Limb joint kinematics during vertical climbing and level running in a specialist climber: *Gekko gecko* Linneus, 1758 (Lacertilia: Gekkonidae)

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ABSTRACT. Previous studies revealed that, despite clear morphological adaptations for climbing, performance and gait characteristics are barely affected when the specialist climbing lizard *Gekko gecko* is forced to run on its non-preferred level substrate. The present study focuses on the detailed joint kinematics of front and hind limbs to investigate whether this lizard modulates its limb movements while running on its non-preferred substrate. The intra-limb (fore and hind limbs) kinematic patterns were determined at three different speeds in *G. gecko* when climbing and running horizontally. Additionally, three-dimensional angles were determined at lift-off and at touch-down for both the fore and hind limbs over a wide range of running and climbing speeds. Generally, the intra-limb movement patterns used during level running are similar to those used when climbing. Moreover, the joint angles at lift-off and touch-down also show a high similarity for climbing and level running. There are some differences in joint angles: during climbing the shoulder and the elbow tend to be more extended at lift-off and touch-down compared to level running, and when the hind foot touches the substrate both the hip and the knee show a greater extension on level surface whereas the ankle is more extended during climbing. These differences can be grouped into two categories: the differences in the hip, ankle and wrist are likely to be related to the observed change in the posture and gait between climbing and level running. The changes in the shoulder, the elbow and the knee angles when *G. gecko* runs over-ground are likely to be the result of differences in the biomechanical constraints encountered during climbing and level-running.

KEY WORDS: *Gekko gecko*, kinematics, locomotion, climbing, level running

INTRODUCTION

In nature, lizards have to perform in a complex, three-dimensional environment. From field observations, some species appear to be restricted to horizontal surfaces or to substrates with a relatively low degree of inclination (e.g. ground dwelling geckoes such as *Eublepharis macularius*), whereas others can move seemingly effortlessly on even very steep inclines (AUTUMN et al., 2000). Given that the mechanical demands for climbing differ largely from those for level running (part of the climbing effort is used to counter the altered effects of gravity; e.g. ZAAF et al., 1999), adaptations or specialisations that allow maximal performance on inclined substrates are expected (BAUER et al., 1996; ZAAF et al., 1999). Results of some experimental studies, in which typically ground dwelling species are induced to run up-hill, indicate that running on

an incline does confront these animals with serious physical constraints. Not only are the metabolic costs considerably higher (e.g. FARLEY & EMSHWILLER, 1996), also the running performance decreases with incline (e.g. FARLEY, 1997; VAN DAMME et al., 1997; IRSCHICK & JAYNE, 1998; JAYNE & ELLIS, 1998; JAYNE & IRSCHICK, 1999; VANHOOYDONCK et al., 2000).

It is often assumed that specialisation for extreme habitat types (e.g. vertical walls) constrains performance in other habitats due to the conflicting demands imposed on the system (LEVINS, 1968). Yet HUEY & HERTZ (1982), could not detect significant negative effects of incline on performance in small ground dwelling agamid lizards. Similarly, in the specialised climbing lizard *Gekko gecko*, no effect of incline on performance was observed (ZAAF, 2000). Whereas one might argue that the case of the agamid lizard is just an example of the 'jack of all trades is the master of none' paradigm (LEVINS, 1968; HUEY & HERTZ, 1984), in the case of highly specialised climbers

such as *G. gecko* this is definitely not true. Apart from the premised features obviously favouring climbing (such as adhesive toe pads, short legs, flattened body shape and posture, appropriate gait, PIANKA & PIANKA, 1976; JAKSIC et al., 1980; CARTMILL, 1985; POUNDS, 1988; SINERVO & LOSOS, 1991; GARLAND & LOSOS, 1994; MILES, 1994; ZAAF et al., 2001), ZAAF et al. (1999) even found subtle functional shifts in the musculature, which could be related to the preferred substrate orientation. Yet, despite these morphological differences, neither the performance nor the gait seem to change markedly when this species is forced to run on its non-preferred (horizontal) substrate (ZAAF, 2000; ZAAF et al., 2001).

These rather unexpected results for *G. gecko* might be explained in two ways. Firstly, adaptations needed to climb vertical structures might not detrimentally affect performance on the horizontal. In this way, high climbing performance does not impede good performance on a level surface (see also VANHOOYDONCK & VAN DAMME, 2001). Secondly, specimens might compensate or accommodate behaviourally for reduced running performance as a result of their adaptations for climbing. In the latter case altered locomotor behaviour should likely be reflected in the spatio-temporal aspects of gait (stride frequencies and lengths, step lengths, duty factors, floating phases). However, as mentioned above, these variables in their relation with speed are largely unaffected by changes in substrate inclination. Despite this, the intra-leg movements used to produce the unchanged foot fall pattern might still differ between substrates (i.e. alternative combinations of joint rotations for similar linear leg displacements), thus reflecting behavioural accommodation.

Moreover, such changes of the intra-leg kinematics, if present, can be expected to be different for the fore and hind limbs. During vertical climbing, tension from the fore limbs is needed to avoid backward tumbling, thus assisting the hind limbs in generating propulsion. During level locomotion of many species, however, the hind limbs are considered as the predominant propulsive element (SNYDER, 1952; REILLY & DELANCEY, 1997a,b). At high speeds, the fore limbs often do not contribute to locomotion at all (SNYDER, 1952, 1962; IRSCHICK & JAYNE, 1999). If this functional shift occurs in *G. gecko*, the fore limb kinematics are likely to change with substrate orientation in a manner differing from that of the hind limbs.

