stride length to increase velocity (Table 3; Fig. 2). From the equations in Table 3, a velocity change from 0.5 to 1.0 m s⁻¹ involved an 18% increase in stride length and a 69% increase in stride frequency. Duty factor in ground-dwelling *E. macularius* decreased with velocity (Table 3;

Table 2. Relationships between gait characteristics and velocity for *Gekko gecko* moving on horizontal and vertical substrata

	Level locomotion (N=15)			Climbing (N=18)		
	r^2	a	b	r^2	a	b
Stride length (m)						
Hind-limbs	0.018	–	–	0.29*	-0.802±0.006	0.191±0.074
Step length (m)						
Fore-limbs	0.02	–	–	0.00001	–	–
Hind-limbs	0.02	–	–	0.00004	–	–
Stride frequency (Hz)						
Hind-limbs	0.90***	0.805±0.012	0.945±0.085	0.87***	0.798±0.006	0.753±0.072
Duty factor						
Fore-limbs	0.09	–	–	0.11	–	–
Hind-limbs	0.02	–	–	0.008	–	–
Sprawling (m)						
Fore-limbs	0.036	–	–	0.130	–	–
Hind-limbs	0.293*	-1.489±0.015	-0.237±0.102	0.336*	-1.379±0.006	0.199±0.070
Limb angle at touch-down (degrees)						
Fore-limbs	0.005	–	–	0.034	–	–
Hind-limbs	0.0003	–	–	0.019	–	–
Limb angle at lift-off (degrees)						
Fore-limbs	0.066	–	–	0.034	–	–
Hind-limbs	0.0563	–	–	0.024	–	–
Relative phase	0.185	–	–	0.156	–	–

Intercepts and slopes (\pm S.E.M.) of least-squares regressions [$\log_{10}(\text{gait characteristic})=a+b\log_{10}(\text{velocity})$] are given for those relationships that had significant r^2 values.

Velocity is expressed in m s⁻¹, stride length and step length in m and stride frequency in Hz.

*Significant at $P=0.05$; ***Significant at $P=0.001$.

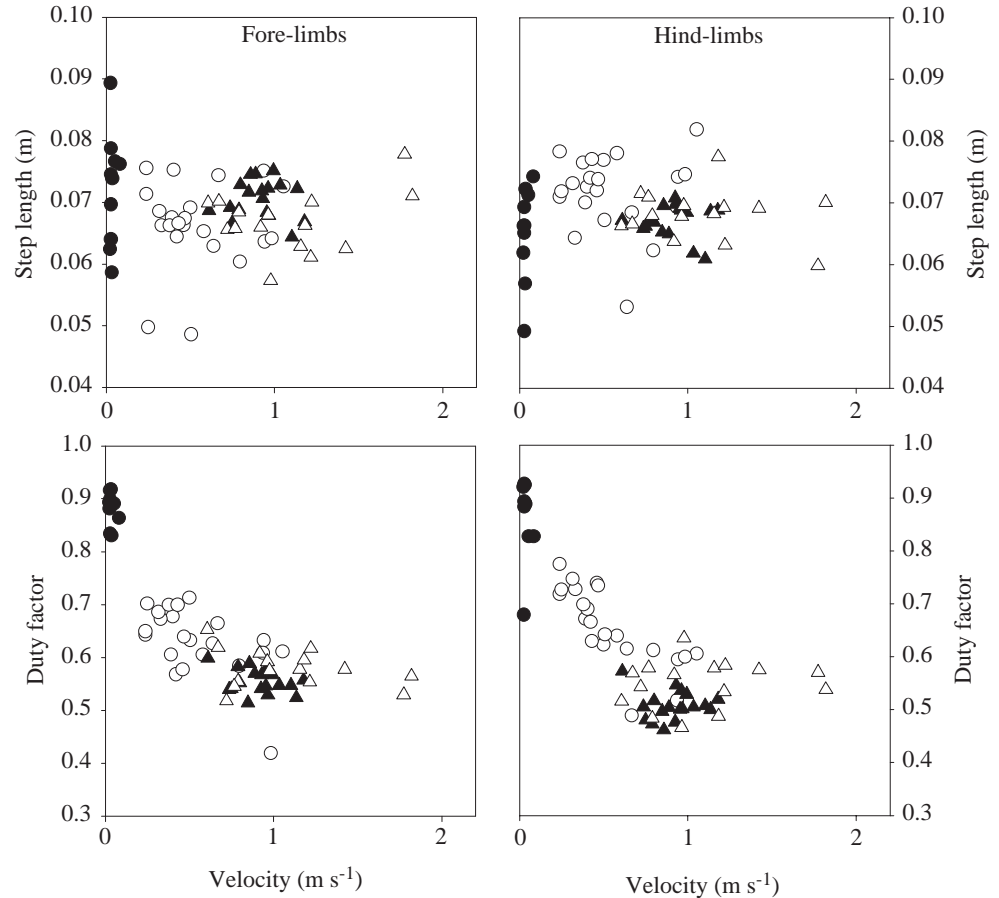


Fig. 3. Step lengths and duty factors for *Gekko gecko* (triangles) and *Eublepharis macularius* (circles) moving at different velocities on vertical (filled symbols) and horizontal (open symbols) substrata.

Fig. 3). Step length and limb angle at lift-off and touch-down did not change with velocity, and neither did the degree of sprawling (Table 3; Figs 3–5). Like the climbing species, the relative fore-limb phase (0.5) did not change with speed (Table 3; Fig. 6).

