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Effect of Slope Degree on the Lateral Bending in *Gekko geckos*

Zhouyi Wang, Lei Cai, Wei Li, Aihong Ji, Wenbo Wang, Zhendong Dai

Institute of Bio-Inspired Structure and Surface Engineering, *Nanjing University of Aeronautics and Astronautics*,
Nanjing 210016, *China*

Abstract

A gecko's habitat possesses a wide range of climbing slopes that pose a number of postural challenges for climbing locomotion. Few studies have examined the relationship between the lateral bending of the trunk of a gecko and other aspects of locomotion when climbing. In this paper, three-dimensional reaction forces and high-speed videos of *Gekko geckos* moving on different slopes are used to reveal how the lateral bending of the animal's trunk responds to changing slopes. The results of such observations indicate that the minimum bending radius continually decreases with an increase in the slope, illustrating that the degree of bending of the trunk becomes significantly greater. Moreover, a lateral bending mechanical model is used to show the interrelation between the lateral bending in the frontal plane and the sagittal deformation of the trunk caused by gravity. Taken together, these results have advanced our understanding of the role of lateral bending of vertebrates when climbing on a slope.

Keywords: slope, lateral bending, reaction force, gecko, ceiling

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1 Introduction

Locomotion is essential to an animal's survival and reproduction, as well as for evading predators and finding suitable mates, prey, and habitats. Of critical importance in vertebrate locomotion is the lateral bending of the trunk. For example, fishes accelerate locomotion and elude predators by the lateral bending of the trunk[1–3], whereas forward propulsion in terrestrial snake locomotion is similarly provided by the lateral bending of the trunk[4]. Moreover, lizards increase their velocity by increasing their degree of lateral bending[5,6], and sandfish continually bend their trunk to "swim" in the sand[7,8]. When a rat is confronted with danger from the side, a sharp lateral bending of its trunk can help it avoid injury in a timely manner and quickly allow it to restore its locomotion[9].

Current research on the lateral bending of an animal's trunk has primarily focused on the following aspects: (1) the differences between animals swimming in a fluid medium versus moving on a horizontal substrate[7,8,10–12], (2) the relationship between lateral bending and gait[5,6,13], (3) the influence of the diameter of the substrate on bending[14,15], and (4) the regulation of bending[16,17]. Taken together, it is clear that different environments make different demands on the locomotor behaviors in animals, helping them adapt to their living environment[18]. So the degree of inclination in an environment is considered as an important factor that effects locomotor behaviors. However, vertebrates climbing on inclined surfaces are rarely studied from the aspect of lateral bending of the trunk[10,15,19–24]. Thus, a question remains: If vertebrates are challenged by an unfamiliar slope, will their trunk actively bend to adapt to the new angle? If so, what is the relationship between the degee of lateral bending and the angle of slope?

The gecko lizard is a proficient climber that utilizes lateral bending to facilitate its locomotion[25]. Furthermore, the mechanics of the gecko's adhesion has previously been investigated[26–29]. Unfortunately, the bending of the trunk in gecko kinematics has largely been ignored in gecko locomotion on slopes[19,22,23,30–32]. However, it is known that the measurement of the reaction forces acting on individual limbs indicates how geckos counteract their instability caused by a lateral bending of their trunk during locomotion[25].

Corresponding author: Zhendong Dai
E-mail: zddai@nuaa.edu.cn

Therefore, in the current paper, we trained *Gekko geckos* to climb on a rotatable force measuring array in order to investigate how they bend their body laterally in response to changes in the slope degree. Furthermore, we also reveal the contributions of the front and hind feet on the lateral bending of the trunk.

2 Materials and methods

2.1 Animals

This study was carried out in accordance with the Guidelines for Laboratory Animal Management in China. The experimental procedures were approved by the Jiangsu Association for Laboratory Animal Science (Jiangsu, China). All efforts were made to minimize the suffering of the animals. Eight, $N = 8$, *Gekko geckos* (mass, 63.4 ± 2.6 g mean ± s.d.; snout-vent length, 137.8 ± 5.5 mm) were purchased from a supplier in Guangxi province (China) and those showing a normal morphology and similar mass (< 5%), and with no history of a broken tail, were selected. The animals were kept under a natural light cycle at a temperature of 25 ± 2 ˚C and a humidity level of 60% to 70%.

2.2 Experimental setup

Our setup consists of two parts: A Force Measuring Array (FMA) and a locomotor behavior recording system (Fig. 1a). The FMA was introduced previously[30], and consists of 16 sensors (2 rows × 8 columns) (Fig. 1b) with smooth glass squares (30 mm × 30 mm) glued on the top with 1 mm clearance (Fig. 1c). This FMA formed the running track for the geckos, and was tilted in fixed increments of 30˚ to provide different slope angles θ of the substrates. A dark plastic box was placed at the end of the track to lure the geckos naturally through the aisle. The measured reaction force data were filtered at a cut-off frequency of 100 Hz according to previous papers[30,32]. Synchronously with the Substrate Reaction Force (SRF) measurement (500 Hz), a high-speed camera (Olympus iSpeed-3, 1280 pixel × 1024 pixel resolution) recorded each trial at 500 Hz. The start of the video recording was triggered by sending a TTL-pulse to the camera and the data acquisition board synchronously using a manual switch. Because the camera was rotated along with the FMA, and was consistently perpendicular to the plane of the array, we obtained standardized dorsal