In this paper we investigate whether, and if so how, accommodation of the locomotor behaviour occurs when *G. gecko* is forced to run on its non-preferred (horizontal) substrate orientation. Therefore, we quantify and compare the three-dimensional joint angles at touch-down and lift-off over a range of speeds. Moreover, the patterns of these angles are compared at three different speeds for running and climb-ing. Given the potential shift in limb pair function and dominance, this is done for fore and hind limb separately.

MATERIAL AND METHODS

Three specimens of *Gekko gecko* 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 separate terraria (60 x 100 x 40 cm) on a 12:12h light dark cycle. Ambient temperature varied from 26°C during daytime 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.

TABLE 1

Morphometrical characterisation of the three *Gekko gecko* specimens used in this study.

	snout-vent length (cm)	mass (g)	fore limb length (cm)	hind limb length (cm)
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

For the experiments, a track was constructed consisting of two removable wooden boxes at each end of a glass-tunnel (140 x 20 x 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 cork-film. To study climbing, the tunnel was placed vertically. The animals were put in the box at the bottom of the tunnel and induced to run through it towards the other box fixed at the top. When the animal entered the top box, boxes were switched and the procedure was repeated.

Animals were marked by white non-toxic paint dots on the tip of the snout, the centre of the pectoral and pelvic girdles, mid-hand and mid-foot, and on all the joints of fore and hind limbs (Fig. 1). In *G. gecko*, the mid-hand and mid-foot are the first limb segments that hit the substrate and the last that leave it (respectively before and after the digits touch and leave the substrate, see RUSSELL, 1975). Therefore, we decided to put markers at the level of the metatarsal and metacarpal bones.

Running and climbing sequences were recorded from above with a NAC-1000 high-speed video system set at 500 frames. A mirror fixed on a wooden support immediately lateral to the glass-tunnel at an angle of 45° provided a simultaneous lateral view. Animals were given at least 15 minutes of rest between successive trials. Only sequences where the animals ran straight and continu-
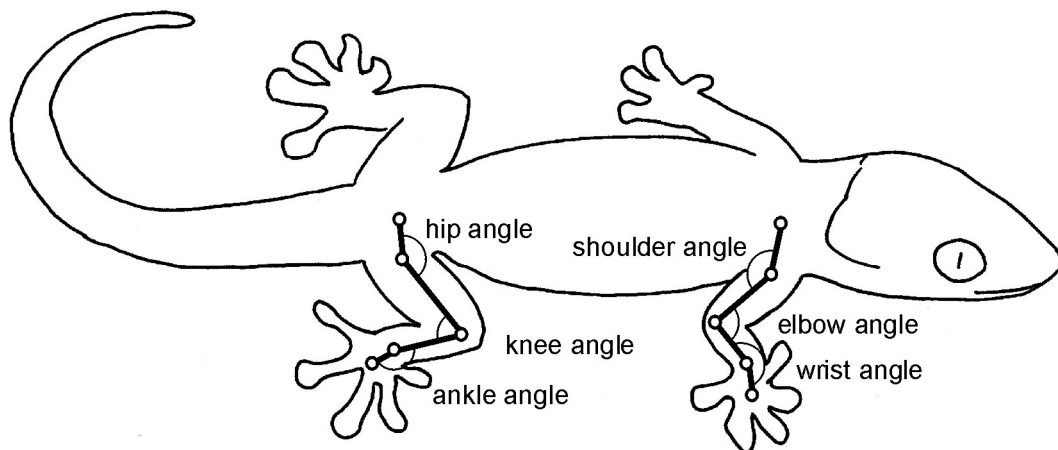
Fig 1. – Landmarks (white dots) and segments (bars) used to calculate the three-dimensional angles in *Gekko gecko*. The angles used in the analysis are indicated.

ously were retained for further analysis. From the positions of the marker on the snout tip, early and late in these sequences, an estimate of running speed was obtained. Based on these estimates, nine climbing sequences were selected for specimens 1 and 2 (Table 1) representing a velocity range as wide as possible. Inducing horizontal running was more difficult in these two specimens. Animals preferred to run on the side-walls of the corridor or simply sat on the side-walls enclosing the tunnel. We obtained only 5 and 2 running bouts respectively. Eight additional running bouts were added from the third specimen (Table 1).

We calculated the angles (3D) between the limb segments (based on the digitised 3D-coordinates of the markers) as indicated on Fig. 1 at the time when the feet touched and left the substrate as this corresponds to the extreme leg configurations. The relationship with forward speed (obtained from the linear regression of the pelvic marker) was established by means of least squares linear regression analysis. T-tests were performed to explore the difference between the joint angles at lift-off and touch-down (and at mid-stance and mid-swing for knee and elbow) and to compare the shoulder, the elbow and the wrist with the hip, the knee and the ankle respectively. A t–test was also performed to see if joint angles are affected by substrate inclination. If the angles were speed dependant, analysis of covariance (ANCOVA, velocity as covariate) was used.