Because of the limited velocity range obtained in our experiments with climbing *E. macularius*, we will not examine the effects of speed on gait characteristics for climbing in this species quantitatively.

Hind-limb versus fore-limb gait characteristics

For symmetrical gaits, steady locomotion should normally yield identical stride lengths and frequencies for the fore- and hind-limb cycles (this was confirmed in preliminary tests). Here, we compare the relevant gait characteristics of the hind- and fore-limbs within one cycle. For level locomotion in *G. gecko*, most gait characteristics for the hind-limb did not differ significantly from those for the fore-limb (paired *t*-tests, all $P > 0.06$). Only the hind-limb angle at lift-off was significantly smaller than that observed for the fore-limb ($t_{1,14} = 8.09$, $P < 0.0001$). During climbing, however, limb angles at lift-off and touch-down did not differ between the front and hind leg (*t*-test, both $P > 0.1$). Moreover, the step lengths and duty factors of the fore-limbs were consistently larger than those of the hind-limbs (paired *t*-tests, step length, $t_{17} = 3.91$, $P = 0.001$; duty factor, $t_{17} = 6.94$, $P < 0.0001$). On average, the step lengths of the

hind-limbs were 4.58% smaller than those of the fore-limbs of the same cycle. For the duty factor, this difference amounted to an average of 8.55%. For level locomotion in *G. gecko*, the degree of sprawling was consistently higher in the hind-limbs than in the fore-limbs ($t_{14} = 5.78$, $P < 0.0001$). For climbing *G. gecko*, the degree of sprawling was consistently higher in the fore-limbs than in the hind-limbs ($t_{17} = 2.70$, $P = 0.01$).

For level data in *E. macularius*, hind-limb step lengths were consistently larger than those for the fore-limbs of the same cycle (paired *t*-tests, $t_{21} = 3.22$, $P = 0.004$). The average within-cycle difference amounted to 2.7%. Despite the larger hind-limb steps, the fore-limb angle at touch-down was larger than that of the hind-limb (*t*-test, $t_{21} = 6.36$, $P < 0.0001$), but the limb angle at lift-off was similar ($P > 0.8$). Duty factors did not differ between fore- and hind-limbs in ground-dwelling *E. macularius* (paired *t*-tests, both $P > 0.18$). In climbing *E. macularius*, the step length of the hind-limb differed significantly from the step length of the fore-limb (paired *t*-test: $t_9 = 2.36$, $P = 0.04$). On average, the step lengths of the hind-limbs were 9.8% smaller than those of the fore-limbs of the same cycle. This is because hind-limb angle at touch-down and lift-off tended to be smaller than those of the fore-limb when climbing (paired *t*-test, $t_9 = 5.46$, $P < 0.0001$ for limb angle at touch-down, and $t_9 = 2.58$, $P = 0.03$ for limb angle at lift-off). In both vertical and horizontal locomotion, the degree of sprawling was higher in the hind-limbs (paired *t*-test,

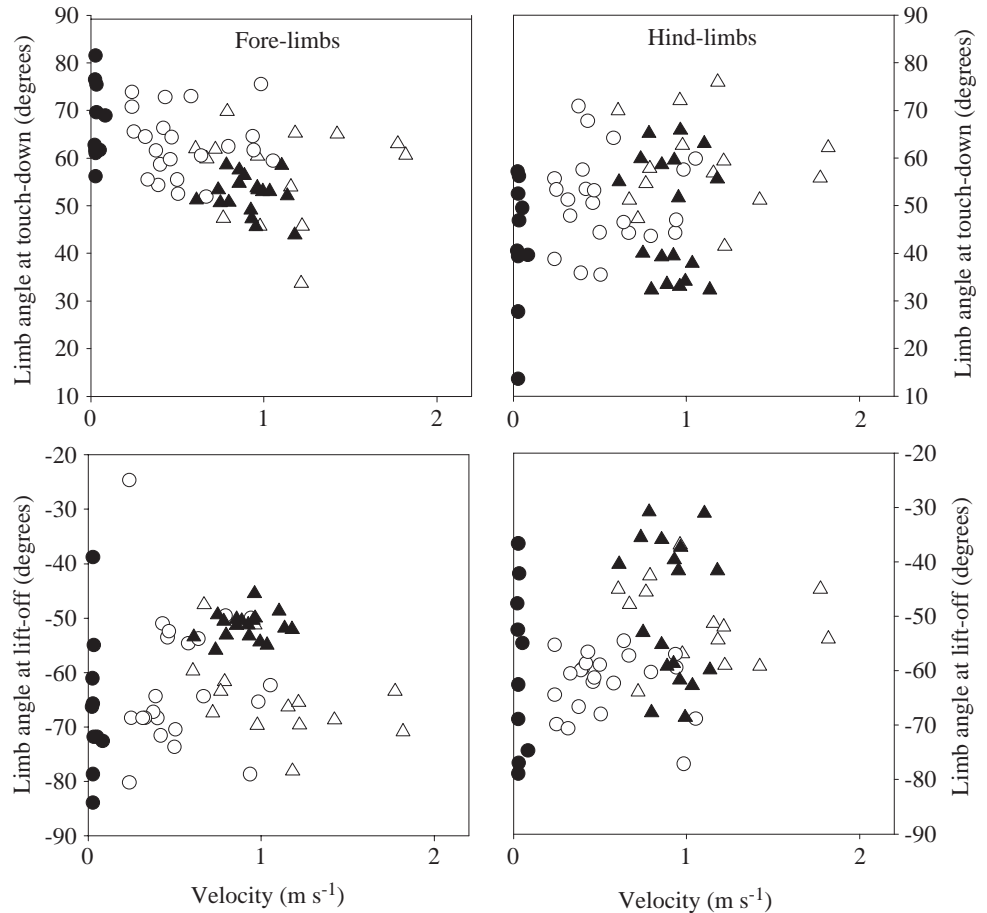


Fig. 4. Limb angles at touch-down (upper graphs) and at lift-off (lower graphs) for the fore- (left side) and hind-limbs (right side) of *Gekko gecko* (triangles) and *Eublepharis macularius* (circles) while climbing (filled symbols) and moving on a horizontal substratum (open symbols).

