

Adaptation Strategy In Attachment–Detachment Cycles When Faced With Changes In Incline And Orientation During Gecko Climbing

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Abstract

Background: Geckos are endowed with the extraordinary capacity to move quickly in various environments; they benefit from efficient control for the complex footpads. Research on the locomotor behavior and contact status in the attachment–detachment (A-D) cycle of the footpads for diverse challenges is linked to the revelation of regulatory strategy. At present, there is a lack of systematic research for the A-D cycle, which limits the understanding of the adhesive locomotion mechanism.

Methods: The A-D cycle that facilitates the level and up–down locomotion on inclined and vertical surfaces of *Gekko gecko* was investigated to clarify the locomotion postures and durations in the release, swing, contact, and adhesion stages, respectively. This reveals the relationship between the structure and function of the attachment devices, and its regulation when faced with changing locomotion demands.

Results: Despite changes in climbing demands, gecko foot locomotion posture (angle extremes and changing trends) in the swing stage, the posture (bending angle: fore 41°, hind 51°) and contact time ratio (7.42%) in the contact stage remain unchanged, which is in contrast with the adjustable postures in the stance phase. Furthermore, the variation range of the forefoot locomotion posture is larger than that of the hindfoot, and the forefoot angle changing trend is opposite to that of the hindfoot, indicating that the combination of anatomical structure and functional demands results in the differentiation in the adaptation mode of the A-D cycle for the fore- and hindfoot.

Conclusions: Gecko's fore- and hindfoot have evolved different structures to undertake differential functions. The function (adhesion) for various locomotion demands relates to footpad deployment in the stance phase but is unaffected by the regulations (postures and durations) in the swing and contact stages. The results demonstrate that the unified adaptation strategy reduces the diversity and complexity of the control. It advances the understanding of the adhesive locomotion mechanism, reflects the structural evolution and adaptation strategy of attachment devices for functional requirements and provides biological inspiration for effective design and control of adhesion robots.

Introduction

Locomotion is the result of the interaction forces between the attachment devices of organisms and the external environment. Some animals, such as some insects[1], tree frogs [2] and geckos, have evolved attachment devices with adhesion function to navigate extremely challenging terrains. Geckos, for instance, can adapt to various locomotion demands and move extremely fast on various surfaces (steep slopes or even ceilings[3]) because of the extraordinary adhesion ability, resulting from the hierarchical adhesion structure[4] and efficient locomotor control on their complex compliant footpads [5, 6]. Studies on adhesion structures found that the pulling angle [7] of setae and softness[8] of lamellar play important roles in the adhesion mechanisms. The realisation of the adhesion function for the microstructure relies on the macroscopic adhesion structure (toes and footpads). Full comprehension of the adhesion-locomotion mechanism requires understanding the adaptation of macrostructures to locomotion

challenges that guarantee effective attachment of the microstructures, such as how the adhesive footpads contact the substrate and swing in the air during the attachment–detachment (A-D) cycle when faced with a variety of locomotion demands. However, only a few studies have investigated the regulatory strategy of the A-D cycle, especially for complex compliant footpads that respond to varying climbing locomotion, coordination between the macro and micro layers of adhesion structures and relationship between the footpad’s regulation and adhesion function.

Locomotion in different environments requires different foot reaction forces [4, 10]. Studies have found that the deployment of footpads is related to the direction or magnitude of the adhesion forces [11–13]. To adapt to various locomotion challenges, geckos adjust foot position, orientation [9–11], postures [12], and locomotion speed [13]. Although some variables may alter in response to changes in locomotion demands, gecko could satisfy their locomotion requirements using an intergraded regulation strategy of their A-D cycles. However, its relationship to the foot reaction force pattern is not systematically analysed yet. In addition, it is unclear if the distinct structure, distributed or compliant, is linked to particular adaptation patterns to ensure adhesion.

