



# Compliant legs enable lizards to maintain high running speeds on complex terrains

François Druelle, Jana Goyens, Menelia Vasilopoulou-Kampitsi, Peter Aerts

## ► To cite this version:

François Druelle, Jana Goyens, Menelia Vasilopoulou-Kampitsi, Peter Aerts. Compliant legs enable lizards to maintain high running speeds on complex terrains. *Journal of Experimental Biology*, 2019, 222 (6), pp.jeb.195511. 10.1242/jeb.195511 . hal-02959453

**HAL Id: hal-02959453**

**<https://hal.science/hal-02959453>**

Submitted on 31 Oct 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

## RESEARCH ARTICLE

# Compliant legs enable lizards to maintain high running speeds on complex terrains

François Druelle<sup>1,\*</sup>, Jana Goyens<sup>1</sup>, Menelia Vasilopoulou-Kampitsi<sup>1</sup> and Peter Aerts<sup>1,2</sup>

## ABSTRACT

Substrate variations are likely to constrain animal performance in natural environments, as running over complex terrains challenges the dynamic stability of the body differently in each step. Yet, being able to negotiate complex terrains at top speed is a strong advantage for animals that have to deal with predators and evasive prey. Little is known on how animals negotiate such terrain variability at high speed. We investigated this in fast-running *Acanthodactylus boskianus* lizards, by measuring their 3D kinematics using four synchronised high-speed video cameras (325 Hz) on an adaptable racetrack. This racetrack was covered with four different substrates, representing increasing levels of terrain complexity. We found that the lizards deal with this complexity gradient by gradually adopting more erect parasagittal leg postures. Legs in a more-erect position are more compliant and are therefore highly adjustable on complex terrains. Additionally, the lizards stabilise their head, which facilitates vestibular and visual perception. Together, compliant legs and head stabilisation enable the lizards to minimise movements of the body centre of mass, even when running on highly irregular terrains. This suggests that the head and the centre of mass are the priority targets for running on uneven terrains. As a result, running performance (mean forward speed) decreases only slightly, and only on the most challenging substrate under investigation.

**KEY WORDS:** *Acanthodactylus boskianus*, Compliant leg, Head stabilisation, Substrate variation, Body dynamics, Control strategy

## INTRODUCTION

Natural environments are complex because of an immense variation in structure and organisation. On a daily basis, animals have to deal with this complexity in their own (micro-)habitat while avoiding predators, catching prey and finding mates. Maintaining a fast running speed over complex terrains is very challenging for legged terrestrial vertebrates, but it may provide an advantage by maximizing fitness (e.g. Garland and Losos, 1994; Irschick and Losos, 1999; Olberding et al., 2012). While there is little data examining the role of locomotion on complex surfaces in relation to fitness, a review considering various animal species showed that sprint speed had a positive effect on fitness in ~50% of cases (Irschick et al., 2008).


Running has been intensively studied in humans and animals in general (e.g. Alexander, 1991; Hirt et al., 2017; Seyfarth et al., 2002; Van Wassenbergh and Aerts, 2013). Through coordinated motor activity, limbs behave like compliant springs during running

(Alexander, 2002). In this context, the spring-mass model has been shown to be very effective for describing the basic mechanics of running (Blickhan, 1989). With proper leg adjustments such as stiffness and the angle of attack, running can even be mechanically self-stabilised above a minimal speed, i.e. the system automatically recovers from small perturbations (Seyfarth et al., 2002, 2003). Running over complex terrains is obviously much more challenging. Each foot placement is disturbed by different orientations and inclinations of the substrate, thus potentially affecting normal, regular dynamics of the centre of mass (CoM) and it seems evident that proper control, minimising the resulting deviations of its trajectory, is needed. It has been shown that animals may rely on mass-spring dynamics to enhance their stability on uneven terrains (Daley et al., 2006; Seyfarth et al., 2003) and it has been hypothesised that compliant limbs, i.e. limbs that easily adjust their functional length according the terrain complexity, may improve stability in these challenging situations (Blum et al., 2011; Daley and Usherwood, 2010; Schmitt, 1999). In general, however, the way animals are able to keep on running at high speed over uneven terrains remains poorly understood (e.g. Biewener and Daley, 2007; Blum et al., 2011; Chadwell and Young, 2015). Maintaining stability on complex terrains relies, in part, on the intrinsic dynamic (spring-damping) properties of the limbs, which have the capacity to resist and recover from (small) perturbations without any neural feedback control (Daley and Biewener, 2011; Daley et al., 2006; Jindrich and Full, 2002) and on controlled corrective actions via supraspinal centres (e.g. Dunbar et al., 2004; Goyens and Aerts, 2018; Larsen et al., 2016; Menz et al., 2003). When and how animals need to switch from self-organised intrinsic dynamic stability to active control strategy to move over complex terrains is a fundamental area of research (e.g. Birm-Jeffery et al., 2014; Daley and Usherwood, 2010; Grimmer et al., 2008).

In studies on humans negotiating obstacles and complex terrains, a combination of strategies has been described, including purely mechanical self-stabilisation and active neuromuscular control (Blum et al., 2010; Ernst et al., 2014; Grimmer et al., 2008; Müller et al., 2012, 2010). Before encountering obstacles, important anticipatory neural mechanisms relying on visual control (Matthis and Fajen, 2014; Matthis et al., 2018) enable foot placement to be monitored so that the height of the CoM can be adjusted (Ernst et al., 2014). Therefore, proper visual perception that relies on head stabilisation (and anticipatory eye movements; Angelaki and Cullen, 2008) also seems crucial for balance control (Dunbar et al., 2004; Goyens and Aerts, 2018; Menz et al., 2003). The vestibular system, situated in the inner ear, allows the detection of head movements as it is highly sensitive to linear and angular accelerations of the head, including gravitational acceleration (e.g. Angelaki and Cullen, 2008; Rabbitt et al., 2004). Furthermore, motor efferent signals allow integration of both exteroceptive information provided by vision and skin sense, and proprioceptive information provided by the muscles and tendons about position of the limbs and body segments (Angelaki and Cullen,

<sup>1</sup>Laboratory for Functional Morphology, Department of Biology, University of Antwerp, Belgium. <sup>2</sup>Department of Movement and Sports Sciences, University of Ghent, Belgium.

\*Author for correspondence (francois.druelle@uantwerpen.be)

 F.D., 0000-0001-9680-6401

2008), making the internal dynamic status of the body immediately and continuously integrated by supraspinal centres. For humans crossing uneven terrains, the objective is to minimise the movements of the CoM by adapting leg parameters through minor adjustments such as leg stiffness, step length and foot strike pattern (e.g. Ernst et al., 2014; Ferris et al., 1999, 1998; Kerdok et al., 2002; Müller et al., 2012, 2010). Although this control strategy is likely to increase locomotor cost and muscle loading, minimising deviations of the body CoM trajectory assures an active control of body dynamic stability and thus minimises the risk of injury (Larsen et al., 2016). The neural control of the body CoM trajectory, via head and gaze stabilisation, and exteroceptive and proprioceptive information, has thus been suggested to be the priority target for running on uneven terrains (e.g. Ernst et al., 2014; Ferris et al., 1999, 1998; Grimmer et al., 2008). Interestingly, birds negotiating obstacles seem to give priority to economy and limb safety rather than CoM motion stability (Birn-Jeffery and Daley, 2012; Birn-Jeffery et al., 2014). These priority strategies remain only poorly known in other animals. Nevertheless, these different results may point to relevant species-specific strategies with regard to their respective morphology and habitat structure (Arnold, 1983; Garland and Losos, 1994).

Overall, running over complex terrains has been shown to require important anticipatory neural mechanisms involving changes in body dynamics and limb postures to target obstacles. Anticipatory strategies via the control of foot placement, body velocity, leg posture etc., seem to be very important in mammals (McFadyen et al., 1999; Mori et al., 2001; Sato et al., 2012) as well as in birds (Birn-Jeffery and Daley, 2012; Birn-Jeffery et al., 2014; Daley and Biewener, 2011) and insects (Watson et al., 2002). Some lizards have also shown anticipation of their behaviour and kinematics via a vertical increase of leg motion and an elevation of head and trunk to improve the negotiation of obstacles (Kohlsdorf and Biewener, 2006; Tucker and McBrayer, 2012). By contrast, *Aspidoscelis sexlineata*, a terrestrial lizard capable of high-speed running, does not exhibit any anticipatory pattern in crossing obstacles (Olberding et al., 2012). Instead, when running bipedally, it only alters the hindlimb kinematics as a 'passive' consequence (according to the authors) of contacting the obstacle, while no variation was observed in either the mean forward speed or in the deviation of the vertical position of the CoM. This surprising result suggests no adjustment of the motor control strategy timing in this species, and no priority for leg safety and economy in comparison to birds, for example (Birn-Jeffery et al., 2014). Yet, the trajectory of the CoM could be an important target of control for successfully crossing obstacles. Because small animals encounter larger terrain variations relative to the length of their limbs, it is likely that their limbs and body reflect specific adaptations for keeping stability on complex terrains. Therefore, it is possible that *A. sexlineata* relies on highly compliant limbs enhancing CoM stability via mass-spring dynamics (Blum et al., 2011; Daley and Usherwood, 2010). Crossing obstacles in this manner should also require an animal to target a direction, or even a physical structure such as a shelter, thus determining, at each moment, the chosen direction of travel. As mentioned previously, an appropriate environmental perception is likely to be performed via gaze and head stabilisation. Although there is no information on the movements of the head in this lizard species when negotiating obstacles, recent experiments performed on *Acanthodactylus boskianus*, another small fast-running lizard, showed that they strongly stabilise their head when running on a flat surface (Goyens and Aerts, 2018). Furthermore, a large and unexpected lateral perturbation causes an increased stabilisation of the head and trunk, therefore highlighting the importance of vestibular perception and

stability control in these fast-running animals. Angelaki and Cullen (2008) stated that the frames of reference of the vestibular system and proprioceptive components differ drastically, being head-centred and body-centred, respectively. Perceiving the position and motion of the body segments relative to the outside world (perception of self-motion) would thus require mapping the two reference frames onto each other.