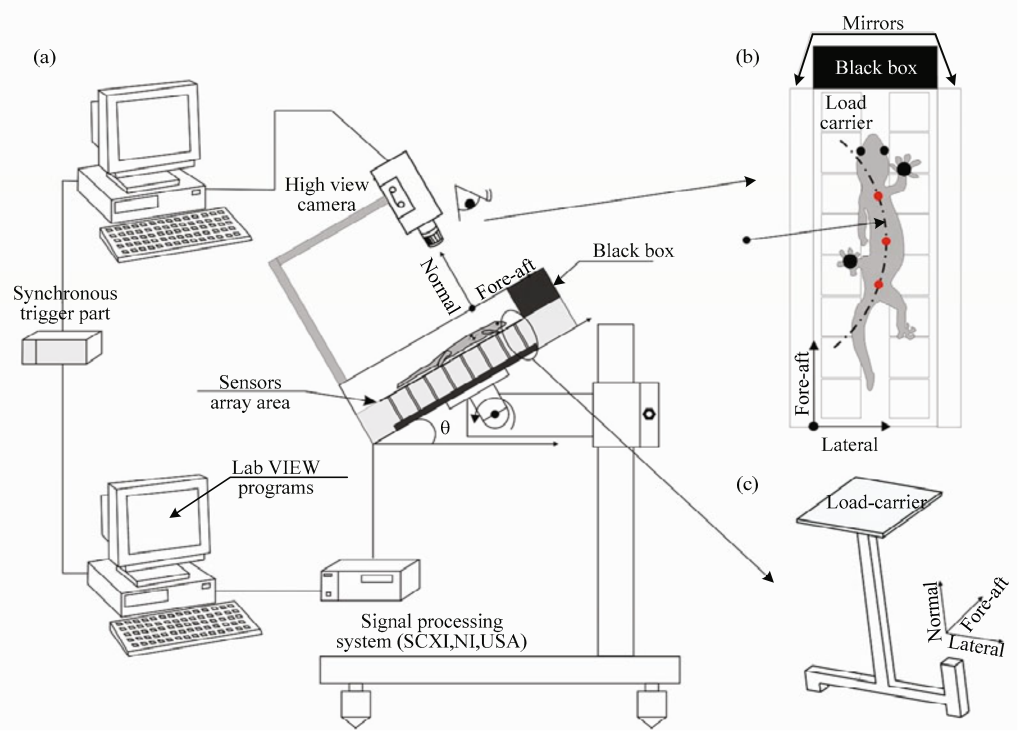


Fig. 1 The system for recording locomotion kinematics and the three-dimensional reaction force measuring system. (a) Animal locomotive behavior recording system and the Force Measuring Array (FMA). The platform of the FMA was rotated (30˚ per step) to enable observation of geckos moving on seven different slopes (θ: sloped angle of platform). (b) Planar view of the platform of the FMA. We calculated the transient lateral bending radius r using the three points on the dorsal of the trunk marked with red dots, and accessed the minimum bending radius ($r_{\min}$) during a step. (c) A single three-dimensional sensor from FMA.

views of the animal movements. Two mirrors were respectively placed on either side of the array channel to obtain lateral views. To simplify the description, we assumed that the median sagittal plane represented the symmetrical plane of the body.

2.3 Data analysis

The timing and position of the feet on and off the substrate were determined from experimental photos recorded using the high-speed camera. Before the trial, the reference points were marked on each gecko's back with nail polish. The coordinates of the reference points on the dorsal midline of each gecko during motion were chosen from experimental photos using i-SPEED Viewer software (i-SPEED 3, Olympus, Inc., Japan). The forward speed of the trial (v) was calculated by the coordinate in fore-aft direction of the mid-point of the left and right shoulder joints. Only trials in which the gecko moved at a near-steady forward speed were evaluated further, if the increases or decreases in forward speed were more than 15% of the average forward speed in this trial, the trial was discarded. Meanwhile the data coordinates of the three marked points on the dorsal spine of the gecko (the mid-points of the left and right shoulder joints, the mid-points of the left and right hip joints, and the midway between the former and latter points on each animal's vertebral column) were used to calculate the transient lateral bending radius (r) of the body, and the minimum bending radius (r_{min}) during the step stance phase was selected to evaluate the degree of lateral bending of the body (Fig. 1b).

The SRFs acting on an individual foot in all three directions were obtained simultaneously using the kinematic data, i.e., the lateral SRF (F_L), fore-aft SRF (F_F), and normal SRF (F_N). We calculated the impulses of the SRFs acting on the individual foot in each dimension during the stance phase (T_S) using Eq. (1), i.e., the lateral impulse (I_L), fore-aft impulse (I_F), and normal impulse (I_N). The positive I_F drives the locomotion during the stance phase, the negative I_L acts on the left foot, pulling away from the gecko's trunk, and the negative I_N indicates the presence of the adhesive force acting on the gecko's foot. The weight component parallel to the plane of the FMA was defined as $F_W^{\parallel}$ ($F_W^{\parallel} = F_W \cdot \sin\theta$). The impulse of $F_W^{\parallel}$ ($I_W^{\parallel}$) during the stance phase was calculated using Eq. (2):

$$I_L = \int_0^{T_S} F_L \mathrm{d}t,\ I_F = \int_0^{T_S} F_F \mathrm{d}t,\ I_N = \int_0^{T_S} F_N \mathrm{d}t, \qquad (1)$$

$$I_W^{\parallel} = \int_0^{T_S} F_W \bullet \sin\theta \mathrm{d}t = \int_0^{T_S} F_W^{\parallel} \mathrm{d}t. \qquad (2)$$

All force data were adjusted for the body weight (BW) before pooling by dividing the force by the body weight, and the length data were adjusted for the body length (BL) by dividing the force by the body length to account for differences in the body size of the samples. The impulses were converted into body weight-seconds (BW·s), and the angular momentums were converted into body weight-body length-seconds (BW·BL·s)

2.4 Statistics

Measured data from all individuals were pooled and analyzed statistically using SPSS software (SPSS15.0, Inc., Chicago, IL). The relationships between the slope angle and each variable (forward speed, minimum bending radius, force impulses (moments)) were determined using least-squares linear regression. Comparisons were made among data for slope angle from 0° to 180° using analysis of co-variance (ANCOVA) to yield p-values, where the slope was set as the independent variable and the dependent variables were minimum bending radius, and force impulses (moments). For each ANCOVA analysis the covariate variables were set as the test animal group and forward speed. Because different animals were used for the seven slopes trials, we did not use repeated-measures ANOVA. Differences were considered statistically to be significant at a value of $p<0.05$. The tested data are presented as mean ± standard deviation (mean ± s.d.).