Many studies have focused on the adhesion function/force in the A-D cycles. The realisation of the adhesion function depends on the distance [14], angle [13, 15], force [16–18] between the setae and the interface, and the footpad deployment in the stance phase. Except in the stance phase, an A-D cycle comprises the contact, release, and swing stages. Time (attach/detach time [19]) and space variables (orientation [20] and angle [21]) are introduced to describe the behaviour at different stages. However, the regulation strategy of the footpads in different stages and how they meet the adhesion requirements need to be explored.

The forefoot of the gecko differs from the hindfoot in terms of physiological anatomy and adhesion potential[6]. The force patterns of the fore- and hind footpads vary at different slopes [22]. In addition, the locomotion/adhesion function of the fore- and hindfoot on a vertical surface in different directions [10] and the response to inclination[23] are disparate. Therefore, it is necessary to investigate if variations in the physiological structure are related to the distinction in the A-D cycle adaptation strategy.

Here, we investigated the A-D cycle of *Gecko Gekko* with complex compliant footpads on substrates at varying inclinations (level, 45° and vertical surfaces) and orientations (up and down). Gecko locomotion is recorded and quantified using a motion capture system. The adaptation strategies of the A-D cycle for diverse locomotion demands are summarized. In addition, the contrasts and similarities in fore- and hindfoot strategies and the coordination mechanism between the footpad structures and adhesion functions are studied. Additionally, a comparison between the adhesive devices of geckos and other adhesion animals is performed. Thus, determination of the integrated A-D cycle adaptation strategies of geckos for diverse locomotion demands will further our understanding of the mechanism of the adhesion function in the hierarchical adhesion structure. This can provide guidance for the design and control strategy of biomimetic adhesion robots.

Materials And Methods

2.1 Animals

Experimental geckos (*Gekko gecko*) were obtained from Guangxi Province (China). They were housed in a greenhouse with controlled humidity (65–75%) and temperature ($27 \pm 2^\circ\text{C}$). Five geckos with similar body size were selected for climbing experiments ($N = 5$; Mass = 60.5 ± 5.2 g; Body length = 255.5 ± 12.2 mm; Tail length = 140.4 ± 8.3 mm; Mean \pm s.d.). The selected geckos were fed with crickets every day and trained to climb on level, inclined and vertical surfaces for approximately 2 weeks.

2.2 Experimental protocol

The experimental setup has four parts: a rotatable motion platform with a channel, motion capture system, three-dimensional (3D) force measuring array and data processing platform (as shown in Fig. 1(a)). The motion capture system comprises four motion capture cameras and motion capture software (Optitrack, USA). The motion channel is constructed using acrylic plates and profiles and is 200 mm in width, allowing the geckos to move freely. It has an open end that serves as an entrance; the other end has a dark box to attract geckos. The 3D force platform comprises 24 3D force sensors, each of which monitors the reaction force of a different footpad [24].

According to the layout method of placing multiple cameras in a small space proposed in [25], four motion-capture cameras are appropriately arranged. Following the marking technology proposed in [26] several markers are pasted on the gecko before each test at the following positions: bregma, cervical spine, middle of spine, caudal vertebrae, left and right shoulders/hip, elbows/knees, wrists/ankles, middle and tip of the tail. In addition, white nail polish was applied on the heel and tip of the middle digit (d3) [23] of the fore- and hindfoot as marking points. The experimental device is placed in a dark room, as shown in Fig. 1(a).

The rotatable motion platform was set to 0° , 45° and 90° . Geckos were trained to climb the 90° and 45° surfaces from top to bottom and bottom to top, respectively. They were placed at the channel' entrance and encouraged to move forward by squeezing the bottom of the tail and tapping the back until they climbed into the dark box. The locomotion behaviour of the gecko was recorded using the motion capture system with camera frame rate of 250 FPS. The geckos' reaction forces were measured using the 3D force measuring array.