Here, we study the running performance and kinematics of a fast-running lizard species, *A. boskianus*, when negotiating complex terrains. The present work aims to fill the gap of knowledge about the interactions between head and CoM stabilisations and gaits. We thus focus on how different levels of terrain complexity influence the kinematics of body segments (head, trunk, tail and leg), which reflect the collective output of the entire neuromechanical control system used to maintain stability along the pathway. We first hypothesise that performing at top speed on more complex terrains will increase the fluctuations of the body mechanics of the animals, therefore requiring increased active head stabilisation needed for controlled minimisation of the deviations of the CoM trajectory. We predict that the amplitude of head motion will reduce while the complexity of the terrain increases. Secondly, we predict that the deviations of the CoM trajectory will be kept at a similar amplitude across terrains, reflecting an active control of body dynamic stability. We also tested the hypothesis postulating that compliant (adjustable) limbs, capable of both leg shortening and lengthening, improve stability in challenging situations (Blum et al., 2011; Daley and Usherwood, 2010). Such a limb strategy could allow lizards to negotiate relatively large terrain perturbations without failure while enhancing stability of the CoM. Finally, we hypothesise that the variance in the motion of the head segment and the body segment (where the CoM is located) should not differ across different substrates, thus reflecting two frames of reference (one head-centred and one body-centred) mapped onto each other. If, on the other hand, one of them shows significantly less variance, this would indicate the less-variable segment to be the primary target of control.

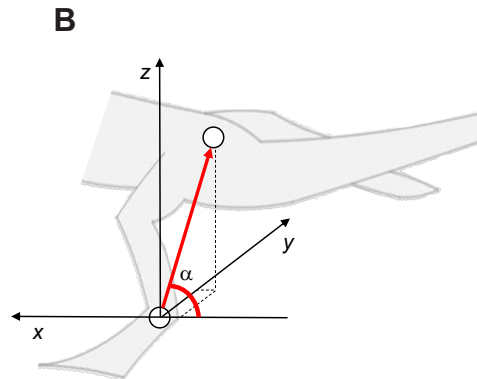
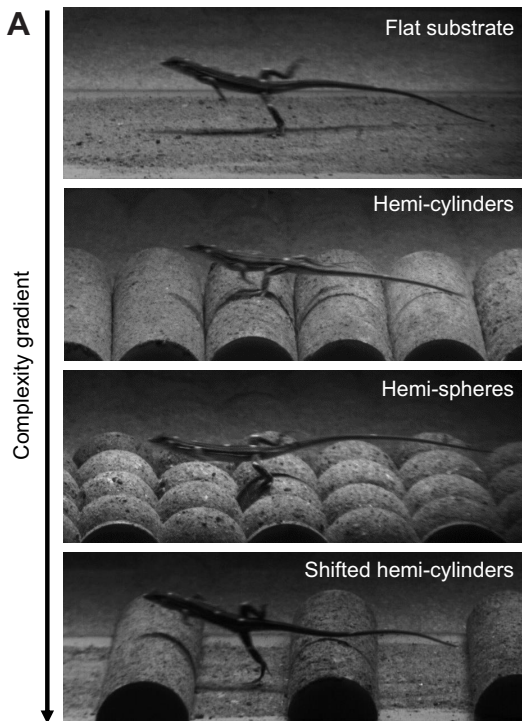
## MATERIALS AND METHODS

### Individuals studied

We sampled seven adult male *Acanthodactylus boskianus* Duméril & Bibron 1839, which were obtained from a commercial dealer (Amfibie, Antwerp, Belgium). The animals were housed individually in vivariums and were fed three days a week (in the afternoon) with crickets. Water was provided *ad libitum*. The overall temperature of the room was kept at  $23.6 \pm 0.1^\circ\text{C}$  with humidity at  $48.05 \pm 4.42\%$  during the period of the experiments. Animals were weighed every day to assess any change in their general physical conditions. A paired permutation test applied between the first (31 October 2017) and the last day (21 November 2017) of the experiments shows that there is no difference during this period in the body mass of the individual tested ( $5.9 \pm 1.7$  g versus  $5.7 \pm 1.2$  g; paired permutation test = 1.4,  $P = 0.63$ ). The protocol was approved by the ethical committee of the University of Antwerp (ECD-dossier 2013-76).

### Experimental protocol

We constructed a  $210 \times 20$  cm racetrack including a central portion of 80 cm that could be covered with 4 different substrates representing a complexity gradient: flat (control), hemi-cylinders, hemi-spheres and shifted hemi-cylinders (the hemi-cylinder substrate in which we removed one unit out of two; Fig. 1A). The radius of the hemi-cylinders and hemi-spheres was 25 mm, i.e. equal to the mean leg length (tibia+femur) of our animal sample ( $24.5 \pm 2.4$  mm). The unit



**Fig. 1. Images and measurements of *Acanthodactylus boskianus* lizards running along increasingly complex substrates.** (A) Zoomed views of a running lizard from the lateral camera. The four substrates are represented with a complexity gradient from the control substrate (top) to the most challenging substrate (bottom). (B) The limb angle  $\alpha$  was calculated using the angle between the functional leg vector (in red) and the vector of the direction of movement (x-axis). White dots indicate position of markers placed on each lizard.

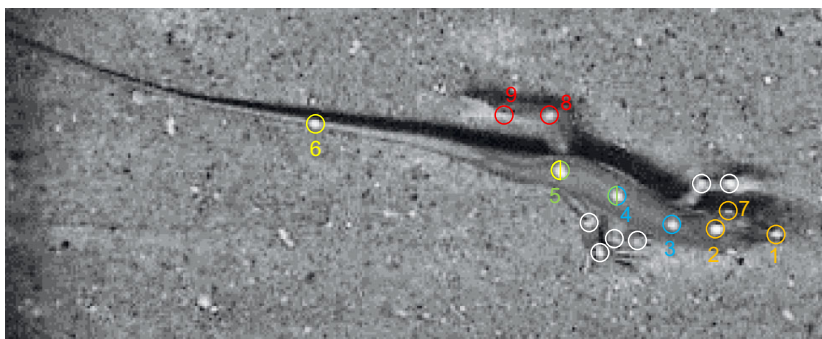
components of the substrates were first made with a 3D printer (Ultimaker B.V.) and then duplicated using a mould and plaster. All the substrate units, as well as the flat surface were painted with adhesive paint. Sand was then glued on all surfaces, which significantly increased the roughness of the substrates providing grip and enabling animals to run at top speed.

All experiments were performed in the morning. Animals were kept in an incubator set at 37°C in order to optimise their sprint performance (Duvdevani and Borut, 1974; Pérez-Mellado, 1992). After 1 h in the incubator, 15 white non-toxic markers were placed at specific anatomical parts on the animals: top of the snout, back of the head, side of the head, shoulder, mid-trunk, hip, mid-tail, knees, proximal part of the feet, elbows and proximal part of the hands (Fig. 2). This allowed collection of detailed head, trunk, tail and limb movements. Over a 3 week period, we tested each lizard on each substrate every day with one or two consecutive trials per substrate and a minimum of 30 min rest (in the incubator) between the different per-substrate trials. The lizards were encouraged to run on the racetrack by hand chasing. Each day, a randomly chosen substrate was placed on the racetrack in order to avoid any order effect. We focused on a field 50 cm long in the middle of the racetrack and recorded the running animals in this field with four synchronised high-speed digital video cameras operating at 325 frames s<sup>-1</sup> and

1/800 shutter speed (NorPix Inc., System 10 GigE Vision, 1920×1080). One camera was positioned perpendicular to the runway to provide a lateral view. One camera was positioned at the top to provide a dorsal view and two cameras were positioned on the diagonal to increase the accuracy of the 3D reconstruction. Calibration of the 3D space was performed using a custom-made calibrated construction (477×143×96 mm). After the recording, digitisation of the body markers was performed manually frame-by-frame using MATLAB DLTdv5 application developed by the Hedrick lab. The sequences were digitised and included in the analysis when the running individuals were crossing the substrate in a straight line and at constant speed. In total, we analyzed 108 strides.