Three climbing and level running sequences of specimen 1 were selected, which covered a speed range (from about 0.60 to 0.90 m/s). Within 1 cm/s the climbing speed was identical to the level running speed. The markers were digitised frame by frame and the 3D-joint angles were calculated as mentioned above. Profiles were smoothed with a zero-phase shift digital low-pass filter (WINTER, 1990; cut-off frequency = 25 Hz). The shoulder, the elbow and the wrist angles were plotted against the relative fore limb cycle (%FF; see Figs 2,3). Similarly, the hip, the knee and the ankle angle were plotted against the relative hind limb cycle (%HF; see Figs 2,3). Zero % corresponds to the time that the fore limb touches the substrate.

RESULTS

General kinematic pattern

Fig. 2 illustrates how the three-dimensional angles within the fore limbs and the hinds limbs vary during their respective stride cycle at three different climbing speeds. The angular patterns for comparable level running speeds by the same individual are represented in Fig. 3.

As soon as the fore foot hits the substrate (0% of the cycle), the extended elbow (± 150°) flexes 40° to 50°. This maximal elbow flexion is reached at all speeds at about 35% of the fore limb cycle. Thereafter, the elbow extends again for the remainder of the stance phase. At lift-off the elbow starts to flex until about – 30% of the fore limb cycle. The amount of flexion during the swing phase is, however, considerably smaller than that observed during stance. This difference appears to become larger with increasing speed. The elbow thus shows a double flexion-extension cycle coinciding with stance and swing. During level running, the elbow shows the same double flexion-extension cycle (with the larger amplitude during stance) as observed for climbing.

At touch-down, the already extended shoulder (± 150°) continues to extend for about 10° during the initial part of stance (± 10% of the limb cycle). Then a sharp flexion of about 60° occurs (retraction of the fore limb), after which the shoulder flexes briefly further (especially at the lowest climbing speed). In the first part of the stance phase fast extension of the shoulder (protraction of the fore limb) takes place. The shoulder thus goes through one simple flexion-extension cycle, which is slightly out of phase with the transitions between stance and swing. At higher running speeds, the pattern of the shoulder angle during level running is very similar to that observed during climbing. At the lowest speed, a flexion-extension cycle is also present, but is somewhat more irregular.

For the wrist angle, no obvious patterns can be discerned. The wrist angle appears to change irregularly with
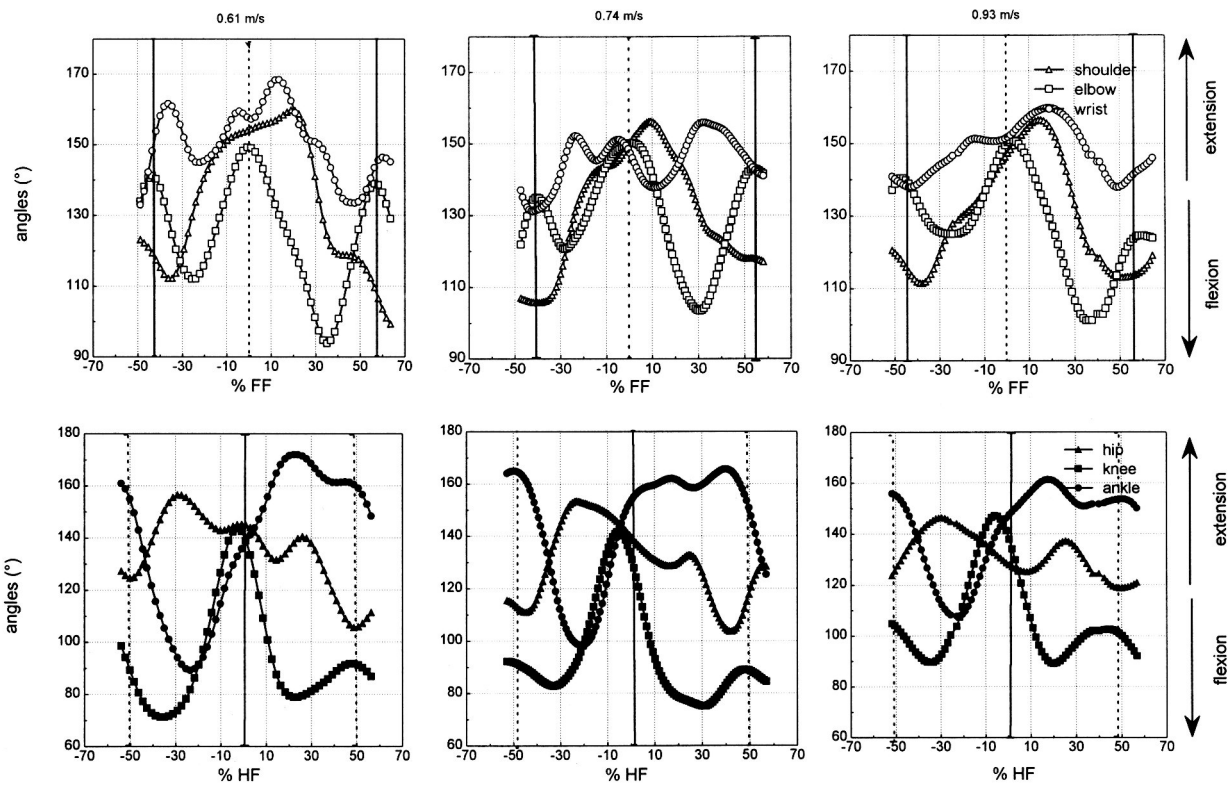
Fig 2. – Three-dimensional angles adjusted to the limb cycle (right body side) of G*ekko gecko* climbing at three speeds (0.61, 0.74 and 0.93 m/s). Shoulder, elbow and wrist are plotted against the fore limb cycle; hip, knee and ankle are plotted against the hind limb cycle. Zero % corresponds to the time when the fore foot hits the substrate. The vertical dashed lines on each plot indicate the time when the foot hits the substrate. The solid lines represent lift-off.