horizontal, $t_{21}=-7.51$, $P<0.0001$; vertical, $t_{21}=-6.26$, $P<0.0001$).

Climbing versus level locomotion

For *G. gecko*, regression lines relating hind-limb stride length and velocity for vertical and horizontal locomotion did not differ in slope (ANCOVA, $F_{1,27}=0.89$, $P=0.35$), but there was a difference in intercepts ($F_{1,28}=6.87$, $P=0.014$). On average, stride lengths were smaller for horizontal than for vertical locomotion.

The stride frequency of the hind-limb increased slightly more rapidly with speed during level locomotion than during climbing (ANCOVA, difference between slopes $F_{1,27}=4.27$, $P=0.048$).

Hind-limb step lengths did not differ between climbing and level locomotion in *G. gecko* (t -test, $t_{31}=0.77$, $P=0.45$), but the fore-limb step lengths of climbing animals were larger than those measured for animals moving on the horizontal substratum ($t_{31}=2.62$, $P=0.01$). Fore-limb angles at touch-down and hind-limb angles at lift-off appear not to be affected

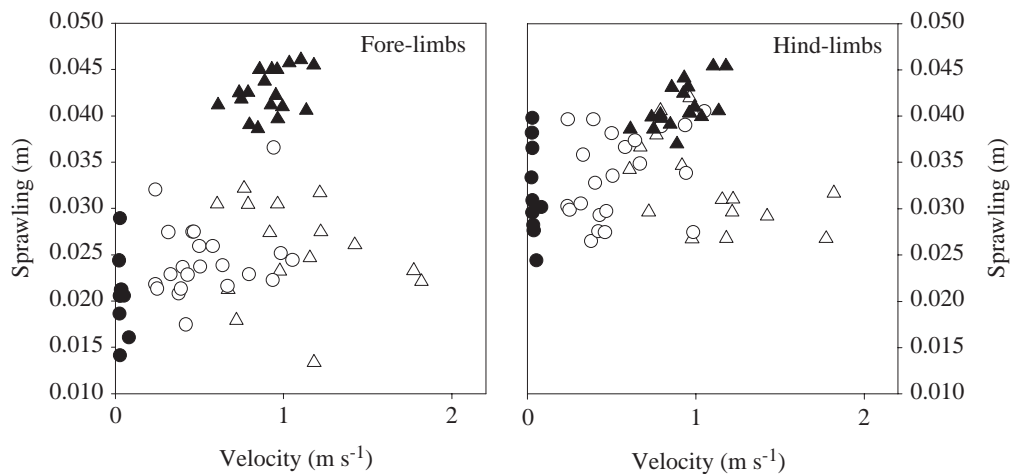


Fig. 5. The degree of sprawling of *Gekko gecko* (triangles) and *Eublepharis macularius* (circles) moving at different velocities on vertical (filled symbols) and horizontal (open symbols) substrata.

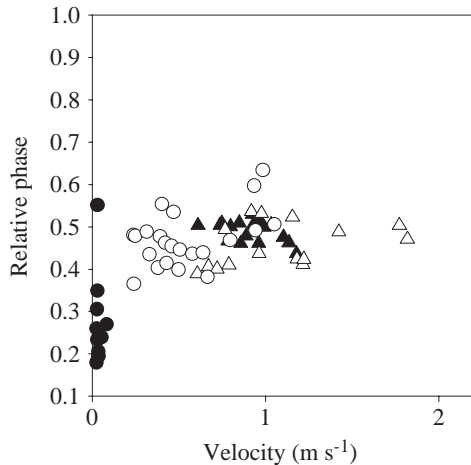


Fig. 6. Relative phase of the fore-limbs *versus* velocity for *Gekko gecko* (triangles) and *Eublepharis macularius* (circles) while climbing (filled symbols) and moving on a horizontal substratum (open symbols).

by inclination (t -test, $P>0.2$), but both fore-limb angle at lift-off and hind-limb angle at touch-down are larger during level locomotion (t -test, $t_{30}=6.62$, $P<0.0001$ for fore-limb angle at lift-off, and $t_{30}=2.75$, $P<0.01$ for hind-limb angle at touch-down).

The degree of sprawling of the fore-limbs is conspicuously smaller on the level surface than during climbing (t -test, $t_{31}=12.25$, $P<0.0001$). The regression lines relating hind-limb sprawling and velocity differ in intercept (ANCOVA, $F_{1,28}=33.23$, $P<0.0001$) but not in slope ($F_{1,27}=0.89$, $P=0.35$). On average, the hind-limbs are more spread on the vertical substratum than on the horizontal one (Table 4).