### Data analysed

Prior to the analyses, we applied a fourth-order low-pass Butterworth filter with a cut-off frequency of 60 Hz. This is well above the mean stride frequency in our study (mean=13.2 Hz; see also Goyens and Aerts, 2018). As few data points were missing at the level of the limbs because of the high-speed movement of the animals and the difficulty to digitise these dots properly during the full strides, we applied a general filter for missing data on our database using a piecewise cubic spline interpolation method. We estimated the position of the body CoM based on the dissections of



**Fig. 2. Dorsal view showing location of markers on *A. boskianus*.** The head is defined with markers indicated by orange circles (3 dots), the proximal trunk markers by blue circles (2 dots), the distal trunk with green circles (2 dots) and the tail with yellow circles (2 dots). The left leg is defined with markers indicated by red circles (2 dots). The markers defined with the white circles were not used in the present analysis. Labels as indicated: 1, top of snout; 2, back of head; 3, shoulder; 4, mid-trunk; 5, hip; 6, mid-tail; 7, side of head; 8, left knee; 9, left proximal foot.

three *A. boskianus* cadavers. After freezing the body, we cut it transversally at positions halfway between the different markers (see above) along the longitudinal axis. The limbs were cut at the hip and shoulder joints. All the segments were subsequently weighed on a micro balance (MT5 Mettler Toledo, Greifensee, Switzerland; precision: 0.01 mg), and each marker was provided with a percentage of the total body mass (for the limbs, we used markers at the knees and elbows to calculate position of the limb CoM) and the weighted arithmetic mean of all markers enabled us to calculate the instantaneous position of the CoM in all digitised frames. In our sample, the average position of the CoM was estimated to be 23.9% of the trunk from the hip joint. Using the trajectory of the CoM in the  $x$ - $y$  plane per stride, i.e. the slope of the regression line, we recalculated the global frame of reference using a rotation matrix, with an  $x$ -axis aligned to the direction of motion, and the  $y$ -axis perpendicular to the  $x$ -axis in a lateral direction, and the  $z$ -axis aligned with the gravity vector.

Overall, nine angles were measured on the running lizards. The three dots on the head allowed pitch, roll and yaw rotations of the head to be determined. The three dots placed on the trunk were used to quantify the yaw and pitch rotations of the proximal and distal trunk parts. The tail pitch and yaw rotations are quantified using the dot at the middle of the tail and the dot at the hip. Each angle amplitude was assessed per stride. The stride was defined as the period between one lift-off of the left hind limb to the following lift-off of the same hind limb, thus including one swing phase and one stance phase.

Running on complex terrains resulted in lots of variation in the use of the limbs. The animals used bipedal running, quadrupedal running and often, a sort of tripedal running gait using one forelimb in part of the stride (see also Irschick and Jayne, 1999). Therefore, the forelimbs were not included in our analysis and we focused on the left hind leg. We calculated the changes in functional leg length during a stride as the absolute distance between the marker at the hip and the marker at the foot. We also calculated the variations in leg angle ( $\alpha$ ) as the angle between the functional leg vector at the foot and the vector of the direction of movement, i.e. the recalculated  $x$ -axis (Fig. 1B).

### Statistical analyses

All data were  $\log_{10}$ -transformed before analysis to permit normality and homoscedasticity assumptions. The strides were compared across speed and substrates; therefore, we first corrected for the size effect. We used the Froude number which is a dimensionless speed value:

$$\text{Froude number} = \frac{v^2}{l \times g}, \quad (1)$$

where  $v$  is the average speed for one complete stride calculated from the slope of the linear velocity of the CoM on the  $x$ -axis aligned with the direction of motion,  $l$  is the length of the tibia, and  $g$  is the gravitational acceleration ( $9.81 \text{ m s}^{-2}$ ). We first tested for differences between substrates in mean dimensionless speed per stride using an analysis of variance (ANOVA). Second, we used analyses of covariance (ANCOVA) to test for differences per stride across substrates including the Froude number as a covariate (independent variables); note that individuals were not used as random factors because size differences had been removed and all the random effect variance appeared to be in the residual term (tested using the lme4 package in R; <https://CRAN.R-project.org/package=lme4>). We thus applied the ANCOVA on various dependent variables: the amplitude of head and body undulations (see the aforementioned angles), the amplitude of markers

displacements on the  $y$ -axis and  $z$ -axis, the amplitude of the functional leg length and leg angle, the gait mechanics (dimensionless stride length, dimensionless stride frequency and duty factor), the amplitude of CoM displacements on the  $y$ -axis and  $z$ -axis and the mean relative height at which the CoM is maintained. When a significant result was observed, we further compared control versus hemi-cylinders, and control versus hemi-spheres.

We also calculated the variance for the motion of the head markers (snout and back of the head) as well as on the trunk, about the CoM (mid-trunk and hip). We calculated the magnitude of the variances in head and trunk, by cumulatively summing the variance of the position of both markers. We used the ANCOVA to test for differences in total variance per stride across substrates including the Froude number as a covariate. Furthermore, we compared the total variance of the head with the total variance of the trunk across the different substrates using paired permutation tests and the total variance of the foot with the total variance of the trunk and head using Friedman tests.

Because only four individuals were able to run on the shifted hemi-cylinders along a straight path without stopping in the middle or refusing to cross the recording section of the track, we applied a specific statistical treatment for the comparison 'control versus shifted hemi-cylinders'. These analyses are the same as those previously performed but only included these four individuals in the control and the shifted hemi-cylinder substrates. Apparently, judging from the high refusal rate, the shifted hemi-cylinders represented the most challenging terrain. Note, however, that the four individuals that are included, cover the morphometric variability (in terms of length, mass and leg length) of the total test sample.

All the statistical analyses were performed using R (v3.3.2; <https://cran.r-project.org>) and the significance level was adjusted to correct for the multiple comparisons performed. We used the false discovery rate procedure to control for falsely rejected null hypotheses. We calculated the Benjamini–Hochberg (B-H) critical values with a false discovery rate of 5% (Benjamini and Hochberg, 1995) and compared it with the original  $P$ -values. After ranking all the significant  $P$ -values in ascending order, we determined which  $P$ -values could still be considered significant (indicated with asterisks in the figures).

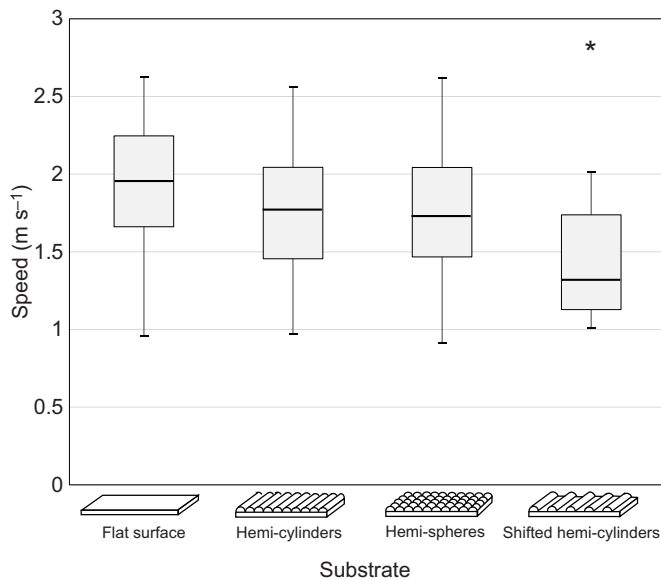
## RESULTS

### Speed performance

The range of speed variation across the four different substrates is shown in Fig. 3. On the control (flat) substrate the average speed per stride was  $1.91 \pm 0.34 \text{ m s}^{-1}$ . The average speed of the seven lizards sampled did not decrease on the hemi-cylinders ( $1.77 \pm 0.32 \text{ m s}^{-1}$ ) or hemi-spheres ( $1.78 \pm 0.37 \text{ m s}^{-1}$ ; ANOVA  $F=0.802$ ,  $P=0.45$ ), but it decreased significantly for the four individuals able to run on the shifted hemi-cylinders ( $1.44 \pm 0.31 \text{ m s}^{-1}$ ; ANOVA  $F=26.17$ ,  $*P<0.0001$ ). The maximal speed recorded during the experiment was  $2.63 \text{ m s}^{-1}$ ; this was reached in two different trials and by two different individuals, one running on the flat surface and one running on the hemi-spheres.

### Head movement

The ANCOVA was run on the angular amplitude of the head taking into account the Froude number. It detected a significant increase in the amplitude of the roll of the head across the three different substrates ( $F=5.52$ ,  $*P=0.005$ ; Fig. 4). The amplitude of the roll of the head was  $9.03 \pm 3.44$  deg on the flat surface and it increased to  $11.72 \pm 3.37$  deg on the hemi-spheres ( $F=9.30$ ,  $*P=0.003$ ). There was also a significant increase in the amplitude of the yaw and roll for the head between the control and the shifted hemi-cylinders ( $4.74 \pm 1.90$  deg versus  $6.34 \pm 2.42$  deg,  $F=7.05$ ,  $*P=0.015$ ; and



**Fig. 3. Box plots of the running speed variation across the different substrates studied.** Box shows 25th and 75th percentiles with median; whiskers are minimum and maximum values. Asterisk indicates a significant difference compared with the control (flat surface);  $P < 0.05$ .  $N = 7$  lizards analysed for the first three conditions and  $N = 4$  lizards analysed for the shifted hemi-cylinders condition.