Fig 3. – Three-dimensional angles adjusted to the limb cycle (right body side) of G*ekko gecko* level running at three speeds (0.60, 0.73 and 0.92 m/s). Shoulder, elbow and wrist are plotted against the fore limb cycle; hip, knee and ankle are plotted against the hind limb cycle. 0 % corresponds to the time when the fore foot hits the substrate. The vertical dashed lines on each plot indicate the time when the foot hits the substrate. The solid lines represent lift-off.
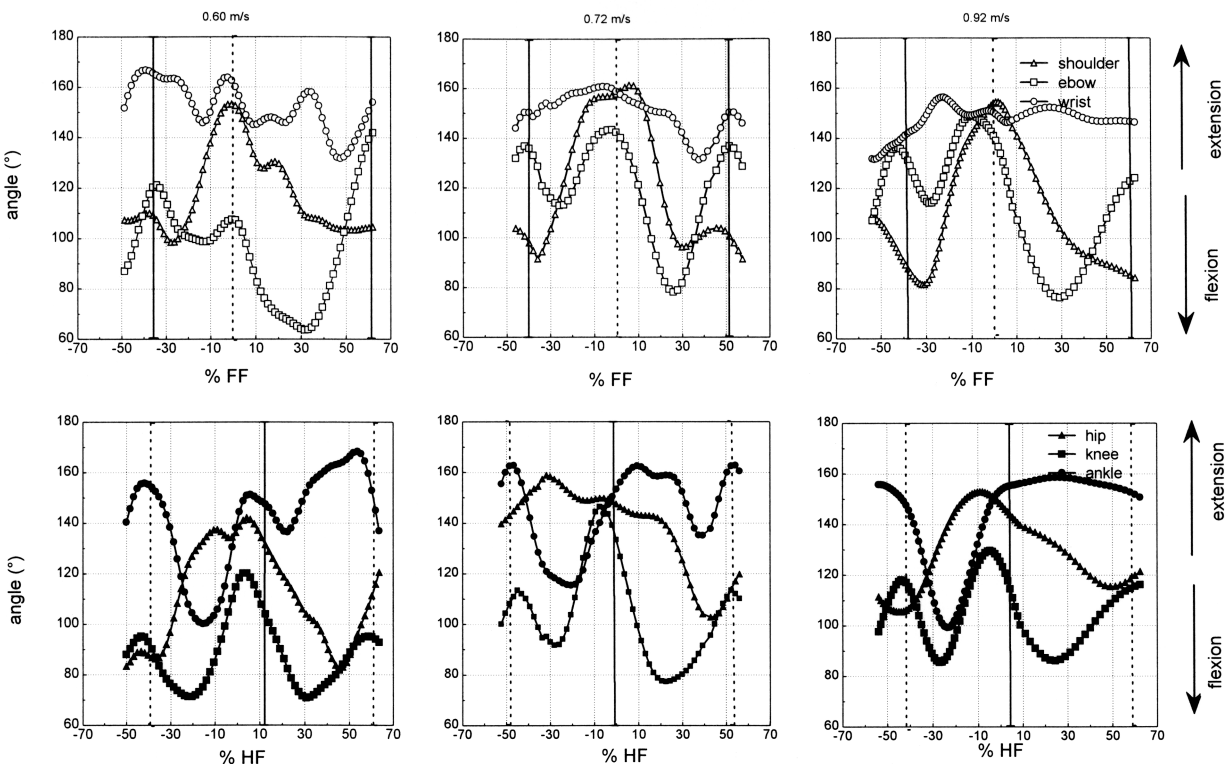
speed. At the lowest speed, the wrist angle pattern approximates a double flexion-extension cycle. At the highest speed this pattern reduces to a single flexion-extension cycle. Wrist angle patterns during level running are rather variable as observed during climbing.

When the hind foot touches the substrate, the knee flexes, starting from an angle of about 90°, for only about 10° to 20° during the first 15% of the limb cycle. Thereafter, it extends 60° to 70° for almost the entire stance phase. A small flexion (about 10°) occurs just prior to lift-off. It proceeds in a very rapid flexion of the knee (about 50°) during the first part of the swing phase. Then the knee extends again (about 10°) towards the end of the swing phase. Thus, the knee goes through a double flexion-extension cycle coinciding with stance and swing respectively. In this case, however, both flexion-extension cycles are extremely asymmetric, with the stance phase being characterized by extension and the swing phase by flexion. The pattern of the knee during level running is generally similar to the pattern observed during climbing, although the extension towards the end of stance appears to be somewhat smaller during level running.