The duty factors of climbing *G. gecko* were on average lower than those of animals moving on the horizontal substratum (hind-limbs, $t_{31}=3.22$, $P=0.003$; fore-limbs, $t_{31}=2.26$, $P=0.03$). Although the relative fore-limb phase was lower on the level (t -test, $t_{31}=2.45$, $P=0.02$) than on the vertical substratum, relative phase values were close to 0.5 in both conditions (Table 4).

The limited velocity range obtained for climbing *E. macularius* precludes statistical analysis of differences in speed modulation strategies between horizontal and vertical locomotion, but Figs 2 and 3 suggest that an animal moving on the horizontal substratum at speeds as low as those realized during climbing would show stride lengths, stride frequencies and duty factors similar to those measured for climbing. The step lengths of the fore-limbs were smaller during horizontal locomotion than when climbing (t -test: $t_{30}=2.041$, $P=0.05$). The opposite was found for hind-limb step length (t -test: $t_{30}=2.57$, $P=0.02$). The relative fore-limb phase also differed between level locomotion and climbing (t -test: $t_{30}=3.16$, $P=0.003$). When climbing, *E. macularius* mainly shifts to a 'lateral single foot' gait pattern (see Hildebrand, 1985) using a relative phase between 0.15 and 0.35 (mean phase 0.28; Table 4; Fig. 6). The degree of sprawling of the fore-limbs was

Table 3. Relationships between gait characteristics and velocity for *Eublepharis macularius* moving on a horizontal substratum

	Level locomotion (N=22)		
	r^2	a	b
Stride length (m)			
Fore-limbs	0.72***	-0.832 ± 0.011	0.2140 ± 0.030
Hind-limbs	0.71***	-0.812 ± 0.012	0.241 ± 0.034
Step length (m)			
Fore-limbs	0.004	—	—
Hind-limbs	0.007	—	—
Stride frequency (Hz)			
Fore-limbs	0.97***	0.819 ± 0.011	0.758 ± 0.031
Hind-limbs	0.97***	0.819 ± 0.011	0.757 ± 0.031
Duty factor			
Fore-limbs	0.26**	-0.240 ± 0.017	-0.126 ± 0.047
Hind-limbs	0.61***	-0.247 ± 0.013	-0.201 ± 0.036
Sprawling (m)			
Fore-limbs	0.025	—	—
Hind-limbs	0.079	—	—
Limb angle at touch-down (degrees)			
Fore-limbs	0.015	—	—
Hind-limbs	0.000015	—	—
Limb angle at lift-off (degrees)			
Fore-limbs	0.007	—	—
Hind-limbs	0.0007	—	—
Relative phase	0.166	—	—

Slopes and intercepts (\pm S.E.M.) of least-squares regressions [$\log_{10}(\text{gait characteristic})=a+b\log_{10}(\text{velocity})$] are given for those relationships that had significant r^2 values.

Velocity is expressed in m s^{-1} , stride length and step length in m and stride frequency in Hz.

Significant at $P=0.01$; *Significant at $P=0.001$.

greater on the horizontal substratum than when climbing (t -test: $t_{30}=2.50$, $P=0.01$), but that of the hind-limbs did not differ between the locomotor substrata (t -test: $P>0.3$).

Inter-specific differences in gait characteristics

Because of the large difference in velocity ranges for which we obtained data on climbing gait characteristics in both species, we did not analyse inter-specific differences in stride length and stride frequency for climbing.

When moving on the horizontal substratum, the mean step length (t -test, fore-limbs, $t_{35}=0.22$, $P=0.83$; hind-limbs, $t_{35}=2.02$, $P=0.051$) and the degree of sprawling (t -tests, fore-limbs, $t_{35}=0.44$, $P=0.69$; hind-limbs, $t_{35}=-0.67$, $P=0.50$) did not differ between the species (Table 4).

The slopes of the regressions of stride length on speed (both log-transformed) differed significantly between the two species (ANCOVA: hind-limbs, $F_{1,33}=7.29$, $P=0.011$). While *E. macularius* increased its stride length to increase its speed on the level, stride length was unchanged in *G. gecko*.

Table 4. Comparison between the gait characteristics of the fore- and hind-limbs in *Gekko gekko* and *Eublepharis macularius* while climbing and moving on a horizontal substratum

	<i>E. macularius</i>		<i>G. gekko</i>	
	Fore-limbs	Hind-limbs	Fore-limbs	Hind-limbs
Level				
Stride length (m)	0.127±0.015	0.130±0.017	0.147±0.014	0.145±0.013
Step length (m)	0.066±0.007	0.072±0.006	0.066±0.005	0.068±0.004
Stride frequency (Hz)	4.076±1.436	4.063±1.143	7.063±2.477	6.880±2.313
Duty factor	0.632±0.063	0.657±0.074	0.579±0.036	0.548±0.045
Sprawling (m)	0.025±0.004	0.034±0.005	0.025±0.005	0.033±0.005
Limb angle at touch-down (degrees)	62.88±62.879	51.0±9.533	56.73±10.048	58.452±9.608
Limb angle at lift-off (degrees)	-61.93±12.372	-62.29±5.739	-64.51±7.880	-50.975±7.527
Relative phase	0.470±0.067		0.456±0.052	
Climbing				
Stride length (m)	0.075±0.009	0.084±0.015	0.156±0.007	0.155±0.009
Step length (m)	0.072±0.009	0.065±0.007	0.070±0.003	0.067±0.002
Stride frequency (m)	0.537±0.019	0.553±0.226	5.830±0.822	5.857±0.784
Duty factor	0.881±0.030	0.865±0.074	0.555±0.023	0.507±0.027
Sprawling (m)	0.020±0.004	0.032±0.005	0.043±0.002	0.041±0.002
Limb angle at touch-down (degrees)	67.44±8.198	42.24±3.52	52.34±4.133	47.57±12.78
Limb angle at lift-off (degrees)	-66.62±12.81	-59.65±15.06	-51.49±2.47	-48.93±12.983
Relative phase	0.280±0.103		0.490±0.024	

Values are means ± S.E.M. (not log-transformed).