3 Results

3.1 The bending radius of the trunk (r)

When a gecko in a sprawled posture climbs a slope, its trunk laterally bends from one side to the other (Fig. 2a). The maximum lateral trunk bending occurred at the initial footfall at 0.04±0.03 of the stance phase, i.e., the lateral bending radius (r) was the lowest; thus, the trunk became rectilinear through the middle stance, making r attain the maximum value, and the trunk then continued bending again, attaining the minimum value of r at 0.88±0.10 of the stance phase (Figs. 2b and 2c).

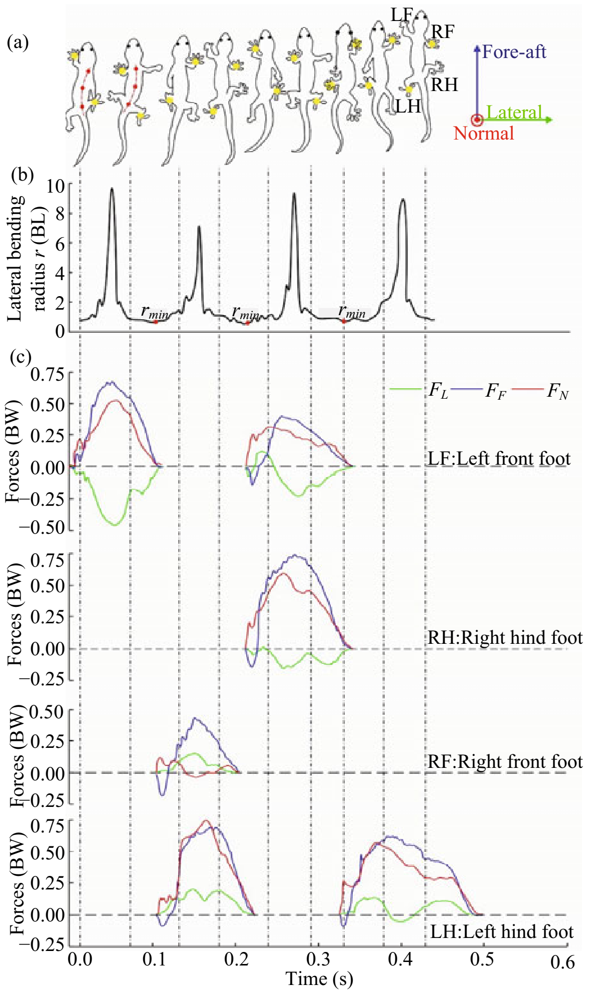


Fig. 2 Gait, lateral bending and substrate reaction forces of a 62.4g *Gekko gecko* running on climbing on a 60° slope. (a) Tracing of gecko climbing where a yellow foot represents a foot in contact with the substrate; (b) the lateral bending radius of a *Gekko gecko* freely climbing on a 60° slope as a function of time; (c) the substrate reaction forces acting on each foot during a step cycle of a *Gekko gecko* freely climbing on a 60° slope as a function of time.

The minimum bending radius ($r_{\min}$) was selected to evaluate the degree of lateral bending of the body during the stance phase. The value of $r_{\min}$ continually decreased with an increase in the slope angle, from 0.88 BL running on a 0° substrate to 0.50 BL climbing on a 180° substrate, which illustrates that, from running on a horizontal surface to climbing up a slope, *Gekko geckos* continuously increase the degree of bending of their body to adapt to a slope increase. The value of $r_{\min}$ clearly decreased when the slope increased from 0° to 30°, whereas, from 150° to 180°, there were no significant changes (Fig. 3a, Table 1).

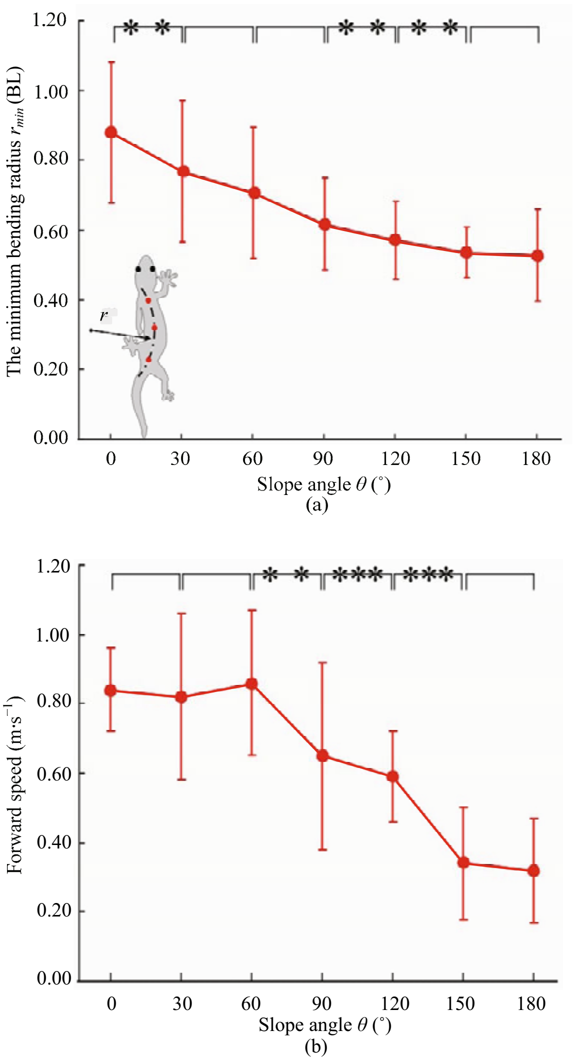


Fig. 3 The forward speed and minimum bending radius of geckos climbing on slopes of different inclinations. (a) The minimum bending radius of a gecko during locomotion; (b) the forward speed of *Gekko geckos* climbing on slopes at seven angles of pitch. On slopes of 60° to 120°, forward speed decreased steeply with increasing slope angle. Black asterisks: the parameters for two successive slope angles are significantly different. *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$.