9.03±3.44 deg versus 16.07±6.13 deg,  $F = 7.38$ ,  $*P = 0.013$ , respectively). The ANCOVA run on the translations of the markers revealed no change along the  $y$ -axis (transverse) across the different substrates. Along the  $z$ -axis (vertical) there was an increase in the amplitude of the displacements of the markers placed on the snout ( $F = 4.47$ ,  $*P = 0.014$ ) and on the back of the head ( $F = 5.86$ ,  $*P = 0.004$ ). When compared one by one with the control substrate, no result remained significant.

### Body movement and CoM

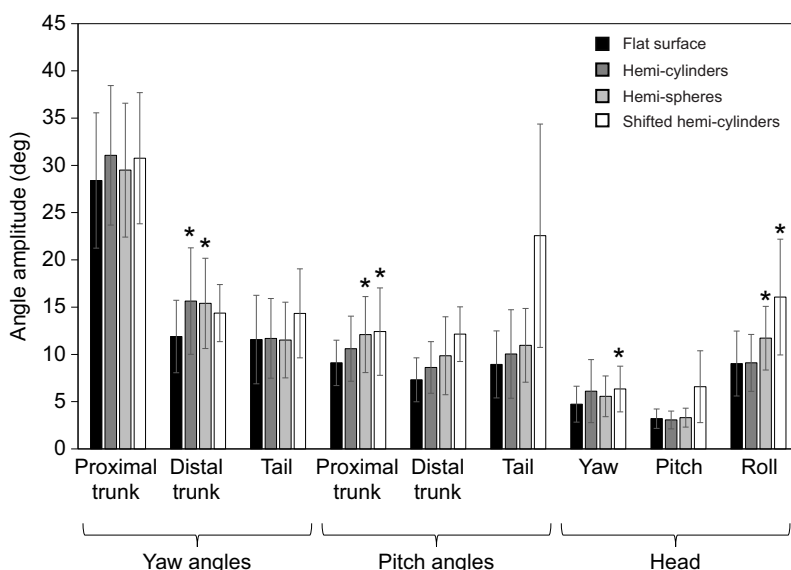
Average movement pattern of the running lizards across the different substrates and its variation was plotted (Fig. 5). The ANCOVA was run on the angular amplitude of the body and tail, taking into account the Froude number and we detected a significant increase in

the amplitude of the yaw of the distal trunk across the three different substrates ( $F = 4.65$ ,  $*P = 0.012$ ). The amplitude of the yaw of the distal trunk was 11.89±3.83 deg on the flat surface and it significantly increased to 15.64±5.63 deg on the hemi-cylinders ( $F = 7.99$ ,  $*P = 0.006$ ) and to 15.4±4.78 deg on the hemi-spheres ( $F = 7.96$ ,  $*P = 0.007$ ). The amplitude of the pitch of the proximal trunk is 9.1±2.4 deg on the flat surface and it significantly increased to 12.09±4.02 deg on the hemi-spheres ( $F = 6.71$ ,  $P = 0.012^*$ ) and to 12.41±4.62 deg on the shifted hemi-cylinders ( $F = 7.29$ ,  $*P = 0.013$ ). The ANCOVA run on the translations of the markers revealed no change along the  $y$ -axis across the different substrates. There was an increase in the amplitude of the displacements of the markers placed on the shoulder along the  $z$ -axis ( $F = 5.56$ ,  $*P = 0.005$ ), but was not significant when compared one by one to the control substrate.

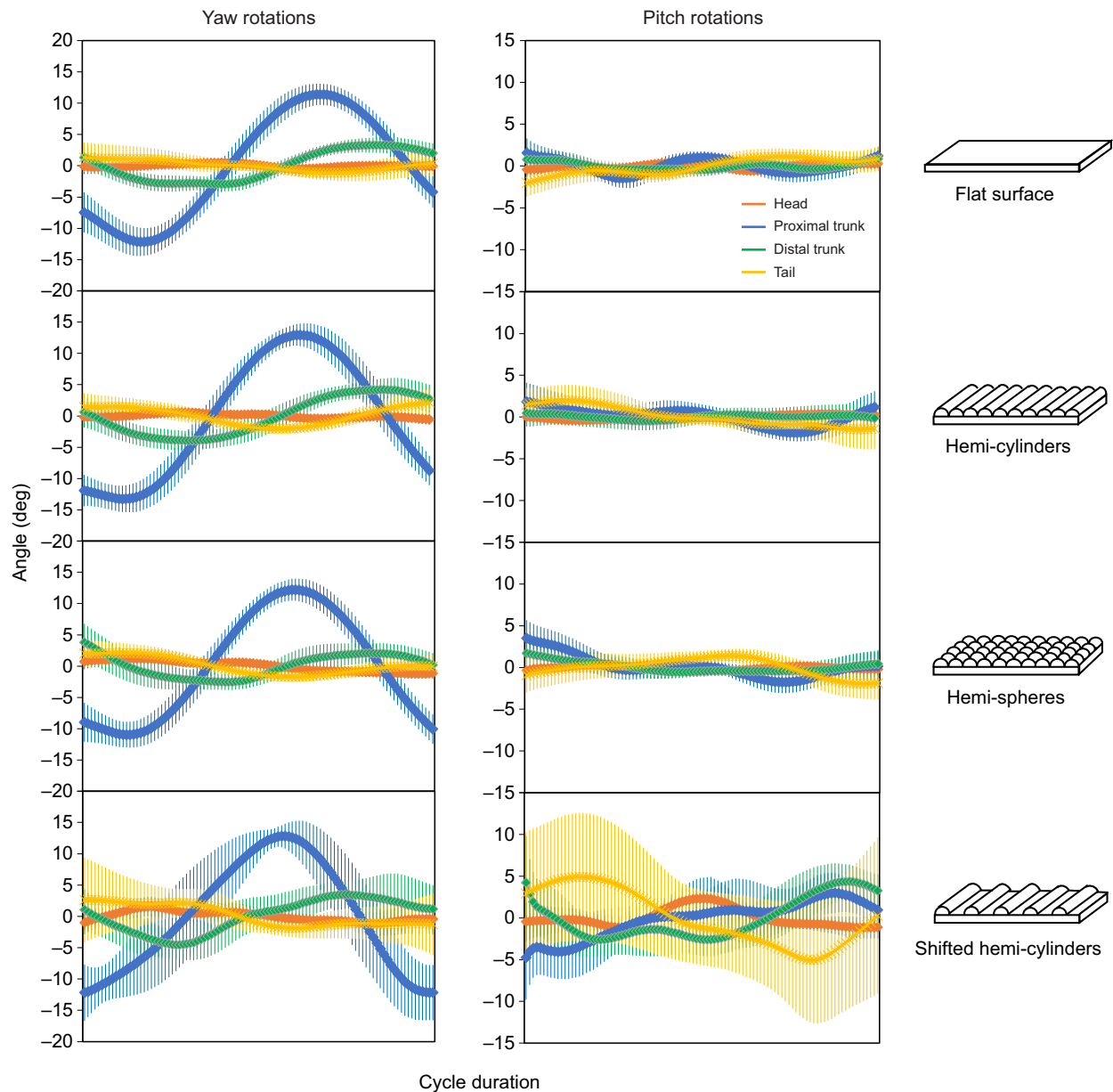
While the angular amplitude of the yaw of the distal trunk and the pitch of the proximal trunk increased, there was no difference in the amplitude of CoM translation in the  $y$ -direction ( $F = 0.10$ ,  $P = 0.91$ ) or  $z$ -direction ( $F = 0.07$ ,  $P = 0.94$ ) across the different substrates (control versus hemi-cylinders versus hemi-spheres). There was also no difference in the amplitude of the movements of the CoM along the  $y$ -axis ( $F = 2.31$ ,  $P = 0.14$ ) and  $z$ -axis ( $F = 3.35$ ,  $P = 0.08$ ) between the control and the shifted hemi-cylinders. By correcting for the height of the substrate (i.e. 25 mm), the CoM was maintained at a lower height relatively on the different substrates compared with the control (17.15±4.85 mm): 15.23±3.67 mm on the hemi-cylinders and 12.44±4.24 mm on the hemi-spheres ( $F = 11.06$ ,  $*P < 0.0001$ ) and 10.07±3.65 mm on the shifted hemi-cylinders ( $F = 13.28$ ,  $*P = 0.002$ ).