The slopes of the regressions of stride frequency on level speed (both log-transformed) also differed between the two species (ANCOVA: hind-limbs, $F_{1,33}=5.83$, $P=0.021$). Stride frequency increased more rapidly with speed in *G. gekko* than in *E. macularius*.

Finally, for the hind-limbs, the slopes of the regressions of duty factor on speed (both log-transformed) differed between the species (ANCOVA: $F_{1,33}=10.46$, $P=0.003$). The duty factor decreased with increasing speed in *E. macularius*, but remained constant in *G. gekko*. Unlike the hind-limbs, no differences were found between the slopes (ANCOVA: $F_{1,33}=0.78$, $P=0.38$) or the intercepts ($F_{1,34}=0.02$, $P=0.88$) of the regression equations of duty factor of the forelimb on speed in the two species.

Discussion

Three working hypotheses are tested in this study (see Introduction). First, does the speed modulation strategy of the climber *G. gekko* differ from that of the ground-dwelling *E. macularius*? It is postulated that in the climber only the temporal aspects (frequency, duty factor) of the gait will change with speed, whereas the spatial variables (stride and step length) will remain constant. Such a speed modulation strategy might ensure the accuracy of leg positioning when moving faster, a requirement that can be assumed to be particularly important when climbing vertical structures. Moreover, throughout the stride, at least one of the legs should always remain in contact with the substratum to deliver an upward force to counter gravity (i.e. a floating phase must be

avoided). If not, the force of gravity will reduce or even reverse the upward momentum of the lizard's body in every stride. From a theoretical point of view, it can even be argued that at least one front leg must exert pulling forces at any time to avoid backwards tumbling due to gravity. Ground-dwelling species, in contrast, do not have these constraints. In theory, they can safely modulate their speed by changing both the spatial and temporal variables of their gait.

According to Russell (Russell, 1976; Russell, 1979), ground dwelling represents the ancestral state within the gekkotans. Therefore, we will first evaluate the locomotion strategy displayed by *E. macularius* on the horizontal and compare it with data available from other non-specialist climbers in order to compare this strategy with that of the specialist climber. Legged animals can increase their velocity by taking larger strides, by increasing their stride frequency or by using a combination of these two strategies. The degree to which stride length and/or frequency are modulated with respect to speed seems to vary among different non-climbing lizard species (White and Anderson, 1994; see Fig. 7). Although a direct inter-specific comparison is hampered by methodological differences and by differences in the range of velocities over which the gait characteristics were measured (Fig. 7), all previously studied lizards seem to modulate their speed using a combination of changes in stride frequency and stride length (Avery et al., 1987; White and Anderson, 1994; Reilly and Delancey, 1997; Fieler and Jayne, 1998; Irschick and Jayne, 1998; Van Damme et al., 1998; Fig. 7).

On its preferred horizontal substratum, *E. macularius* shows a speed modulation strategy comparable with those of the other