During about the first third of stance the hip extends rapidly 30° to 40° starting from an angle of about 120°. During stance, the hip starts to flex, slowly, and continues

into the swing phase. About half way through the swing phase a brief period of extension, coinciding with the transition from flexion to extension in the knee, occurs. Overall, the angular rotation in the hip remains small (amplitude about 30° to 40°) and is characterized by a strong temporal asymmetry. The angular rotations in the hip for level running *G. gecko* are somewhat larger than those for climbing animals (about 40° to 50°). The marked brief extension during swing observed in climbing is absent during level running.

Contrary to the wrist, ankle patterns appear more stable during climbing. Over the first half of the stance phase, the ankle flexes from about 160° to about 70°. Next, during the stance phase the ankle extends to about 145° after which the ankle angle remains constant until the next touch-down. The ankle thus shows a single, but temporally strongly asymmetric, flexion-extension cycle. Except at the lowest speed, the ankle pattern for level running is highly similar to that observed during climbing.

Effect of speed

Table 2 summarises the effect of speed on the joint angles at lift-off and touch-down as well as at the time when the foot leaves and hits the substrate (expressed as %

TABLE 2

Relationships between angular variables (at lift-off and touch-down) and velocity for *Gekko gecko* moving on horizontal and vertical substrates. Intercepts and slopes (± se) of least squares regressions (angles = b +a ∗ velocity) are given for those relations that had significant r^2-values. Velocity is expressed in ms^{-1}, angles in degrees.

	level running (*N* = 18)			climbing (*N* = 15)		
	r^2	slope ± se	intercept ± se	r^2	slope ± se	intercept ± se
			fore foot			
			lift-off			
%FF	0.0369	-	-	0.020	-	-
shoulder	0.001	-	-	0.011	-	-
elbow	0.237	-	-	0.001	-	
wrist	0.006	-	-	0.072	-	-
			touch-down			
%FF	NT	-	-	NT	-	-
shoulder	0.00002	-	-	0.124	-	-
elbow	0.138	-	-	0.003	-	-
wrist	0.164	-	-	0.0007	-	-
			hind foot			
			lift-off			
% HF	0.09	-	-	0.061	-	-
hip	0.0004	-	-	0.027	-	-
knee	0.0157	-	-	0.441**	27.76±0.187	72.73±7.23
ankle	0.063	-	-	0.001	-	-
			touch-down			
% HF	0.162	-	-	0.072	-	-
hip	0.615***	49.14±10.781	73.18±12.273	0.019	-	-
knee	0.097	-	-	0.079	-	-
ankle	0.513**	-31.39±8.47	173.62±9.648	0.074	-	-

significant at *P* = 0.01.; * significant at *P* = 0.001. %FF, timing of touch-down/lift-off expressed as a proportion of the front foot cycle; %HF, timing of touch-down/lift-off expressed as a proportion of the hind foot cycle; NT, not testable as fore foot touch-down was considered as time zero by definition.
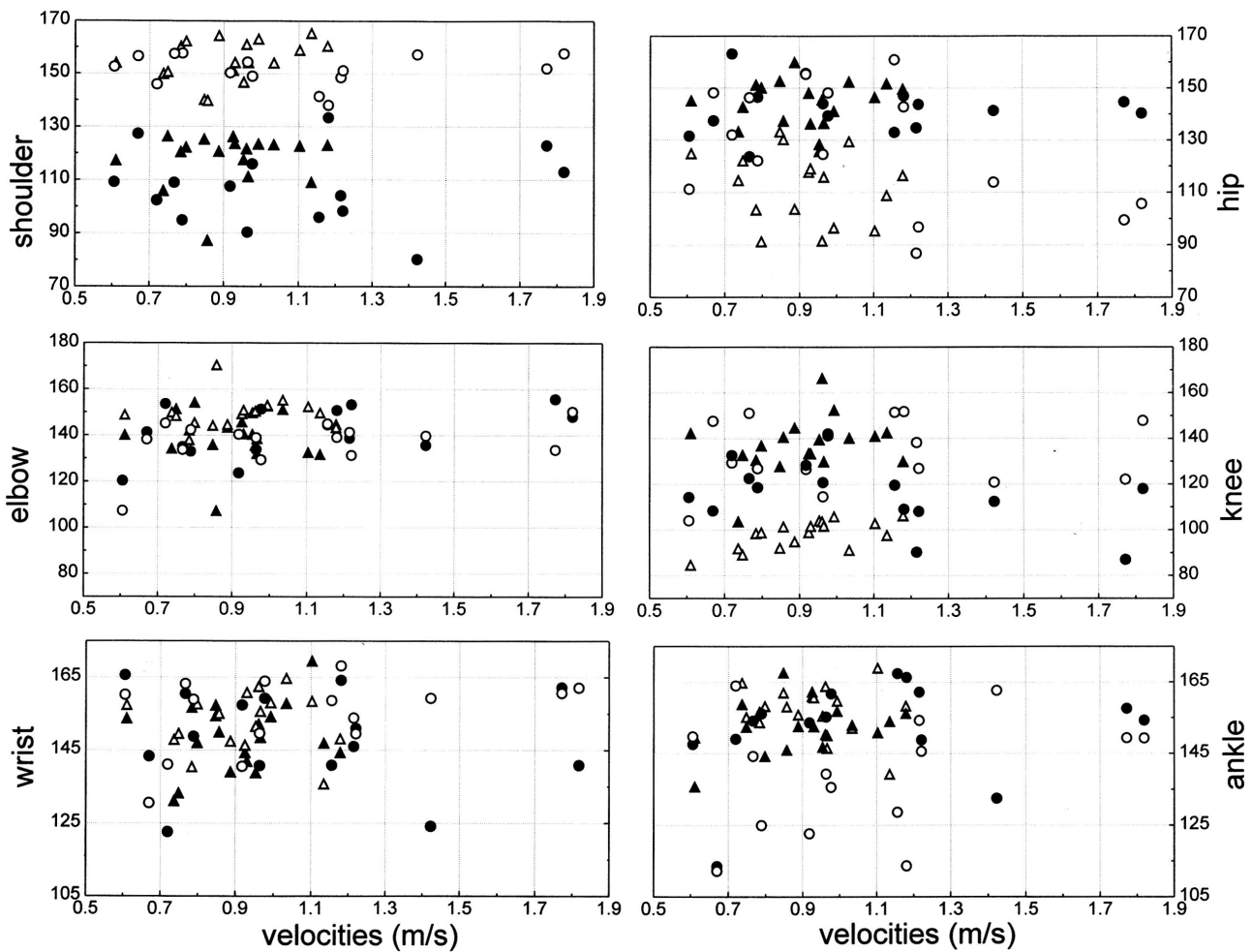
Fig 4. – The three-dimensional angles of the fore and hind limbs of G*ekko gecko* determined at touch-down (open symbols) and at lift-off (filled symbols) versus speed. Triangles and circles represent running vertically and horizontally respectively.