3.2 Forward speed (*v*)

In spite of our great effort to obtain the equivalent forward speeds at different inclines, the geckos slowed their forward motion when encountering an increased slope angle, and the thus forward speed ranged from 1.02 $\mathrm{m{\cdot}s^{-1}}$ to 0.19 $\mathrm{m{\cdot}s^{-1}}$. When encountering slopes ranging from 0° to 60° (shallow slopes) there was no significant reduction in the forward speed, and the mean of the forward speed was 0.84 ± 0.19 $\mathrm{m{\cdot}s^{-1}}$ (N = 84). Similarly, the forward speed showed no clear difference when the geckos climbed up 150° and 180° slopes

Table 1 Mean of forward speed, bending radius and three-dimensional force impulse of gecko moving on different slopes

Project	Foot	0	30	60	90	120	150	180
Forward speed (m·s^{-1})		0.84±0.12(28)	0.82±0.24(26)	0.86±0.21(30)	0.65±0.27(24)	0.59±0.13(22)	0.34±0.16(23)	0.32±0.15(27)
Minimum bending radius (BL)		0.88±0.30(28)	0.77±0.21(26)	0.71±0.18(30)	0.61±0.13(24)	0.57±0.11(22)	0.56±0.07(23)	0.50±0.08(27)
Lateral force impulse (10^{-3}·BW·s)	front	−3.7±2.3(19)	−8.4±2.3(15)	7.2±3.1(24)	19.9±9.8(11)	58.4±16.8(15)	81.5±27.2(17)	242.6±131.6(20)
	hind	−2.0±1.1(14)	−7.8±3.9(11)	−7.0±4.2(15)	9.1±7.1(14)	34.7±17.0(15)	69.3±25.9(16)	157.4±71.7(21)
Fore-aft force impulse (10^{-3}·BW·s)	front	−2.5±0.8(19)	5.6±3.7(15)	13.7±10.1(24)	40.6±17.6(11)	60.8±26.7(15)	125.7±44.5(17)	287.4±157.2(20)
	hind	3.4±0.9(14)	32.2±12.0(11)	38.0±18.0(15)	48.4±17.2(14)	36.7±13.6(15)	−52.8±22.5(16)	−170.0±85.7(21)
Normal force impulse (10^{-3}·BW·s)	front	26.5±4.5(19)	24.9±6.1(15)	13.7±4.3(24)	−12.1±5.9(11)	−40.5±9.2(15)	−97.5±38.3(17)	−212.4±106.3(20)
	hind	19.8±4.4(14)	33.3±8.1(11)	26.5±6.9(15)	6.7±3.7(14)	−22.2±8.7(15)	−51.9±33.2(16)	−112.9±64.6(21)
Bending angular momentum (10^{-3}·BW·BL·s)		2.1±1.4(14)	3.3±1.1(11)	16.5±7.8(15)	18.3±5.7(14)	30.3±4.6(15)	36.4±5.8(16)	54.1±6.6(21)

BW: body weight, BL: body length

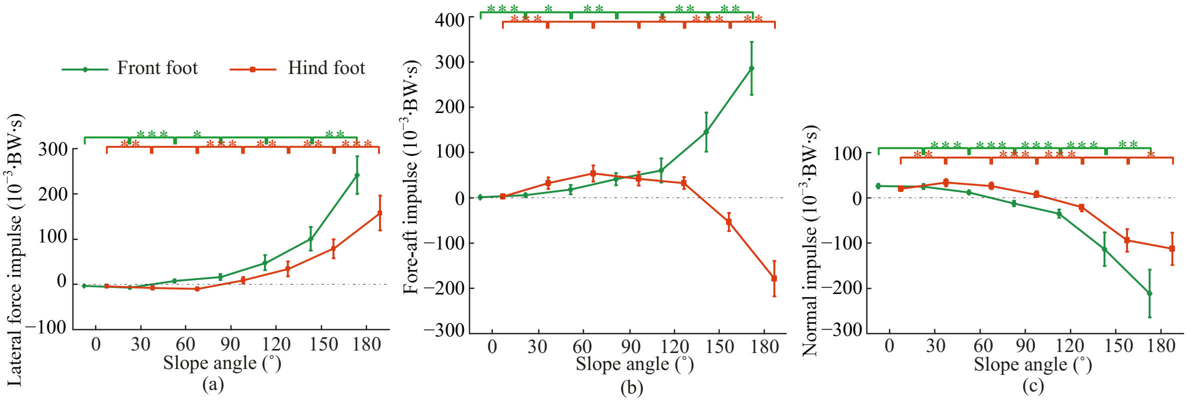
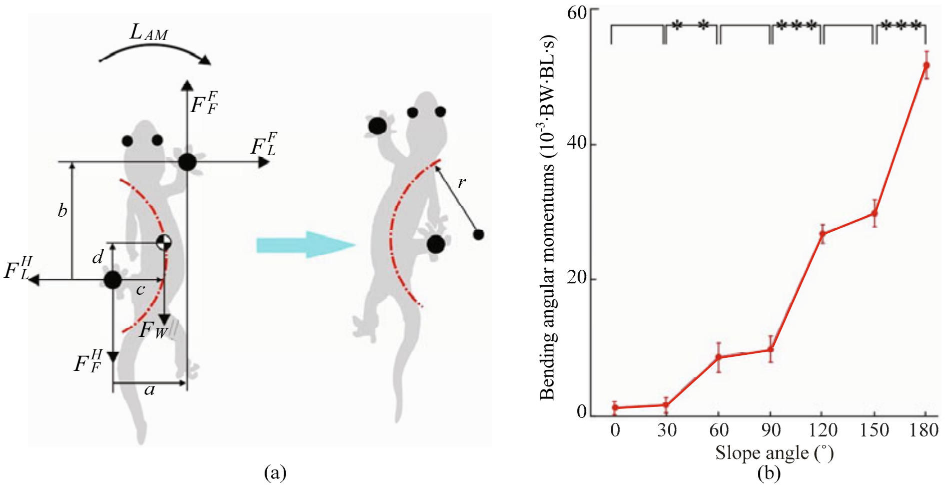