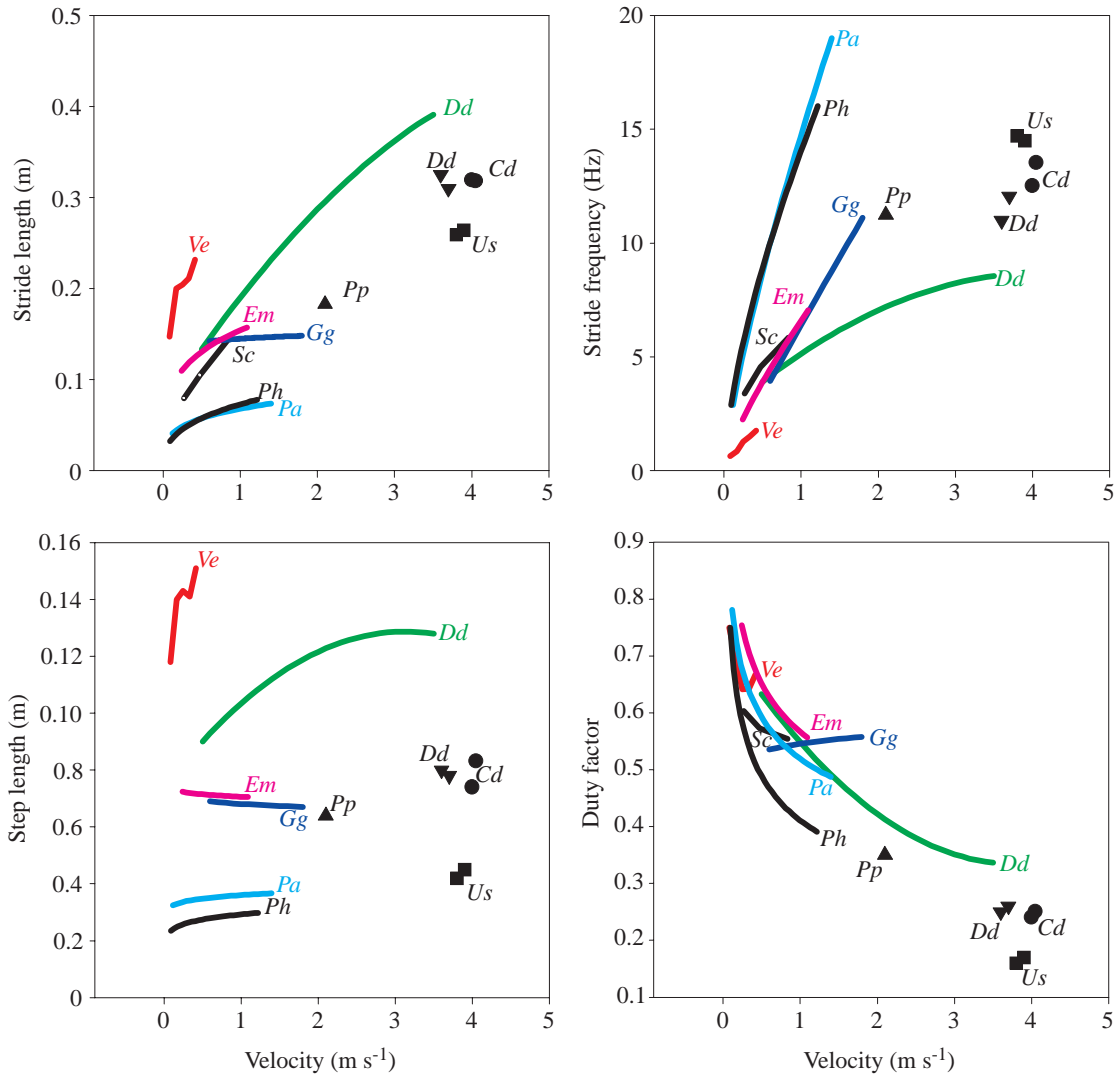


Fig. 7. Gait characteristics for moving on a horizontal substratum at different speeds for *Gekko gecko* (Gg) and *Eublepharis macularius* (Em) compared with data for other lizards (Ve, *Varanus exanthematicus*, Jayne et al., 1990; Dd, *Dipsosaurus dorsalis*, Fieler and Jayne, 1998; Sc, *Sceloporus clarkii*, Reilly and Delancey, 1997; Pa, *Podarcis hispanica atrata*, Van Damme et al., 1998; Ph, *Podarcis hispanica hispanica*, Van Damme et al., 1998). Also indicated are the gait characteristics of *Phrynosoma platyrhinos* (Pp), *Uma scoparia* (Us), *Callisaurus draconoides* (Cd) and *Dipsosaurus dorsalis* (Dd) running at maximal speed (Irschick and Jayne, 1999).

ground-dwelling lizards (Fig. 7). Both stride length and stride frequency increase significantly with speed, although faster locomotion is achieved mainly by increasing the stride frequency. To increase stride length, step length may be increased and/or the duty factor may be reduced (less overlap in the support by several legs, leading to the incorporation of a floating phase in the stride). *E. macularius* keeps its step length constant (see Table 3) and avoids floating phases in its strides. Only occasionally do duty factors drop somewhat below 0.5. The fact that step length does not change with speed suggests that this variable is maximised at all speeds, being set by morphological and mechanical constraints (leg length, girdle rotation, maximal excursions at the joints between leg segments). Such a constant step length is not exceptional. Other lizard species (e.g. lacertids, Van Damme et al., 1998;

see Fig. 7) and also other tetrapods (e.g. walking cats and dogs, McMahon, 1984) show a constant step length over a range of speeds.

Combined with the constant step length, however, the absence of a floating phase in this ground-dweller is remarkable because this seriously constrains stride length and, hence, maximal speed. In ground-dwelling animals, no reasons seem to exist to exclude floating phases from the running strides, and many lizards do show floating, especially at higher speeds (e.g. Van Damme et al., 1998; P. Aerts and R. Van Damme, personal observations). At first glance, the evolutionary retention of 'climbing control' (in which contact with the substratum is essential; see above) cannot be put forward as a possible explanation because it is assumed that *E. macularius* represents the ancestral, ground-dwelling condition

of the gekkotans. This implies that *E. macularius* is either unwilling to include a floating phase into its limb cycle (at least in our experiments) or cannot do so because of biomechanical constraints (floating phases will only occur when the push-off forces exceed a certain level). This may at least partly explain why the maximal velocity on the level is relatively low for *E. macularius* compared with the maximal velocities attained by other species of similar size (as illustrated in Fig. 7). As an alternative explanation, it could be argued that the absence of a floating phase is an artefact of the actual measured velocity range being too narrow and that further stride length increase by including floating might have occurred if higher speeds had been recorded. The maximum speed of *E. macularius* we have recorded was approximately 1.8 m s^{-1} (measured on a race-track; A. Zaaf and R. Van Damme in preparation), which is higher than the maximal speeds attained during the present experiments (approximately 1.1 m s^{-1}).