2.3 Data analysis

To obtain the x, y and z coordinates of the markers at the bregma, left and right shoulders/hip, cervical spine, caudal vertebrae, elbow/knee, wrist/ankle, heel and tip of the third digit of fore- and hindfoot, the DLT6 software [27] based on MATLAB platform (version R2019a, MathWorks, Natick, MA, USA) was used for digitising the recorded videos. The y, z, x-axis represent the forward and backward motion parallel to the direction of travel, the back–abdominal motion perpendicular to the moving surface, and the mid-lateral motion perpendicular to the yoz plane, respectively.

A global coordinate system (O_0) was established, as shown in Fig. 1(a). The movement direction of the geckos is the positive direction of the y-axis, the xoy plane is parallel to the movement plane, and the direction perpendicular to the xoy plane is the positive direction of the z-axis. According to the Cartesian coordinate system, the x-axis is positive, and the movement direction is perpendicular to the yoz plane. The angle rotation around the x- and z-axis is the pitch and yaw angle, respectively. In addition, distinct coordinate systems (O_{lf} , O_{rf} , O_{lh} , O_{rh}) for the four feet are established. The origin coordinates are set at the wrist/ankle joint; the xoy plane is parallel to the motion plane. The y-axis direction is consistent with the motion direction; the x-axis direction points to the outside of the body (the right and left foot points to the right and left, respectively).

2.4 Parameters definition

During the movement process, the support phase is responsible for generating thrust, whereas the swing phase moves the foot forward to start the next step. The A-D cycle can be divided into four stages: release (R), swing (S), contact (C), and adhesion (A). The contact stage represents the moment when the footpad touches the substrate until the entire footpad is in full contact with the base; the release stage refers to the stage where the footpad begins eversion and detach until the entire footpad is about to leave the substrate. The time spent in the four stages (T_R , T_S , T_C , T_A) and the percentage of each of these periods (Df_R , Df_S , Df_C , Df_A) are obtained.

Foot bending angle θ

After the footpad goes the swing phase, the digit is rolled up when the footpad touches the base and starts to adhere. The angle between the line of the tip of the third digit and the heel and the base plane is defined as the bending angle.

Bending angular velocity ω

Bending angle θ divided by contact phase time T_C .

Foot pitch angle α

When the footpad is in the swing phase, the digits are also in a rolled-up state. The angle between the line of the digit tip and the heel of the third digit in the plane of the movement direction is defined as the pitch angle.

Foot yaw angle γ

During the swing phase of the front and rear feet, the angle between the third digit and the y-axis direction of movement direction defined as the foot yaw angle. A positive value indicates that the footpad points in the positive direction of the y-axis, and a negative value indicates that the footpad points in the direction opposite to the y-axis direction.

Contact angle β

When the footpad touches the base, the angle between the calf (the line between the wrist/ankle joint and elbow/knee joint) and the base is defined as the contact angle.

Initial contact force $F_{n_initial}$

This is the force perpendicular to the substrate surface when the footpad touches the base upon collision.

2.5 Statistical analyses

Seventy tests were chosen from more than 200, including 20 trials each of vertical-up, and vertical-down, 10 trials each at 45° slope-up, 45° slope-down, and horizontal. Only trials in which the geckos moved in a straight line were chosen. Every selected trial had a velocity of $\pm 15\%$ of the average speed and at least a complete gait cycle video clip.

SPSS software (SPSS 22.0, Inc., Chicago, IL, USA) was used to analyse the selected data statistically. Comparisons were made among data for 0°, 45°, and 90° in two directions (up and down), using ANCOVA with the Scheffe method for post hoc tests to examine the variables: time rate, yaw angle, pitch angle, and bending angle. ANCOVA was used again for the variables of foot contact angle, initial contact force, and bending angular velocity. Welch's analysis of variance (ANOVA) with the Games–Howell test was used when the variance homogeneity was not satisfied. A significance level of 0.05 was used throughout. Pearson correlation analysis was adopted to test the relationship between movement speed and time or time percentage of each stage and was deemed correlated when the Pearson correlation coefficient P was larger than 0.4. The results of the tests are expressed as the mean \pm standard deviation (mean \pm s.d.).