Fig. 4 The three-dimensional reaction force impulse of front and hind feet during the stance phase in relation to slope angle. (a) Lateral force impulses. In order to describe the lateral force impulses of the left and right feet, the lateral force directing the mid-line of the body is defined as the negative lateral impulse (foot pushing away from the body), whereas, the positive lateral force impulse is the opposite (foot pulling toward the body). (b) Fore-aft force impulses. The positive fore-aft force impulse means that the foot drives the body upwards. (c) Normal force impulses. The negative normal impulse means that the feet adhere to the substrate of the slope. Red asterisks: the hind feet between two successive slope angles are significantly different. Green asterisks: the front feet between two successive slope angles are significantly different. *: $p<0.05$, **: $p<0.01$; ***: $p<0.001$.

(inverted slopes), and the mean of the forward speed was 0.33 ± 0.15 m·s^{-1} ($N = 50$). However, there was a significant reduction in the forward speed when encountering slopes ranging from 60° to 150° (steep slopes), i.e., a forward speed range of 0.43 m·s^{-1} to 0.82 m·s^{-1}, with a mean = 0.65 ± 0.27 m·s^{-1} ($N = 24$), was shown on a 90° slope, whereas a forward speed range of 0.32 m·s^{-1} to 0.72 m·s^{-1}, with a mean = 0.59 ± 0.13 m·s^{-1} ($N = 22$), was demonstrated on a 120° slope (Fig. 3b; Table 1).

3.3 The impulses of a substrate reaction force acting on an individual foot

The lateral impulses (I_L) acting on the front and hind feet increased with respect to the sloped angles, and the I_L action on a front foot increased faster than such action on a hind foot. When the sloped angle ranged from 0° to 30°, the front foot of the geckos pushed outward, and the lateral force impulse action on the front foot pointed to the midline of the body, whereas at any sloped angle beyond 60°, the front foot pulled inward and its I_L pointed toward the outside of the body. When the geckos moved on a shallow slope (sloped angle < 60°), their hind foot pushed outward, and I_L acting on the hind foot pointed toward the midline of body; in contrast, when the sloped angle was larger than 60°, their hind foot pulled inward (Figs. 2c and 4a, Table 1). The fore-aft impulse (I_F) acting on the front foot increases with the sloped angle. The front foot generated a positive I_F when the geckos moved on a non-horizontal surface. On slopes ranging from 0° to 60°, the I_F acting on the hind foot increased, whereas from 60° to 180°, it decreased. The hind foot generated a positive I_F, which appeared to act as a source of propulsion over an angled slope of 0° to 120°, but changed into a braking behavior from 150° to 180° (Figs. 2c and 4b, Table 1). The normal impulses (I_N) acting on the front and hind feet decreased



(a) (b)

Fig. 5 The bending angular momentums induced by the reaction force acting on the feet during a step. (a) Diagram of the calculation for bending angular momentum, where the centre of mass as the centre of bending moment was used to calculate the bending angular momentum generated by the feet. (b) Mean values of the bending angular momentum of geckos climbing on different slopes. BG: body weight; BL: body length. Black asterisks: the bending angular momentums between two successive slope angles are significantly different. *: $p<0.05$, **: $p<0.01$; ***: $p<0.001$.

as the sloped angles increased. The value of I_N acting on the front foot decreased faster as compared to that acting on the hind foot (Figs. 2c and 4c, Table 1).

3.4 The bending angular momentum

A lizard in a sprawled posture bends its body laterally into a *C*-shaped wave and propels forward in an *S*-shaped wave[6]. Thus, the supporting feet need to generate a sufficient bending moment during the stance phase to make the trunk laterally bend from one side to the other so as to maintain an *S*-shaped movement. Because the movement results from a continuous action of force or force moment, impulses or angular momentum caused by the forces acting on the feet were introduced to show the contribution of the feet on the locomotion of the animal.

In accordance with what occurs in nature, to reveal the contributions of the front and hind feet on the lateral bending during a slope locomotion (Fig. 4a), we calculated the bending angular momentum (L_{AM}) through Eq. (3), using the center of mass (COM) of the gecko as the center of the bending moment.