This unexpected aspect of the speed modulation strategy of the ground-dwelling species means that nearly all the spatio-temporal variables of the specialist-climber's strides resemble the presumed ancestral style rather well when performing on the preferred vertical substratum! Both stride length and frequency increase significantly when *G. gecko* climbs faster. Moreover, this occurs in a very similar manner to that observed for the velocity increase by the ground-dwelling species (compare the regression constants of the equations relating stride length and frequency to speed; see Tables 2, 3). Furthermore, step length remains constant in both species. Therefore, it is likely that the invariability of the duty factor, as it appears from the regression model (Table 2), is a statistical artefact resulting from the fact that we did not record low-speed climbing by *G. gecko* in our experiments (Fig. 3; Table 2). Indeed, it is impossible to increase stride length while keeping both step length and duty factor constant. However, as in *E. macularius*, duty factors rarely drop below 0.5. For the fore-limbs, they were always above 0.5, whereas those of the hind-limb were below 0.5 for only a minor fraction of the cycle (less than 4%; see Fig. 3). This conforms to our predictions concerning the constraints on climbing: a front leg is always in contact with the substratum, and floating phases are absent. In practice, two diagonal legs are always in contact with the substratum, except for those rare cases in which hind-limb duty factors fall below 0.5.

Thus, our results show that *G. gecko* uses a speed modulation strategy, both during climbing and when moving on level surface, that is very similar to that of the level runner *E. macularius*. This is because the latter species seems to apply a locomotor strategy that conforms more to that predicted for a climber than to that for a level runner. Indeed, although stride length increases significantly with speed in both species, it is mainly increases in cycle frequency that achieve speed increases: on their preferred substratum, both species apply a gain factor of 1.26 to stride length, but a factor of 2.28 to frequency, when the speed triples (from 0.5 to 1.5 m s^{-1} ; obtained from the regression equations of the hind legs in Tables 2, 3). Moreover, *E. macularius* keeps its step length

constant and probably avoids floating phases in its strides. Extrapolation of the regression equation for duty factor (Table 3) to the maximal speed of 1.8 m s^{-1} predicts a duty factor of 0.5! These two features are attributable to a specialist climber (see above). So, does the locomotor style of *E. macularius* resemble the presumed ancestral state of a horizontal runner or were the ancestral gekkotans (as suggested by Russell, 1976; Russel, 1979) climbers, although not necessarily as specialised as *G. gecko*, rather than ground-dwellers? It could also be argued that the strategy used by both species represents a basic non-specialised locomotor behaviour, which can be considered as an exaptation for highly specialised climbing. In this respect, it is worthwhile considering the modulation strategy of the two *Podarcis* species plotted in Fig. 7 (see also Van Damme et al., 1998). Both species resemble the gekkotans of the present study fairly well: stride length modulation is small compared with frequency modulation and step length is kept constant. Nevertheless, one species is a ground-dweller (*P. h. atrata*), whereas the other must be considered as a climber (*P. h. hispanica*). However, it is still possible that climbing represents the primitive state in this case too (see Van Damme et al., 1998).

The second working hypothesis formulated above stated that *G. gecko* retains its climbing style of speed modulation when moving on a level surface because this style is an expression of the intrinsic properties of the system, leaving no room for behavioural modulation. From this perspective, these intrinsic properties are considered to be tuned by natural selection to a specialised climbing life-style. In general, we must conclude that *G. gecko* performs on the level surface in the same way as when it climbs: i.e. frequency-modulated, with a constant step length and keeping at least one (fore) limb always on the ground.

Compared with climbing, stride lengths are somewhat smaller on the level substratum, while frequencies are higher. But, in this case and in contrast to the climbing results, stride length does not change with speed. The constant step lengths are identical to those used in climbing, which provides further support for the suggestion that this variable is maximized at all speeds and is set by morphological and mechanical constraints (leg length, girdle rotation, maximal excursions at the joints between leg segments, etc.). On only a few occasions do the duty factors of the hind legs drop below 0.5. In all other cases, even at the highest speeds, they remain well above this value (see Fig. 3). The degree of sprawling differs between climbing and level locomotion (see Table 4). On the level, sprawling is reduced, with the front legs, especially, placed nearer the body. As a result, the body is presumably lifted from the substratum. To climb vertically, it is essential to keep the body close to the substratum (see above). Since gravity acts parallel to a vertical surface, this does not necessarily imply significant frictional forces. On the level, the body weight would induce frictional forces unless *G. gecko* lifts its body from the ground.

That smaller stride lengths were observed in *G. gecko* when moving on the horizontal is remarkable because, theoretically, there are no constraints on stride length when moving on a

horizontal substratum (see above). Therefore, stride length would be expected to be at least equal to that for similar climbing speeds. Zaaf et al. (Zaaf et al., 1999) showed that the muscular system of *G. gecko* appears to be fine-tuned to its climbing life-style. It is therefore not inconceivable that the altered leg configuration required to lift the body above the substratum during horizontal movement constrains muscle performance (or joint motions) in the stride direction, resulting in a decrease in the stride length. Since step length does not change with substratum orientation, this must express itself through an extended overlap in ground contact of diagonal pairs of legs. Indeed, the average duty factors are somewhat larger during level locomotion (see Table 4).

So, concerning this second hypothesis, we must conclude that the basic coordination of the limb movements does not change when *G. gecko* changes to a novel substratum orientation. This basic coordination resembles that of the ground-dwelling *E. macularius*, since climbing in the former species was fairly similar to level locomotion in the latter (see above). Provided that level locomotion is the ancestral locomotor state of the gekkotans (Grismer, 1988; Russell, 1976; Russell, 1979) and that the strategy applied by both species represents a basic non-specialised locomotor behaviour (see above), *G. gecko* (or specialist climbers in general) apparently retained this strategy with minor alterations when adopting their new life-style. In this context, the ancestral locomotor state must be considered an exaptation for climbing allowing for superb performance as soon as adhesive pads emerged. However, assuming a scansorial life-style as the ancestral state (Grismer, 1988; Russell, 1976; Russell, 1979; see above), it can be hypothesized that the intrinsic properties of the locomotor system are so attuned to this life-style that the specific spatio-temporal behaviour (i.e. the collective result of these properties) is inevitably exhibited on whatever substratum the animals perform. This suggestion would be disproved if *E. macularius* alters its spatio-temporal behaviour when climbing (see below).