Results

3.1 Time proportions of different stages

The time variables of each stage, the proportion of swing and adhesion time have a certain correlation with the movement speed ($P_1 = 0.407$; $P_2 = 0.601$), whereas the proportion of contact time and release time has no obvious correlation with the movement speed ($P_1 = 0.114$; $P_2 = -0.064$).

Contact stage: The contact time proportion of the fore- and hindfoot exhibits no significant difference on different slopes and motion direction (all of the p values > 0.05 , as shown in Supplementary material, Table 2), and the contact time percentage of the forefoot is similar to that of the hindfoot (forefoot: $7.42 \pm 0.97\%$; hindfoot: $7.42 \pm 0.61\%$).

Release stage: The release time percentage of the fore- and hindfoot show no significant difference in various slopes (all p values > 0.05 , as shown in Supplementary material, Table 3), whereas there are obvious differences in various slopes. For example, the forefoot release time percentage during upward vertical climbing is significantly different from that of downward climbing on a 45° slope ($p < 0.001$), horizontal plane ($p = 0.001$), and vertical surface ($p < 0.001$; $p = 0.026$).

3.2 Posture changing trend

The fore- and hindfeet movement changes the pitch and yaw angle during an A-D cycle in the level, 45° slope and vertical surface, as shown in Fig. 3 (a–d). The variation trend in the yaw angle is similar, which first decreases and then increases. The forefoot pitch angle decreases and then increases, whereas that of the hindfoot increases and then decreases.

The locomotion posture of the fore- and hindfoot did not alter considerably under varied movement situations, according to the videos of gecko climbing up and down in vertical, 45° slope, and horizontal surfaces. Therefore, the video sequence of downward locomotion on the vertical surface is chosen to exhibit the entire process of fore- and hindfoot postures. Figure 2 (e) and (f) show the posture changes of the fore- and hindfoot in a complete movement cycle (observed from the side and dorsal view), including the four stages of adhesion, release, swing and contact.

3.3 Locomotion posture angles

Yaw angle and pitch angle

The maximum, minimum and range of forefoot yaw angle show no significant change ($p > 0.05$); when moving upward on the vertical and 45° inclined surfaces, the range of the hindfoot's yaw angle is slightly larger than that of the downward locomotion. The range of the forefoot yaw angle ($163.09 \pm 6.16^\circ$) is larger than that of hindfoot ($134.37 \pm 11.14^\circ$).

There is no difference in the minimum ($-156.92 \pm 15.70^\circ$), maximum value ($151.76 \pm 13.73^\circ$), and the range ($308.68 \pm 20.42^\circ$) of forefoot pitch angle. The maximum, minimum and range of hindfoot ($-25.56 \pm 31.45^\circ$, $138.44 \pm 15.76^\circ$, $164.00 \pm 32.46^\circ$) also display no significant difference ($p > 0.05$). The pitch range of the forefoot is significantly larger than that of the hindfoot ($p < 0.05$).

Foot bending angle and the angular velocity

The bending angles of the fore- and hindfoot were $40.99 \pm 5.01^\circ$ and $50.91 \pm 8.21^\circ$ respectively; there is no significant difference in the horizontal plane, 45° inclined plane, and vertical plane when moving upward and downward ($p > 0.05$). The bending angles of fore- and hindfoot in the horizontal plane are $45.82 \pm 6.16^\circ$ and $56.36 \pm 11.04^\circ$, respectively, and are larger than those of the inclined and vertical planes.

On the vertical and 45° surfaces, the bending angular velocity of the forefoot is lower than that of the hindfoot ($p < 0.05$); on the horizontal plane, there was no significant difference between the fore- and the hindfoot ($p > 0.05$).