During the duration of the stance phase (T_S), the lateral and fore-aft forces acting on the hind feet (F_L^H and F_F^H), and the lateral and fore-aft forces acting on the front feet (F_L^F and F_F^F), were measured using the FMA. The lateral distance between the left and right support feet in each step (a), the fore-aft distance between the left and right support feet in each step (b), the lateral distance between the COM and the hind support foot (c), and the lateral distance between the COM and the hind support foot (d) were obtained from the high-speed video recordings (Fig. 5a). The values of a and b remain constant[31], whereas, c and d change with the lateral bending of the trunk. Therefore, to simplify the integral calculation in Eq. (3), c and d were considered to be $0.5a$ and $0.3b$, respectively. Thus, Eq. (3) can be simplified as Eq. (4). In Eq. (4), I_L^H and I_F^H are the lateral and fore-aft impulses acting on the hind feet, respectively, and similarly, I_L^F and I_F^F are the same impulses acting on the front feet. These results of the impulses are shown in Fig. 4. A previous study described the results of a and b in detail[31]. Thus, the bending angular momentum (L_{AM}) was obtained using Eq. (4), and is shown in Fig. 5b. When the geckos climbed up different slopes, the bending angular momentum used to maintain their movement increased as the slope increased, and increased sharply on slopes above 90°. Minimum bending was found at 0°, and maximum bending occurred at 180°, with the latter being

$$L_{AM} = \left| \int_0^{T_S} -\vec{c} \times \vec{F}_F^H \mathrm{d}t + \int_0^{T_S} -\vec{d} \times \vec{F}_L^H \mathrm{d}t + \int_0^{T_S} (\vec{a} - \vec{c}) \times \vec{F}_F^F \mathrm{d}t + \int_0^{T_S} (\vec{b} - \vec{d}) \times \vec{F}_L^F \mathrm{d}t \right|. \tag{3}$$

$$\begin{aligned} L_{AM} &= \left| \int_0^{T_S} -0.5\vec{a}\times\vec{F}_F^H\mathrm{d}t + \int_0^{T_S} -0.3\vec{b}\times\vec{F}_L^H\mathrm{d}t + \int_0^{T_S} (\vec{a}-\vec{c})\times\vec{F}_F^F\mathrm{d}t + \int_0^{T_S} (\vec{b}-\vec{d})\times\vec{F}_L^F\mathrm{d}t \right| \\ &= \left| \int_0^{T_S} -0.5\vec{a}\times\vec{F}_F^H\mathrm{d}t + \int_0^{T_S} -0.3\vec{b}\times\vec{F}_L^H\mathrm{d}t + \int_0^{T_S} (\vec{a}-\vec{c})\times\vec{F}_F^F\mathrm{d}t + \int_0^{T_S} (\vec{b}-\vec{d})\times\vec{F}_L^F\mathrm{d}t \right| \\ &= \left| -0.5\vec{a}\times\int_0^{T_S} \vec{F}_F^H\mathrm{d}t - 0.3\vec{b}\times\int_0^{T_S} \vec{F}_L^H\mathrm{d}t + 0.5\vec{a}\times\int_0^{T_S} \vec{F}_F^F\mathrm{d}t + 0.7\vec{b}\times\int_0^{T_S} \vec{F}_L^F\mathrm{d}t \right| \\ &= \left| -0.5\vec{a}\times\vec{I}_F^H - 0.3\vec{b}\times\vec{I}_L^H + 0.5\vec{a}\times\vec{I}_F^F + 0.7\vec{b}\times\vec{I}_L^F \right|. \end{aligned} \tag{4}$$

approximately twenty-times greater than the former (Fig. 5b, Table 1).

4 Discussion

4.1 The lateral bending and dorsoventral deformation of the trunk

The trunk of lizard in a sprawling posture was laterally bended into a *C*-shaped flexure[6,8], and the increased degree of lateral bending increases the stride length and locomotor speed on a horizontal surface[6]. The forward speed of a *Gekko gecko* shows a ladder change when the slope angle changes from 0° to 180°, whereas the speed on the whole decreases as the slope increases (Fig. 3b). This contradiction between the changes in lateral bending of the trunk and the forward speed illustrates that a sharp lateral bending of the trunk on inverted slopes (slope angle >120°) may not be a means of speed control.

The cross-section plane of a lizard's trunk is similar to an ellipse[33], and thus the trunk of a gecko can be simplified through the elliptical pillar model (Fig. 6a). The approximate volume can be calculated using as

$$V_1 = A_1 \cdot L_1, \tag{5}$$

where A_1 is the elliptical area of the section plane of an elliptical pillar, and L_1 is the pillar length.

Because the body of a gecko bends laterally in a *C*-shaped flexure during locomotion, we adjusted the above model to that of the bending of an elliptical pillar in the frontal plane (Fig. 6b). Moreover, the body was simplified to approximate a compressed model of an elliptic pillar in the median sagittal plane (Fig. 6c). The volume of bending in an elliptical pillar can be calculated as

$$V_2 = A_2 \cdot L_2, \tag{6}$$

where A_2 is the elliptical area of the section plane of a bending elliptical pillar, and L_2 is the pillar length.

In accordance with the principle of constancy for the volume of a trunk:

$$A_1 \cdot L_1 \approx A_2 \cdot L_2, \tag{7}$$

apparently,

$$L_1 > L_2, \ A_l < A_2. \tag{8}$$

We found that when the geckos moved on inverted slopes, their body was dorsoventrally deformed along the median sagittal plane as a result of gravity increasing the distance between the COM and surface. Ignoring the weight of both the head and tail, the trunk and limbs of a quadruped standing on a horizontal surface were considered as similar to a beam supported at both ends, which is analogous to a bridge supported by piers along the median sagittal plane[34]. Thus, in the median sagittal plane, we established a mechanical model of a simply supported beam to analyze the dorsal-ventral deformation of the beam under the influence of a uniformly distributed load caused by mass (Fig. 6d). The maximum deformation in the dorsal-ventral direction is equal to[35]

$$h_{\max} = \frac{5qL_2^4}{384EI_x}, \tag{9}$$

where

$$I_x = \int_{A_2} x^2 \mathrm{d}A. \tag{10}$$

Here, $h_{\max}$ is the maximum deformation during the action of a uniformly distributed load, q is a uniformly distributed load caused by mass, L_2 is the effective length of a beam, E is the elasticity modulus, and I_x is the inertia moment about the x-axis.