of the stride cycle). During climbing and level running, the joint angles of the fore limbs do not change with speed (all P > 0.06; Fig.4). When the hind foot leaves the substrate, none of the hind limb angles change with speed (all P > 0.25; Fig.4). However, at touch-down, during level running the hip angle increases (P < 0.01) and the ankle angle decreases (P < 0.01) with increasing speed (Fig.4). An increase in level running speed from 0.5 to 1 m/s results in an increase by 20% of the hip angle, and a decrease in ankle angle of about 11% (both calculated from the regression equations). During climbing, only the knee angle at hind foot touch-down increases with speed (Table 2). Consequently, an increase in speed from 0.5 to 1 m/s (based on the regression equations) results in an increase of 14 % in knee angle at hind foot-fall. None of the timing parameters calculated change with speed (all P > 0.13).

(Table 3, paired t-test, t_{17} = -2.78, P = 0.01 and t_{14} = -1.04, P < 0.01, for climbing and level running respectively). Additionally, the hind foot touches the substrate before the fore foot leaves it (t_{17} = 4.28, P < 0.01 and t_{14} = 3.36, P < 0.01 for climbing and level running respectively).

TABLE 3

Comparison of the timing when the front and hind feet of *Gekko gecko* hit, and leave the substrate (expressed as a proportion of the fore/hind foot cycle respectively). Time zero is defined at front foot contact. Values are means ± standard error.

	vertical		horizontal	
	lift-off	touch-down	lift-off	touch-down
front foot	-44.97 ± 2.558	0	-42.88 ± 3.954	0
hind foot	2.057 ± 2.985	-48.22 ± 2.559	5.52 ± 4.301	-46.21 ± 4.692

Hind limb versus fore limb timing

During both climbing and level running, the hind limb leaves the ground after the fore foot hits the substrate

Difference within limbs

The elbow and the knee flex twice during a cycle, during the stance and the swing phase respectively (Figs 2,

3). Therefore, the elbow and the knee angles cannot only be compared between footfall and lift-off, but also between mid-stance and mid-swing.

During climbing, the elbow is more extended at touch-down than at lift-off (t-test for dependent samples, t_{17} = -2.513, P = 0.02), amounting up to an average of 6.21% difference. However, during level running, touch-down and lift-off, elbow angles are comparable. Additionally, the elbow is consistently more extended at mid-swing than at mid-stance, for both level and vertical running (t-test for dependent sample, climbing t_{17} = 4.42, P < 0.01; level running: t_{14} = 7.61, P < 0.01). On average, at mid-swing the elbow is 11.27% more extended during climbing and 28.9% more extended during level running.

In contrast, the knee is more extended when the hind foot leaves the substrate than at touch-down (t-test for dependent samples, climbing; t_{17} = -13.71, P < 0.01; level running: t_{17} = -4.17, P < 0.01). The average differences are 28.4% and 13.5% during climbing and level running respectively. The knee is also more extended at mid-stance than during mid-swing in climbing (t-test, t_{17} = 4.438, P < 0.01). In level running, mid-stance and mid-swing knee angles are comparable.

Climbing versus level running

The shoulder is more extended during climbing than during level running when the fore foot leaves the substrate (t-test for independent samples, t_{31} = -2.69, P = 0.01), but not when it touches it (t_{31} = -1.55, P = 0.13). On average the shoulder extends 9.5% more during climbing. At lift-off the degree of the elbow extension is comparable for climbing and level running (t_{31} = 0.35, P = 0.72), but the elbow extends further during climbing (t_{31} = -4.07, P < 0.01). At both footfall and lift-off, the wrist angle is identical for horizontal and vertical running (P > 0.5).