### Limb movement

On the control substrate, the average stride frequency was 13.19±2.13 Hz, the average stride length was 141±21 mm and the average duty factor was 27±6%. Across the different substrates (i.e. hemi-cylinders and hemi-spheres), we found no significant difference in the dimensionless stride frequency ( $F = 3.09$ ,  $P = 0.0502$ ) or in the dimensionless stride length ( $F = 3.079$ ,  $P = 0.0508$ ). The duty factor was significantly higher on the hemi-spheres than on the flat surface (33±7%;  $F = 8.33$ ,  $*P = 0.006$ ). On the shifted hemi-cylinders, the average stride frequency was 12.76±2.33 Hz, the average stride length was 103±15 mm and the duty factor was 40±6%. The dimensionless stride frequency and the dimensionless stride length



**Fig. 4. Average amplitudes of yaw and pitch angles for the trunk and tail, and yaw, pitch and roll angles for the head.** Significance is shown relative to the control substrate (in black). Dark grey bars represent the hemi-cylinders, grey bars represent the hemi-spheres and white bars represent the shifted hemi-cylinders. Results are means±s.d. of  $N = 7$  lizards analysed for the first three conditions and  $N = 4$  lizards analysed for the shifted hemi-cylinders condition.  $*P < 0.05$ .

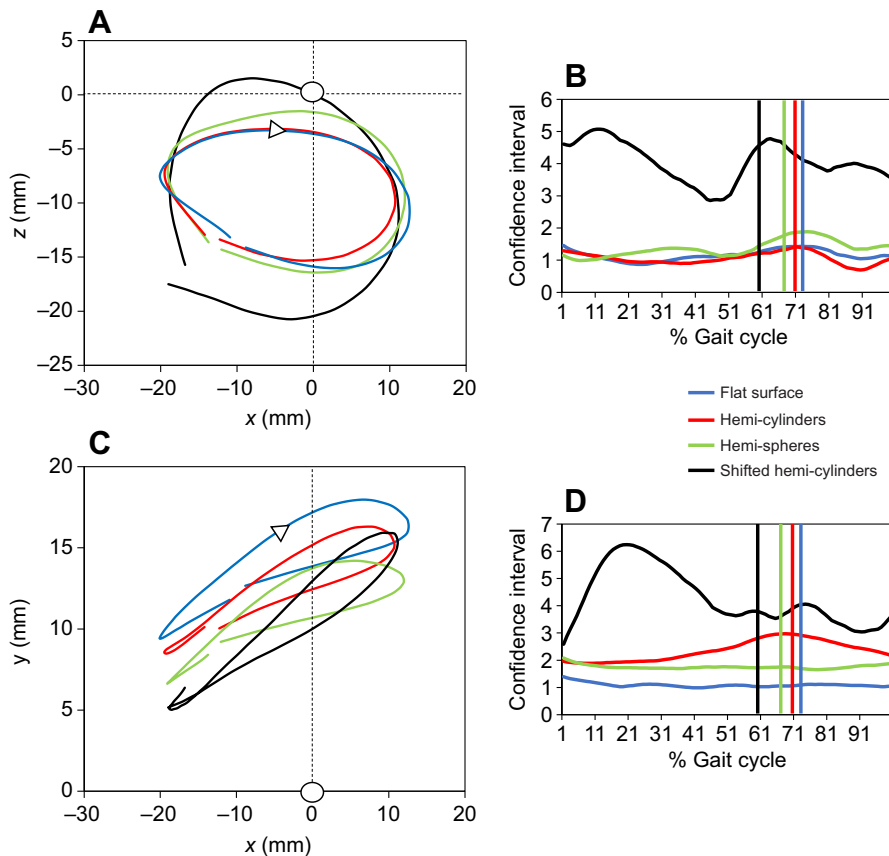


**Fig. 5. Kinematic profiles for yaw (on the left) and pitch (on the right) angle rotations of the head, trunk and tail on the four different substrates studied.** All graphs show average profiles. Average profiles are presented with 95% confidence intervals.

were significantly lower than on the control substrate ( $F=10.38$ ,  $*P=0.004$  for both) and the duty factor was significantly greater ( $F=28.28$ ,  $*P<0.0001$ ). Furthermore, the amplitude of displacement of the foot along the  $z$ -axis increased significantly on the complex substrates ( $F=7.38$ ,  $*P=0.001$ ) but not along the  $y$ -axis ( $F=2.18$ ,  $P=0.12$ ). The amplitude of the movements of the foot along the  $z$ -axis was  $15.23\pm3.54$  mm on the flat surface and increased to  $18.95\pm4.36$  mm on the hemi-spheres ( $F=14.64$ ,  $*P=0.0003$ ) and to  $26.13\pm4.84$  mm on the shifted hemi-cylinders ( $15.23\pm3.54$ ;  $F=12.55$ ,  $*P=0.002$ ).

Fig. 6 shows the average movement of the foot relative to the hip in the sagittal plane (Fig. 6A) and in the frontal plane (Fig. 6C) according to the terrain complexity. The orbit in the sagittal plane remained similar on the flat surface, hemi-cylinders and hemi-spheres. In the frontal plane, the foot was gradually held closer to the hip with increasing complexity, i.e. lizards adopt a less sprawled posture. On the shifted hemi-cylinders, individuals also adopt a less

sprawled posture than on the less challenging substrates, but with more lateral movement (i.e. a more diagonal orbit in the frontal plane). Average kinematics of the leg parameters for the leg angle and the functional leg length were plotted (Fig. 7). Lizards flex their legs across the stride with a slight flexion during the stance phase and a stronger flexion during the swing phase. The phase plots are asymmetric with a bias toward limb retraction. There was no difference in the amplitude of leg angle across the different substrates ( $F=1.48$ ,  $P=0.23$ ) and with the shifted hemi-cylinders ( $F=0.133$ ,  $P=0.72$ ), but we found a significant difference in the amplitude of the functional leg length ( $F=8.15$ ,  $*P=0.0005$ ). The amplitude of the functional leg length was  $9.22\pm2.55$  mm on the flat surface and it increased to  $11.42\pm2.52$  mm on the hemi-spheres ( $F=14.92$ ,  $*P=0.0003$ ) and to  $13.5\pm2.61$  mm on the shifted hemi-cylinders ( $F=8.26$ ,  $*P=0.009$ ). Fig. 8 shows two strategies for the kinematics of the leg parameters on the shifted hemi-cylinders. When the leg contacts the top of the hemi-cylinder at



**Fig. 6. Movement of the foot relative to the hip on the sagittal and frontal planes.** Mean trajectories are shown for each surface on (A) sagittal and (C) frontal planes. The hip is represented with a white circle. The arrowhead on the blue trajectory indicates the direction of movement for all the orbits. The respective confidence intervals for the mean trajectories on (B) sagittal and (D) frontal planes expressed according to gait cycle. The vertical bars indicate the beginning of the stance phase on each terrain.

touch-down, it remains highly flexed along the stance phase (Fig. 8C,D). When the leg contacts the ground (between two hemi-cylinders), it is fully extended (Fig. 8A,B).

#### Variance of head, body and foot movements

Fig. 9 shows that there was no significant difference in the total variance of the head motion or in the trunk motion across substrates. Furthermore, we did not find any significant difference between the head and the trunk. There was a significant increase of the variance of the foot movement with the complexity gradient

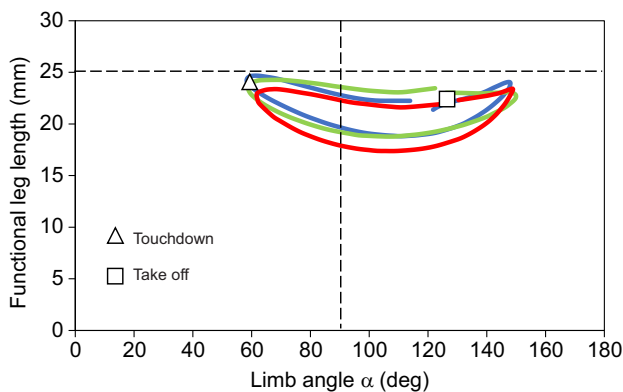
( $F=10.52$ ,  $*P<0.0001$ ), it increased on the hemi-spheres ( $F=18.82$ ,  $*P<0.0001$ ) and on the shifted hemi-cylinders ( $F=14.2$ ,  $*P=0.001$ ). Additionally, the magnitude of variance of the foot movement is always higher than the total variance of the head and trunk movements (Friedman test: 96.46,  $*P<0.0001$ ).