Eqs. (9) and (10) show that the maximum deformation of the beam ($h_{\max}$) is reduced by increasing its section area or by decreasing its effective length when a uniformly distributed load (q) is constant. Moreover, according to Eq. (8), the resistance to dorsal-ventral bending in the median sagittal plane is increased and results in a dorsal-ventral deformation that primarily occurs following lateral bending. The adhesion system of a gecko has an asymmetric characteristic because it

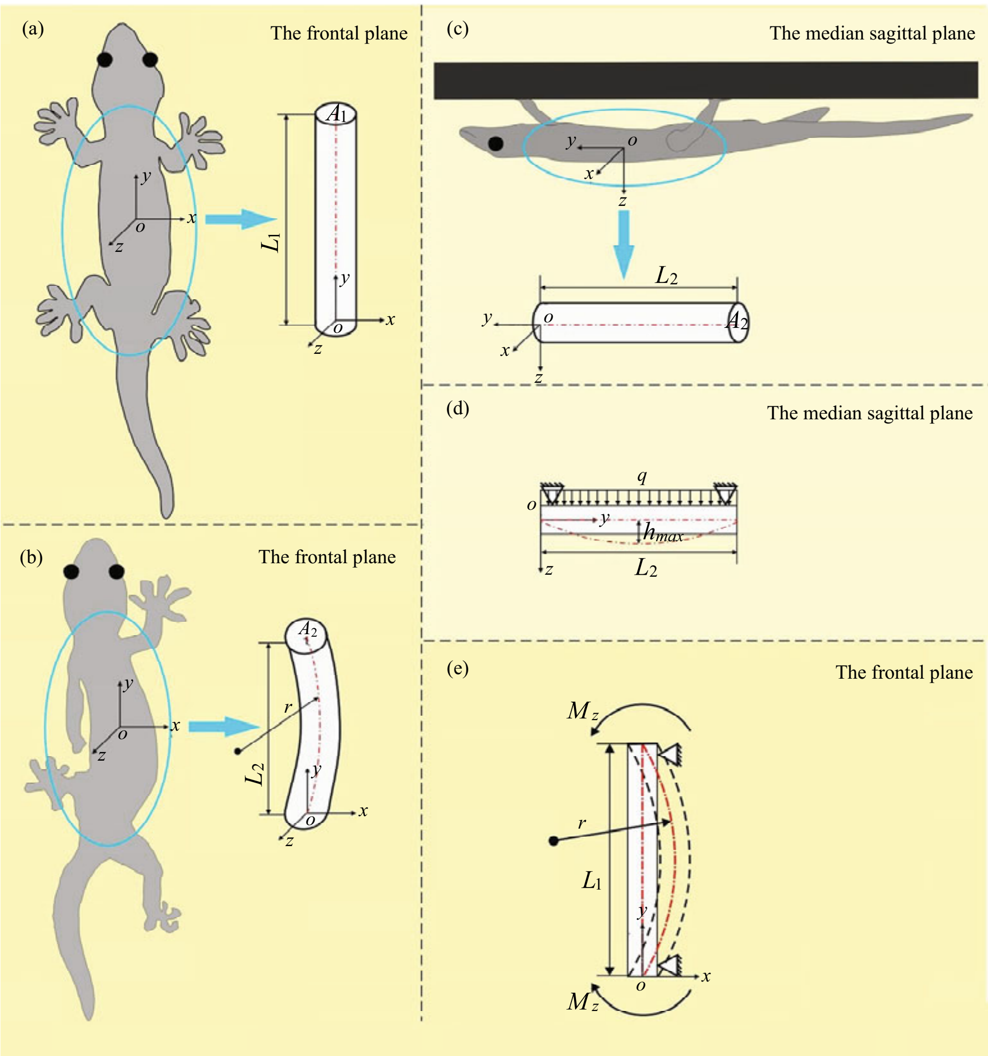


Fig. 6 Bending mechanical models of *Gekko geckos* in the frontal body and median sagittal planes. (a) The trunk in static state was simplified as an elliptic pillar. (b) The bending trunk during gecko movement was simplified as the bending elliptic pillar. (c) During movement the body was simplified as a compressed model of an elliptic pillar. (d) The deformation of the beam supported at both ends under the uniformly distributed load induced by mass. (e) In the frontal plane, the mechanical model of a supported beam in bending moment.

can resist a larger shear force compared with a normal force[26,36]. For safe adhesion while moving, a proper contact angle between the foot and substrate is necessary[31]. Because a significant amount of dorsal-ventral deformation will result in an increase in the contact angle, thereby making the normal direction of the adhesion system share more load, and finally causing a failure of the adhesion system, to ensure that the contact angle between the foot of the gecko and the slope is located within a range allowing safe adhesion, the gecko increases the lateral bending in its frontal plane to enhance the bending strength about the *x*-axis, and inhibits a dorsoventral deformation of the trunk resulting from the gravitational forces, thereby making on inverted slopes more load are distributed to the shear direction of the adhesion system .

4.2 The reaction forces acting on the foot in response to lateral bending

In the frontal plane, at the beginning of a step, the diagonally opposing feet both step forward simultaneously, and a *C*-shaped curve opens toward the side of the hind limb before shifting to the opposite side during the next step. Based on the elliptical pillar model, we established a mechanical model of a simply supported beam in the frontal plane to obtain the relationship between the bending radius and lateral bending moment (Fig. 6e), i.e.,[37]

$$M_Z = \frac{EI_z}{r}, \tag{11}$$

where M_Z is the lateral bending moment about the z-axis, E is the elasticity modulus of a beam, I_Z is the inertia moment about the z-axis, and r is the lateral bending radius.