The ground-dwelling species, *E. macularius*, has potentially more flexibility in its speed modulation strategy since the constraints associated with vertical climbing are absent. This increased flexibility should allow this species to adjust its strategy when climbing. From the results and the above discussion, it is clear that this does not occur: overall, ground-dwelling *E. macularius* modulate their speed in a similar way to *G. gecko* climbing or moving on a level surface. So, how does *E. macularius* alter its locomotor behaviour when climbing? As mentioned above, the narrow, slow speed range obtained for climbing in the present study precludes statistical comparison. However, visual inspection of the frequency, stride length and duty factor data (Figs 2, 3) suggests that, if level-surface locomotion had been recorded for *E. macularius* at such slow speeds, frequency, stride length and duty factor would probably have been very similar to those measured for climbing. This suggestion is reinforced when the log/log regressions for level locomotion presented in Table 3 are extrapolated to the speeds obtained for climbing. The speed

range 2.5–8.5 cm s⁻¹ gives predicted stride lengths ranging from 6 to 9 cm, frequencies between 0.4 and 1.02 Hz and duty factors of 0.92–0.79. These predicted values coincide strikingly well with our measurements made for climbing (see Figs 2, 3). Step lengths are independent of speed but change slightly with substratum orientation (the step lengths of the fore-limbs were longer when climbing, those of the hind-limbs were shorter; see Table 4).

A major difference seems to be that *E. macularius* shifts from a walking trot to a 'lateral single foot' sequence when moving from a horizontal to a vertical substratum. This is obvious from the relative phase between the fore- and hind-limbs. Again, however, this apparent change in style might be the result of the very low speeds recorded rather than being induced by the difference in incline. When moving slowly, most tetrapods (including lizards and salamanders) use this sequence of footfalls because it provides the highest stability (Hildebrand, 1985; Hildebrand, 1988). Only when moving faster do they change to a walking or running trot because the time then available for the centre of mass to move away from the diagonal line of support becomes too short.

Unlike in *G. gecko*, sprawling in *E. macularius* appears to decrease slightly on the vertical substratum (not statistically significant for the hind-limb; see Table 4). A qualitative evaluation of the video sequences of climbing *E. macularius* suggests that this reduction is because the specimens try to minimize the distance between the body and the substratum in an alternative way. The intra-leg configurations during stance differ from those observed during level locomotion: the legs are kept close to the sides of the body, with the shoulder and hip lowered below the elbow and knee respectively (i.e. the elbows and knees point upwards). It is surprising that this drastic change does not affect the step length to a larger extent. This provides support for the suggestions that gekkotans maximize their step length when possible and that this step length is determined mainly by rotational constraints at the level of the hip and shoulder joint.

To summarise, it appears that the overall pattern of coordination in climbing *E. macularius* does not differ from its level locomotion strategy. This is not really unexpected because the level locomotion style already corresponds to that presumably appropriate for climbing (see above). However, it is obvious that a vertical incline presents *E. macularius* with serious problems. When observing animals climbing, it is clear that the low speeds achieved are not a matter of motivation but are a direct consequence of the lack of adhesive structures.

So, despite the fact that it has been shown in the literature that substratum inclination can affect absolute sprint performance (for lizards over 40 g; Huey and Hertz, 1984), the net cost of transport (Farley and Emshwiller, 1996) and the detailed limb kinematics and gait characteristics (Irschick and Jayne, 1998; Jayne and Irschick, 1999) we demonstrate here, for two gecko species with clearly different preferred habitats, that only slight adjustments in gait characteristics are made when they are forced to move on a non-habitual substratum. In addition, the gait characteristics differ little between these two

species. Given the large niche differences and assuming the existence of selective pressure on spatio-temporal gait variables, this resemblance is probably dictated by historical (phylogenetic) constraints. If level locomotion represents the ancestral state for gekkotans (Russell, 1976; Russell, 1979), it is surprising to find that this common strategy suits climbing (fixed spatial variables, no floating phases) rather than level locomotion. Presumably, constraints other than those strictly coupled to locomotion must be considered to explain this.

Ancestral gekkotans are thought to be nocturnal (Autumn et al., 1994; Autumn et al., 1997). The accuracy of foot placement (through fixed spatial gait variables) might be essential when visual inspection of the substratum is hindered by low- or no-light conditions. From this point of view, nocturnality could be considered an exaptation for climbing. The development of adhesive pads allowed *G. gecko*, as well as other true geckos, to exploit the climbing niche to its extremes (i.e. on smooth vertical or overhanging surfaces) without affecting their performance on less-demanding substrata (sub-vertical, horizontal). This could explain why the level performance of the specialist climber is not inferior to that of the ground-dwelling gekkotan (the basic control strategy is applied in all circumstances), but also why the two species we studied apparently move considerably slower than other (non-climbing) lizards of similar size (see Fig. 7; i.e. the basic control strategy is not optimized for running). This further implies that the poor climbing performance of *E. macularius* is probably a consequence of the extreme experimental conditions (vertical, smooth surface), rather than being an expression of an intrinsic inability to climb. Detailed performance analyses, including tests on sub-vertical inclines, could provide insight into this problem. Such analyses are the subject of our current research.

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