At hind foot lift-off, none of the hip, the knee or the ankle angles vary between climbing and level running (t-test, all P > 0.3). At touch-down, however, these angles do change with substrate orientation. The regression lines relating the hip angle at footfall with speed during climbing and level running differ in slopes (Analyse of covari-

ance, $F_{1,29}$ = 6.71, P = 0.015), but not in intercepts ($F_{1,30}$ = 1.28, P = 0.27). The hip angle at footfall increases during level running. The regression lines relating knee and ankle angles with speed do not differ in slopes ($F_{1,29}$ = 0.78, P = 0.3 and $F_{1,29}$ = 2.97, P = 0.09 for the knee and ankle respectively), but do differ in intercepts ($F_{1,30}$ = 16.48, P < 0.01 and $F_{1,30}$ = 12.41, P < 0.01 for the knee and the ankle respectively). On average the knee angle at footfall is larger during level running and that of the ankle is larger during climbing (see Table 4).

DISCUSSION

ZAAF and co-workers (2001) observed that *G. gecko* takes somewhat larger strides at a lower frequency while climbing, and smaller front limb steps while running on the horizontal. Duty factors are constant over speed, but are somewhat larger during running, while during climbing sprawling is significantly larger. Based on these findings ZAAF et al. (2001) concluded that the spatial aspects of climbing are kept fairly constant and that this strategy is retained when switching to a horizontal substrate. In the following section, we examine in more detail how the joint angles change between climbing and running.

The hip angle at the time when the hind foot leaves the substrate shows the same amount of extension whether the animal is running or climbing (table 4). However, at touch-down the hip angle increase slightly with speed during level running. By increasing the hip angle with speed at footfall during level running, *G. gecko* presumably modifies the point of contact of the foot with the substrate in order to deliver force. Although we do not provide a direct measurement on the femur retraction-protraction and rotation, it is likely that that the higher hip angle on the level surface means that the femur is less protracted at touch-down (see Fig.1). Probably, this difference in protraction is a consequence of the postural change that takes place when *G. gecko* shifts to a horizontal surface. ZAAF et al. (2001) showed that sprawling was reduced on the flat (probably to reduce potential friction with the surface), which might constrain femoral protraction. As the degree of sprawling decreases with increasing level running speeds, the velocity effect on the hip angle at touch-down supports this hypothesis. REILLY & ELIAS (1998) found similar results in the alligator when it changed from a sprawling gait to a high walk. In this species, a greater femoral excursion in the sprawling gait (in comparison with the high walk) is realised by a greater femur protraction just prior to touch-down. This is similar to what happens in sprawled climbing by *G. gecko*. The stronger protraction of the femur may thus allow a more anterior placement of the hind foot, which can increase the step length. This is, however, not observed in *G. gecko*

TABLE 4

Mean values (± SE) of the amount of joint angles at lift-off and touch-down in *Gekko gecko* when running and climbing.

| | vertical | | horizontal | |
	lift-off	touch-down	lift-off	touch-down
shoulder	118.22±9.676	155.12±7.691	106.90±14.313	151.33±6.040
elbow	139.91±10.896	149.17±7.085	141.27±11.042	137.07±9.930
wrist	148.18±9.545	152.90±7.64	148.46±13.482	154.65±10.478
hip	144.92±8.130	113.33±13.62	141.684±9.665	126.237±23.41
knee	137.15±12.482	98.09±6.1819	133.37±14.987	115.35±14.220
ankle	152.69±7.094	156.91±7.008	152.00±13.674	139.74±16.368

(see ZAAF et al., 2001), which implies that the larger upper limb rotation is counteracted by decreased rotations at the level of other joints (e.g. smaller knee extension). Moreover, the movement of the femur is not restricted to simple retraction-protraction, but it can also rotate about its long axis to generate thrust (i.e. JAYNE & IRSCHICK, 1999). According to these authors, the amount of femoral rotation is minimised on inclined surfaces in the generalized lizard *Dipsosaurus dorsalis,* to keep the body close to the substrate. However, in contrast to *G. gecko, D. dorsalis* reduces its degree of sprawling on inclined surfaces.

Our results show that the shoulder and hip react differently to the physical demands imposed by the substrate orientation. Whereas the femur is more protracted at touch-down on the vertical substrate, and retracts equally far whether *G. gecko* is running or climbing, the humerus excursion is reduced on the vertical substrate as a result of a decrease of the degree of retraction at lift-off. This suggests that front steps are smaller on the vertical substrate, but this appears to be compensated for by the increased elbow extension at touch-down (ZAAF et al., 2001). Maybe, the less retracted state of the upper arm is required to ensure a sufficient backward pointing force transmission to the vertical substrate throughout stance.

Both the elbow and the knee show a flexion-extension cycle during both the swing and stance phases of the locomotor cycle. The amount of flexion of the elbow during the stance phase is higher than that occurring during the swing phase. This is undoubtedly linked to the need for fore limb pulling forces just mentioned. This suggests that, contrary to horizontal locomotion by specialised runners where elbow extensor activity can be expected to brake initial elbow flexion during stance, forceful elbow flexor activity (m. brachialis and m. biceps) adds to the propulsion in vertical climbing. ZAAF et al. (1999) showed that these elbow flexors are better developed in *G. gecko* than in a ground dwelling gecko.