#### DISCUSSION

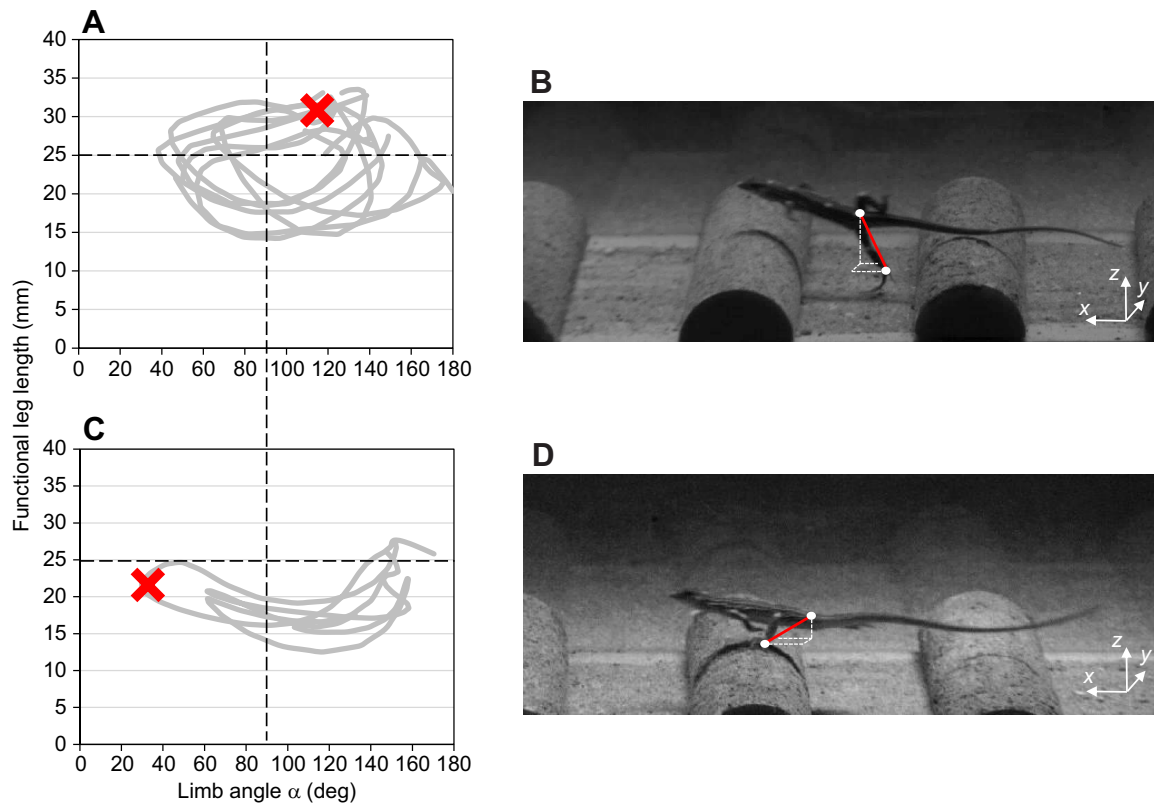
We found that the small, fast-running specialist *A. boskianus* is able to cope with different levels of substrate complexity at top speed. This capacity relies on the leg movements that adjust to the substrate variations and enhance, in this way, the stability of the head and CoM. Indeed, the lizards do not experience any change in mean forward running speed when the amplitudes of the head and CoM movements are kept similar to those observed when they are running on the flat surface. Interestingly, the performance decreased on the most challenging terrain (i.e. shifted hemi-cylinders), while the head movement amplitude increased in both roll and yaw rotations. Whether these capacities to negotiate complex terrains are specific for these running specialists or common for lizards in general remains to be tested.

#### Head stabilisation

We first predicted that performance on more complex terrains would require the animals to reduce head motion, reflecting an increased control of head stabilisation (which we did not measure directly). In the control situation (i.e. running on a flat surface), we found that the range of pitch of the head was smaller ( $3.2\pm1.03$  deg) than the range of yaw ( $4.74\pm1.9$  deg), which was, in turn, smaller than the range of roll ( $9.03\pm3.44$  deg). The amplitude of head displacements for the yaw was very similar to the amplitude of head movements found by Goyens and Aerts



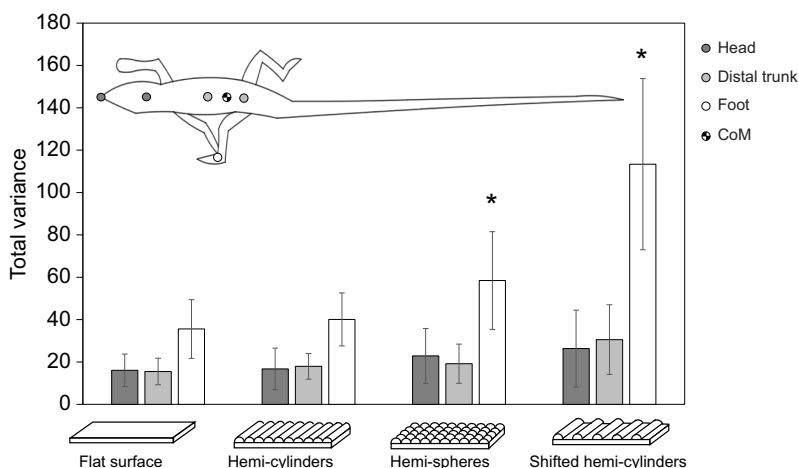
**Fig. 7. Relationship between leg angle ( $\alpha$ ) and functional leg length across the different substrates.** The mean trajectory is represented in blue for the flat substrate, in red for the hemi-cylinders, and in green for the hemi-spheres. The direction of movement is clockwise; the vertical dashed line indicates when the functional leg vector is at 90 deg with the vector of the movement direction and the horizontal dashed line indicates the average anatomical leg length of our sample.



**Fig. 8. Relationship between leg angle ( $\alpha$ ) and functional leg length during running strides on shifted hemi-cylinders.** Two different patterns were observed. (A,B) When the leg falls between the hemi-cylinders there is a lengthening of the functional leg length during the stance phase. (C,D) When the leg falls on the hemi-cylinder there is a shortening of the functional leg length during the stance phase. The red crosses in A and C indicate the position of the depicted screenshots during the running strides in B and D. Red lines in B and D indicate functional leg length; dots indicate location of markers.

(2018) for the same species ( $4.76 \pm 1$  deg). However, contrary to their results and to our prediction, we did not observe a decrease in the amplitude of head motion (i.e. an increase in head stabilisation) when the entire system was more perturbed (note that the nature of the perturbation is different in our study). When comparing substrates, our results show an increased head roll amplitude on the hemi-spheres and an increased yaw and roll on the shifted hemi-cylinders. The higher head motion (roll and yaw) may be the direct result of mechanical perturbations imposed by complex terrains to the system without change of the underlying control. Alternatively, there may be an increased control effort for head stabilisation, yet insufficiently to

compensate the mechanical perturbations imposed by the more challenging substrates entirely. It is worth noting that there is a significantly increased proximal trunk pitch amplitude on the hemi-spheres and shifted hemi-cylinders, while the head pitch does not change. The head is, however, mechanically connected to the trunk. Hence, the absence of increased head pitch supports the assumption that the animals indeed increase the control effort to stabilise the head pitch on these two very challenging substrates. As a result, the head is always maintained horizontally in the direction of movement, indicating the importance of an appropriate perception of the upcoming environment in the direction of travel. The observation that the variance in head



**Fig. 9. Total variance for the head, distal trunk and foot across the different substrates.** The head and the distal trunk are always moving with the same magnitude of variance. The magnitude of variance of the foot increases significantly with the complexity gradient. Values are means  $\pm$  s.d. of  $N=7$  lizards analysed for the first three conditions and  $N=4$  lizards analysed for the shifted hemi-cylinders condition. \* $P < 0.05$

motion does not change across the substrates, also suggests an actively controlled head stabilisation.

Interestingly, the increased head roll on the hemi-spheres did not impair performance. On the shifted hemi-cylinders, however, where both head roll and yaw increase, the mean forward speed is affected. Hence, the most challenging terrain produces mechanical changes that may not be fully compensated by the head stabilisation control. Therefore, the present study and that by Goyens and Aerts (2018) suggest that head stabilisation, supporting vision and vestibular perception, is crucial for lizards when they run at high speed and through complex terrains. In other words, maintaining high-speed locomotion requires head stabilisation.

### Controlling the CoM trajectory

Head (and gaze) stabilisation offers a head-centred frame of reference that may help to control the body CoM trajectory. A stable CoM trajectory seems to be the target during running (e.g. Ernst et al., 2014; Ferris et al., 1999, 1998; Kerdok et al., 2002; Müller et al., 2012, 2010) and this is likely to be mapped on the movements of the head (Angelaki and Cullen, 2008). In this context, we predicted that the deviations of the CoM trajectory will be kept at a similar amplitude across terrains and that the total variance in head motion and (distal) body motion (where the CoM is located) should not differ across different substrates. Our results support these two assumptions, thus suggesting comparable control strategies between the head and the distal trunk. Body stability is thus targeted through an active control of the CoM, also minimising external mechanical work during running. This dynamic stability occurs despite changes in the amplitude of body movements. For instance, on hemi-cylinders and hemi-spheres, the yaw of the distal trunk increases significantly. On the most challenging substrate, the performance (mean forward speed) significantly reduced for the four individuals able to negotiate this substrate. The pitch of the trunk increased significantly, yet the motion of the CoM still does not deviate more than on the control substrate. Furthermore, the height of the CoM was kept at 17 mm on average on the flat surface while the lizards generally ran keeping the CoM slightly, but significantly, closer from the top of the complex substrates, i.e. 15 mm for the hemi-cylinders, 12 mm for the hemi-spheres and 10 mm for the shifted hemi-cylinders. This decrease in CoM height follows the complexity gradient of the substrates and is related to the opportunities for foot placement. Indeed, the respective shapes of the complex terrains determine where the lizards could step. However, interestingly, the distribution of footfalls does not show any location consistency. The lizards stepped on the front, top, back and side (hemi-spheres) edges of the substrate units, therefore suggesting no active foot placement by the animal, as also observed in Olberding et al. (2012).