The bending is a result of continuous action of the bending force moment during locomotion; meanwhile, there is a proportional relationship between the bending moment and bending angular momentum, which can be expressed as

$$L_{AM} = \int_0^{T_S} M_z \mathrm{d}t. \tag{12}$$

Eqs. (11) and (12) show that the amount of bending angular momentum is inversely proportional to the lateral bending radius. Because the lateral bending radius on inverted slopes is smaller than that on shallow slopes (Fig. 3a), to accomplish a movement on an inverted slope, a gecko needs to generate a greater bending moment allowing its body to contort more sharply into a *C*-shape. However, the question of how a gecko generates such a large lateral bending moment remains unanswered.

During the stance phase, L_{AM} caused by the reaction force acting on the feet is favorable for not only a transition of forces between the front and hind feet, but also for a continuity of the locomotion. On a shallow slope (slope angle < 60°), the lateral force of the front foot generates a disadvantageous negative bending angular momentum, which inhibits the body from bending. On a horizontal surface, the negative fore-aft force acting on the front foot generates a positive bending angular momentum, illustrating that a negative fore-aft force acting on the front foot brakes the locomotion, which is advantageous for a lateral bending. On a 30° slope, the gecko makes full use of shear gravity to produce an opposite bending angular momentum. On steep slopes (60°< sloped angle < 120°) and inverted slopes (sloped angle > 120°), the bending angular momentum is mainly generated by the lateral force of the front foot; a small lateral force can generate a larger bending angular momentum to facilitate bending. Moreover, the sum of the lateral force impulses acting on the left and right supporting feet increase with the incline, resulting in a greater amount of lateral bending. A positive fore-aft force produced by the front foot generates a disadvantageous bending angular momentum that also hinders the bending of the body. On the whole, large differences in the lateral and fore-aft force impulses acting on both the front and hind feet help supply the necessary angular momentums for lateral bending when the geckos move along a shallow incline. As the hind feet contribute less and less to a positive fore-aft impulse (Fig. 4b), the larger lateral impulse acting on the front feet help the body bend laterally when a gecko climbs up an inverted slope.

Specifically, inclines greater than 90° are associated with an increased bending angular momentum, such that this momentum on a 180° slope is two times greater than that on a 90° slope (Fig. 4b). This result indicates that body bending becomes increasingly difficult owing to the increased gravitational forces exerted on inverted slopes, thereby forcing the gecko to use a considerable amount of energy to continuously bend its body. Moreover, the contraction of the axial and lateral muscles can be used in the control of its lateral bending[38]. Previously, great deformations of the muscles have been shown to generate and release a significant amount of power[39], resulting in a high consumption of energy. The gradual decrease in the bending radius indicates that a gecko requires more energy consumption to climb up a steeper slope.

4.3 Anatomy basis for lateral bending of the trunk

Utilizing an integrated approach with previous studies from a variety of vertebrates we find that the bending planes of the trunk are different in different animals. Some animals' trunks are curved in the frontal plane during movement[4,6,40], while others mainly show vertical bending[41,42]. The reasons that underlie vertical bending may be associated with different gait patterns and the decoupling of footfall cadence from vertebral column movement. Terrestrial animals have adapted to the sway of their trunks between the front and hind feet in both the vertebrae and muscles by: (a) increasing the contact area between adjacent vertebra to enhance the supporting of the body weight; (b) evolving the dorsal longitudinal muscle along the spine, allowing constriction to increase the curvature, enhance the stiffness of the trunk, and support the body weight[34,43].

Gekko gecko is different from other terrestrial animals and could inhabited inclined or even inverted surfaces[31,44,45]. The previous study showed that lizards from cluttered areas have large number of presacral vertebrae than those from open areas. Lizards from open habitat, densely vegetated habitat and highly cluttered habitat have the number of presacral vertebrae 24.5 (31 species), 26 (36 species) and 26.5 (29 species) respectively[46]. Dissection of the skeletal system of *Gekko gecko* showed that the number of presacral vertebrae is 26 in *Gekko gecko*[47]. The large number of presacral vertebrae would be benefit for the trunk bending in a wide range in the frontal plane, which in turn helps to reduce the length of the body, decrease the distance between the barycenter and feet, and diminish the avulsion effects of gravity on the adhesive feet, thereby increasing its stability during ceiling movement. Meanwhile, geckos have evolved the Dorsal Longitudinal Muscle (DLM)[48], and the contraction of DLM enhances the stiffness and bending range of spine so as to prevents the trunk deformation in the median sagittal plane. At the same time, the contraction of DLM allows the barycenter to be closer to the contact surface and facilitates security and stability even while climbing on inverted slopes.

5 Conclusion

Using a novel three-dimensional SRF measurement array and a synchronous high-speed recording system, we obtained the bending behavior of the trunk of a *Gekko gecko* during its locomotion, and subsequently measured the detailed 3D substrate reaction forces acting on the individual limbs at varying slopes. We found that a gecko enhances the stiffness of its trunk in the dorsoventral direction by increasing its lateral bending, thereby decreasing the angle between the substrate and the animal's adhesive foot as much as possible, allowing the gecko to successfully climb along inverted slopes. However, lateral bending has been generally ignored in the design of climbing robots, which has seriously decreased the performance of wall-climbing robots. Thus, to efficiently improve the performance of a wall-climbing robot it is necessary to exploit the coupling of various factors, such as an adjustment of its behavior and the characteristics of its adhesion system. The above strategies governing the climbing locomotion of a gecko may inspire future structural designs and novel control mechanisms in the creation of climbing robots.

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