At touch-down the amount of the elbow extension was significantly larger on a vertical substrate. This additional extension of the elbow at touch-down during climbing results in a more anterior placement of the foot. Thus, tensile flexor forces in the elbow are ensured over a larger distance.

As for the elbow, the knee angles at lift-off were comparable between level running and climbing (Table 4, Fig. 4). However, at touch-down, and unlike what is observed for the elbow, the amount of the knee extension was larger on the level than on a vertical substrate (Table.4, Fig. 4). This can clearly be related to the more parasagittal leg posture on the horizontal substrate. Through a reduction in the degree of flexion at touch-down, forceful pushing can dominate the stance phase. Obviously, the reduced excursion in the knee during climbing is compensated for by the increased femoral retraction (see above). Despite differences in limb postures and morphology, the knee is in many vertebrates, lizards and others, more flexed at touch-down when the animal is locomoting on an incline. For example, in cats (SMITH & CARLSON-KUHTA, 1995), squirrel monkeys (VILENSKY et al., 1994), turkeys (ROBERTS et al., 1997), and the lizard *Dipsosaurus dorsalis* (JAYNE & IRSCHICK, 1999), the knee was more flexed at touch-down during uphill locomotion. Moreover, ZAAF et al. (2001) show that a specialist level running gecko (*Eublepharis macularius*) reduces the degree of sprawling, and hence flexes its limbs when induced to climb vertically. By doing this, the level runner tries to minimise the distance between the body and the vertical substrate in order to reduce the moment about its centre of gravity and to gain additional friction between the body and the substrate. The specialist climber *G. gecko*, on the other hand, spreads its hind limbs to bring its body closer to the substrate when running vertically (ZAAF et al., 2001). Thus, presumably the decreased extension of the knee at touch-down in climbing *G. gecko* is involved in thrust generation as suggested above. Increased flexion of the knee at touch-down on a vertical substrate probably puts the foot and the lower leg in a position allowing the production of sufficient force to initiate forward propulsion.

The pattern of movement of the wrist shows irregular but generally small flexion-extension cycles during climbing (Fig. 2). For level running, wrist movements seem to be more regular with peaks of extension occurring mostly at lift-off and touch-down (Fig. 3, at least for the first two speeds). As *G. gecko* raises its body from the ground during level running by reducing the degree of sprawling, and by increasing the flexion of the elbow at touch-down (see higher), the observed flexion-extension movement at the wrist could be a mechanism for generating thrust by ultimate palmar flexion. On a vertical substrate, however, thrust generation through palmar flexion-extension movements seems more difficult. The fact that the wrist angle does not change over the cycle during climbing suggests that the front foot is rotated while the fore limb is retracted as was observed on high-speed recordings.

The amount of the ankle extension is comparable between lift-off and touch-down during level running. However, during climbing the hind foot hits the substrate more extended than when it leaves the ground (Fig. 4, Table 4). Again this must be related to the large sprawling during climbing. In a sprawled leg, initial plantar contact is only possible with largely extended ankles, whereas in a more parasagittal limb posture (as used for level running), plantar contact requires a more flexed ankle. However, in the alligator, REILLY & ELIAS (1998) found that the ankle was more flexed at touch-down during a sprawling gait, and in *Dipsosaurus dorsalis* the ankle angle was not affect in uphill running (JAYNE & IRSCHICK, 1999).

In most reptiles the ankle flexes early during the stance phase and a biphasic flexion-extension is observed during the stance and swing phase respectively (BRINKMAN, 1981; GATESY, 1991; REILLY & DELANCEY, 1997a;

REILLY & ELIAS, 1998; JAYNE & IRSCHICK, 1999). As mentioned already, flexion extension during stance is important for propulsion (REILLY, 1995, REILLY & DELANCEY, 1997a,b). Probably, the flexion of the ankle after lift-off is required for level runners so that their long digits do not hit the substrate while their feet are moving forward. Our data show that the ankle in *G. gecko* only flexes significantly during the propulsive phase. During limb protraction, no significant change in the ankle angle was observed. As the digits in *G. gecko* are capable of hyperextension (RUSSELL, 1975, 1976) they can compensate for the lack of ankle extension.

In the light of the hypotheses formulated in the introduction, we summarise the results as follows. To a large extent, *G. gecko* conserves the angular patterns of the leg joints when shifting from its preferred vertical substrate to the horizontal. However, like the spatio-temporal gait characteristics (see ZAAF et al., 2001) some small changes do show up. We group these differences into two categories. Changes such as the altered hip, ankle or wrist angles probably result from the reduction in sprawling when the animal movies on a horizontal surface; these could be considered as behavioural accommodations to movement on a level surface. Reduced sprawling is needed to lift the body above the surface and the observed alterations are thus an inherent consequence of this. A second category of changes can be linked to the absence of the specific constraints on propulsion in climbing, when the animal moves over ground (i.e. pulling forces at the fore limbs, continuous pushing at the hind limbs). The changes observed at the level of the knee, the elbow and the shoulder belong to this group. Climbing in *G. gecko* thus seems to go along with extensive morphological specialisation allowing good performance on both vertical and horizontal substrates. Yet, despite these morphological specialisations few alterations in the movement patterns are observed (ZAAF et al., 2001; this study).

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