### Movement of compliant legs

Lizards commonly adopt sprawl postures, but it has been shown that the general mechanics of their locomotion is very similar to that of (legged) animals with an erect posture (Farley and Ko, 1997) and lizards are also capable of running with extended legs (Brandt et al., 2015; Clemente et al., 2008; Kohlsdorf and Biewener, 2006; Olberding et al., 2012; Van Wassenbergh and Aerts, 2013). We hypothesised that being able to easily change functional leg length while running (i.e. running with compliant legs) should improve stability in challenging situations. Our results support this assumption as the lizards appear to use a 'Groucho'-like running style (Irschick and Jayne, 1999), from strongly flexed to extended leg postures, to negotiate the complex terrains. We thus observed large amplitudes of foot clearance and a significant increase of this amplitude, as well as

of the magnitude of variance, when running on the hemi-spheres and the shifted hemi-cylinders. This is achieved by adopting a less-sprawled posture with more-erect parasagittal legs (see Fig. 6C) and by increasing the functional leg length by knee flexion and extension. This leg adjustability may even be (partly) achieved in a passive way via the spring-damper properties (as in a car suspension) of the limb. However, overall, the movements of the legs remain very similar across the substrates and were also very similar to that observed in running birds, resembling a clock-driven pendulum movement (Blum et al., 2011). *A. boskianus* commonly adopts leg movements in an orbital shape on the control, hemi-cylinders and hemi-sphere substrates. Running on the shifted hemi-cylinders reveals two different leg strategies and points to the great flexibility of these compliant legs in responding to the substrate during the stance phase. Although the swing dynamics do not seem to be very variable between the substrates, the animals can adopt both very extended legs and very flexed legs during the stance phase (see Fig. 8). In other words, the trajectory of the CoM is kept stable by extending and flexing the legs while adopting more erect parasagittal leg postures. Consequently, the joint dynamics varies substantially when running on complex terrains and it increases with the complexity gradient. As a result, the compliant legs minimise the variance in the CoM trajectory while the animals encounter important mechanical perturbations caused by the substrate. They have a similar function to the spring-damper suspension system in cars.

While such extreme variations in leg postures should strongly increase the required muscle forces (e.g. Biewener, 1989a; Bishop et al., 2008; Daley and Biewener, 2011), the small size and mass of *A. boskianus* ( $\approx 6$  g) allow these lizards to run with highly crouched postures (Biewener, 1989b) and they are likely to run bipedally and quadrupedally without increased energetic costs (Fedak and Seeherman, 1979; Irschick and Jayne, 1999). Furthermore, small animals live in inherently complex environments, and they frequently encounter large terrain variations relative to leg length. Compliant legs thus offer more 'flexibility', as the legs are capable of both lengthening and shortening (Birn-Jeffery and Daley, 2012; Birn-Jeffery et al., 2014; Blum et al., 2011; Schmitt, 1999). This leg adjustability allows negotiation of relatively large terrain perturbations (as for instance the shifted hemi-cylinders in the present study) without failure, while enhancing stability of the CoM. Whereas birds moving on uneven terrain seem to give priority to economy and limb safety, rather than to CoM motion stability (Birn-Jeffery and Daley, 2012; Birn-Jeffery et al., 2014), our study shows that the way lizards use their limbs stabilises the CoM. Nevertheless, comparisons with the bird experiments on the negotiation of one or two obstacles should be made cautiously. It is possible that the capacity to keep running on complex terrains (when foot placement is disturbed by the orientation and inclination of the substrate) requires stabilisation of the CoM, in birds as well. This, however, remains to be tested.

An optimal match between morphology and performance, and performance type and habitat structure certainly is advantageous (maximises fitness) for an animal given the behavioural contexts encountered (e.g. Garland and Losos, 1994; Higham et al., 2015; Irschick and Losos, 1999; Losos and Sinervo, 1989; Sathe and Husak, 2015). Here, it seems that the morphology of *A. boskianus* is strongly adapted for fast running, but also for maintaining this performance on complex terrains. For example, this species exhibits a caudal position of the CoM. It has been shown to be related to manoeuvrability (Aerts et al., 2003; Carrier et al., 2001) and to the occurrence of bipedal running bouts (Aerts et al., 2003; Clemente, 2014). In such a small animal, economy of the locomotor system may be less important than the need for maintaining stability along

the pathway and manoeuvrability. Indeed, these small animals generally do not cross long distances anyway, but they absolutely need to be able to escape rapidly to the nearest hiding place from potentially larger (and faster) predators.

## Conclusion

*A. Boskianus* is a terrestrial lizard capable of high-speed running. On complex terrains, we observed that it is able to keep running at high speed while maintaining the head stable and minimising the deviations in CoM trajectory. To do so, it relies on compliant legs that are used by adopting more-erect parasagittal leg postures. In this way, the legs can be fully extended when encountering valleys and strongly flexed at the peaks. With regard to the way this locomotor system is able to negotiate complex terrains and its high-speed component, it is likely to be exclusively controlled by the neuronal circuits situated within the spinal cord, without supraspinal control. We hypothesise that the legs are following a rhythmic neural motor pattern which remains stable along the running sequence and that the legs can react (almost) instantaneously (in flexing the knee) to the substrate variations via neural reflexes.

## Acknowledgements

We are very grateful to Jan Scholliers for his valuable help for designing and building the complex terrains. We thank Lise Eerdeken and Nick Van Hul for their help in digitising a large number of running sequences. We are also very grateful for the work of two anonymous reviewers, who provided useful comments that improved the first version of the manuscript.

## Competing interests

The authors declare no competing or financial interests.

## Author contributions

Conceptualization: F.D., J.G., P.A.; Methodology: F.D., J.G., P.A.; Software: F.D., J.G., P.A.; Validation: F.D., J.G., P.A.; Formal analysis: F.D., M.V.-K.; Investigation: F.D., M.V.-K.; Resources: F.D., M.V.-K.; Data curation: F.D.; Writing - original draft: F.D.; Writing - review & editing: F.D., J.G., M.V.-K., P.A.; Visualization: F.D., J.G., M.V.-K., P.A.; Supervision: J.G., P.A.; Project administration: P.A.; Funding acquisition: P.A.

## Funding

This work was supported by Fonds Wetenschappelijk Onderzoek (FWO project GOE02.14N). J.G. was funded by an FWO postdoctoral fellowship (12R5118N). M.V.-K. was funded by the Department of Biology, University of Antwerp.

## Data availability

Datasets supporting the present work are available from the corresponding author upon request.

## References

- Aerts, P., Van Damme, R., D'Août, K. and Van Hooydonck, B. (2003). Bipedalism in lizards: whole-body modelling reveals a possible spandrel. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **358**, 1525-1533.
- Alexander, R. M. (1991). Energy-saving mechanisms in walking and running. *J. Exp. Biol.* **160**, 55-69.
- Alexander, R. M. (2002). Tendon elasticity and muscle function. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **133**, 1001-1011.
- Angelaki, D. E. and Cullen, K. E. (2008). Vestibular system: the many facets of a multimodal sense. *Annu. Rev. Neurosci.* **31**, 125-150.
- Arnold, S. J. (1983). Morphology, performance and fitness. *Am. Zool.* **23**, 347-361.
- Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. B* **57**, 289-300.
- Biewener, A. A. (1989a). Mammalian terrestrial locomotion and size. *BioScience* **39**, 776-783.
- Biewener, A. A. (1989b). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**, 45-48.
- Biewener, A. A. and Daley, M. A. (2007). Unsteady locomotion: integrating muscle function with whole body dynamics and neuromuscular control. *J. Exp. Biol.* **210**, 2949-2960.
- Birn-Jeffery, A. V. and Daley, M. A. (2012). Birds achieve high robustness in uneven terrain through active control of landing conditions. *J. Exp. Biol.* **215**, 2117-2127.
- Birn-Jeffery, A. V., Hubicki, C. M., Blum, Y., Renjewski, D., Hurst, J. W. and Daley, M. A. (2014). Don't break a leg: running birds from quail to ostrich prioritise leg safety and economy on uneven terrain. *J. Exp. Biol.* **217**, 3786-3796.
- Bishop, K. L., Pai, A. K. and Schmitt, D. (2008). Whole body mechanics of stealthy walking in cats. *PLoS ONE* **3**, e3808.
- Blickhan, R. (1989). The spring-mass model for running and hopping. *J. Biomech.* **22**, 1217-1227.
- Blum, Y., Lipfert, S. W., Rummel, J. and Seyfarth, A. (2010). Swing leg control in human running. *Bioinspir. Biomim.* **5**, 026006.
- Blum, Y., Birn-Jeffery, A., Daley, M. A. and Seyfarth, A. (2011). Does a crouched leg posture enhance running stability and robustness? *J. Theor. Biol.* **281**, 97-106.
- Brandt, R., Galvani, F. and Kohlsdorf, T. (2015). Sprint performance of a generalist lizard running on different substrates: grip matters. *J. Zool.* **297**, 15-21.
- Carrier, D. R., Walter, R. M. and Lee, D. V. (2001). Influence of rotational inertia on turning performance of theropod dinosaurs: clues from humans with increased rotational inertia. *J. Exp. Biol.* **204**, 3917-3926.
- Chadwell, B. A. and Young, J. W. (2015). Angular momentum and arboreal stability in common marmosets (*Callithrix jacchus*). *Am. J. Phys. Anthropol.* **156**, 565-576.
- Clemente, C. J. (2014). The evolution of bipedal running in lizards suggests a consequential origin may be exploited in later lineages. *Evolution* **68**, 2171-2183.
- Clemente, C. J., Withers, P. C., Thompson, G. and Lloyd, D. (2008). Why go bipedal? Locomotion and morphology in Australian agamid lizards. *J. Exp. Biol.* **211**, 2058-2065.
- Daley, M. A. and Biewener, A. A. (2011). Leg muscles that mediate stability: mechanics and control of two distal extensor muscles during obstacle negotiation in the guinea fowl. *Philos. Trans. R. Soc. B Biol. Sci.* **366**, 1580-1591.
- Daley, M. A. and Usherwood, J. R. (2010). Two explanations for the compliant running paradox: reduced work of bouncing viscera and increased stability in uneven terrain. *Biol. Lett.* **6**, 418-421.
- Daley, M. A., Usherwood, J. R., Felix, G. and Biewener, A. A. (2006). Running over rough terrain: guinea fowl maintain dynamic stability despite a large unexpected change in substrate height. *J. Exp. Biol.* **209**, 171-187.
- Dunbar, D. C., Badam, G. L., Hallgrímsson, B. and Vieilledent, S. (2004). Stabilization and mobility of the head and trunk in wild monkeys during terrestrial and flat-surface walks and gallops. *J. Exp. Biol.* **207**, 1027-1042.
- Duvdevani, I. and Borut, A. (1974). Mean body temperature and heat absorption in four species of Acanthodactylus lizards (Lacertidae). *Herpetologica* **176**-181.
- Ernst, M., Götze, M., Müller, R. and Blickhan, R. (2014). Vertical adaptation of the center of mass in human running on uneven ground. *Hum. Mov. Sci.* **38**, 293-304.
- Farley, C. T. and Ko, T. C. (1997). Mechanics of locomotion in lizards. *J. Exp. Biol.* **200**, 2177-2188.
- Fedak, M. A. and Seeherman, H. J. (1979). Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. *Nature* **282**, 713.
- Ferris, D. P., Louie, M. and Farley, C. T. (1998). Running in the real world: adjusting leg stiffness for different surfaces. *Proc. R. Soc. B Biol. Sci.* **265**, 989-994.
- Ferris, D. P., Liang, K. and Farley, C. T. (1999). Runners adjust leg stiffness for their first step on a new running surface. *J. Biomech.* **32**, 787-794.
- Garland, T., Jr and Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In: *Ecological Morphology: Integrative Organismal Biology* (ed. P. C. Wainwright and S. M. Reilly), pp. 240-302. Chicago: University of Chicago Press.
- Goyens, J. and Aerts, P. (2018). Head stabilisation in fast running lizards. *Zoology* **127**, 114-120.
- Grimmer, S., Ernst, M., Günther, M. and Blickhan, R. (2008). Running on uneven ground: leg adjustment to vertical steps and self-stability. *J. Exp. Biol.* **211**, 2989-3000.
- Higham, T. E., Birn-Jeffery, A. V., Collins, C. E., Hulse, C. D. and Russell, A. P. (2015). Adaptive simplification and the evolution of gecko locomotion: morphological and biomechanical consequences of losing adhesion. *Proc. Natl Acad. Sci. USA* **112**, 809-814.
- Hirt, M. R., Jetz, W., Rall, B. C. and Brose, U. (2017). A general scaling law reveals why the largest animals are not the fastest. *Nat. Ecol. Evol.* **1**, 1116.
- Irschick, D. J. and Jayne, B. C. (1999). Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *J. Exp. Biol.* **202**, 1047-1065.
- Irschick, D. J. and Losos, J. B. (1999). Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *Am. Nat.* **154**, 293-305.
- Irschick, D. J., Meyers, J. J., Husak, J. F. and Le Galliard, J. F. (2008). How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evol. Ecol. R* **10**, 177-196.
- Jindrich, D. L. and Full, R. J. (2002). Dynamic stabilization of rapid hexapedal locomotion. *J. Exp. Biol.* **205**, 2803-2823.
- Kerdok, A. E., Biewener, A. A., McMahon, T. A., Weyand, P. G. and Herr, H. M. (2002). Energetics and mechanics of human running on surfaces of different stiffnesses. *J. Appl. Physiol.* **92**, 469-478.
- Kohlsdorf, T. and Biewener, A. (2006). Negotiating obstacles: running kinematics of the lizard *Sceloporus malaciticus*. *J. Zool.* **270**, 359-371.

- Larsen, R. J., Jackson, W. H. and Schmitt, D. (2016). Mechanisms for regulating step length while running towards and over an obstacle. *Hum. Mov. Sci.* **49**, 186-195.
- Losos, J. B. and Sinervo, B. (1989). The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.* **145**, 23-30.
- Matthis, J. S. and Fajen, B. R. (2014). Visual control of foot placement when walking over complex terrain. *J. Exp. Psychol. Hum. Percept. Perform.* **40**, 106.
- Matthis, J. S., Yates, J. L. and Hayhoe, M. M. (2018). Gaze and the control of foot placement when walking in natural terrain. *Curr. Biol.* **28**, 1224-1233.
- McFadyen, B. J., Lavoie, S. and Drew, T. (1999). Kinetic and energetic patterns for hindlimb obstacle avoidance during cat locomotion. *Exp. Brain Res.* **125**, 502-510.
- Menz, H. B., Lord, S. R. and Fitzpatrick, R. C. (2003). Acceleration patterns of the head and pelvis when walking on level and irregular surfaces. *Gait Posture* **18**, 35-46.
- Mori, F., Tachibana, A., Takasu, C., Nakajima, K. and Mori, S. (2001). Bipedal locomotion by the normally quadrupedal Japanese monkey, *M. Fuscata*: strategies for obstacle clearance and recovery from stumbling. *Acta Physiol. Pharmacol. Bulg.* **26**, 147-150.
- Müller, R., Grimmer, S. and Blickhan, R. (2010). Running on uneven ground: Leg adjustments by muscle pre-activation control. *Hum. Mov. Sci.* **29**, 299-310.
- Müller, R., Ernst, M. and Blickhan, R. (2012). Leg adjustments during running across visible and camouflaged incidental changes in ground level. *J. Exp. Biol.* **215**, 3072-3079.
- Olberding, J. P., McBrayer, L. D. and Higham, T. E. (2012). Performance and three-dimensional kinematics of bipedal lizards during obstacle negotiation. *J. Exp. Biol.* **215**, 247-255.
- Pérez-Mellado, V. (1992). Ecology of lacertid lizards in a desert area of eastern Morocco. *J. Zool.* **226**, 369-386.
- Rabbitt, R. D., Damiano, E. R. and Grant, J. W. (2004). Biomechanics of the semicircular canals and otolith organs. In *The vestibular system* (ed. S. M. Highstein R. R. Fay and A. N. Popper), pp. 153-201. Berlin: Springer.
- Sathe, E. A. and Husak, J. F. (2015). Sprint sensitivity and locomotor trade-offs in green anole (*Anolis carolinensis*) lizards. *J. Exp. Biol.* **218**, 2174-2179.
- Sato, Y., Aoki, S. and Yanagihara, D. (2012). Gait modification during approach phase when stepping over an obstacle in rats. *Neurosci. Res.* **72**, 263-269.
- Schmitt, D. (1999). Compliant walking in primates. *J. Zool.* **248**, 149-160.
- Seyfarth, A., Geyer, H., Günther, M. and Blickhan, R. (2002). A movement criterion for running. *J. Biomech.* **35**, 649-655.
- Seyfarth, A., Geyer, H. and Herr, H. (2003). Swing-leg retraction: a simple control model for stable running. *J. Exp. Biol.* **206**, 2547-2555.
- Tucker, D. B. and McBrayer, L. D. (2012). Overcoming obstacles: the effect of obstacles on locomotor performance and behaviour. *Biol. J. Linn. Soc.* **107**, 813-823.
- Van Wassenbergh, S. and Aerts, P. (2013). In search of the pitching momentum that enables some lizards to sustain bipedal running at constant speeds. *J. R. Soc. Interface* **10**, 20130241.
- Watson, J. T., Ritzmann, R. E., Zill, S. N. and Pollack, A. J. (2002). Control of obstacle climbing in the cockroach, *Blaberus discoidalis*. I. Kinematics. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **188**, 39-53.