Contact angle

The contact angles of the fore- and hindfoot change depending on the surfaces and motion directions. The forefoot contact angle is significantly different from the hindfoot angle ($p < 0.05$). When moving upwards vertically, the forefoot contact angle ($43.10 \pm 6.33^\circ$) is significantly larger than that of hindfoot

($32.21 \pm 7.12^\circ$), whereas is significantly smaller ($26.26 \pm 3.05^\circ$) than that of the hindfoot ($43.65 \pm 5.98^\circ$) when moving downwards. The forefoot contact angle ($17.12 \pm 2.69^\circ$) is significantly smaller than that of the hindfoot ($50.88 \pm 3.05^\circ$) when moving upwards on 45° slope, whereas it is $24.99 \pm 5.60^\circ$ significantly larger than that of the hindfoot ($7.46 \pm 5.10^\circ$) when moving downwards. The forefoot contact angle is approximately half of the hindfoot during level walking.

Discussion

4.1 Structure-function relationship in different limbs

The anatomical structure and geometry of joints often reflect their movement and function. The forelimb of geckos includes muscle tissue that can rotate between the radius and ulna (as shown in Fig. 2 in [28]), and the skeletal system of the forelimb is more sophisticated than that of the hindlimb (as shown in Fig. 3 in [6]). The experimental results reveal that the fore- and hindfeet have distinct locomotion postures and that the ranges of the forefoot pitch and yaw angles in the swing process are much larger than those of the hindfoot. The pitch and yaw angle extremes of the forefoot do not change considerably, but the yaw angle range of the hindfoot is wider during upward motion than downhill. This is because the legs are twisted rearward, and the footpads and hindlimbs undergo substantially more movement changes than the forelimbs [23]. During the swing stage (Fig. 1(a–d)), the dynamic postures of the fore- and hindfeet exhibit clear differences: the forefoot digits are rolled up and detached at the beginning of the swing phase, whereas the wrist joints roll toward the direction of motion. The footpad swings in the air after quick detachment, all the digits curl up and close together, and the footpad changes the pitch angle significantly around the wrist joint. The footpad rises, then lowers, then rises again, finally drops to make contact with the substrate. All the digits bend upward but do not noticeably curl up together during the swing stage of the hindfoot. The five digits are separated, and the footpad creates a perceptible yaw angle change around the wrist joint; the footpad first swings backward (against the motion direction), and then forward (motion direction) until it is ready to enter the support phase and makes contact with the substrate for adhesion. The angle variation during the swing stage was connected to the postures and was considerably different (Fig. 3). The pitch angle of the forefoot tends to drop first and then rise, whereas the pitch angle of hindfoot first increases and then decreases. Because the footpads are in parallel contact with the substrate, the pitch angle of the fore- and hindfeet in the support phase should be ideally close to 0° . However, owing to the segmented digit bone structure and bent phalanges [17], the initial pitch angle determined using data from the digit tip and heel is not zero (as shown in Supplementary material Table 5). The digit rotates backwards around the heel (lateral view) as the forefoot enters the swing phase, resulting in the digit tip being below the digit heel. The pitch angle also becomes negative and drops to a minimum. The digit then spins forward, causing the foot to extend forward. The digit tip progressively rises beyond the heel, increasing the pitch angle until contact is made. When the hindfoot reaches the swing phase, the digits hyperextend, increasing the pitch angle; nonetheless, the digit tip does not fall clearly into the air, and the foot surface remains parallel to the moving surface. The foot then enters the contact phase, during which the pitch angle begins to drop until

it reaches its lowest point, as the foot enters the support phase. Distributed digits enable the footpad to augment the normal adhesion force by coupling the reverse digits [40]. By contrast, during the swing, the forefoot bends and collects all digits. We speculate that the function of the separate layout of digits has been weakened or even ignored, and the curling posture is conducive to reducing the resistance of the air swing, whereas the hindfoot does not have an obvious curling state due to the different physiological structure and locomotion functions of the fore- and hindlimbs. First, the joint or organ that bears the weight of the swing process need overcome the motion resistance. The forefoot position is the most forward when the forelimb swings in the movement direction, whereas the knee joint is the most forward component to move as the hindlimb swings. Furthermore, the bending angle of the forefoot is much less than that of the hindfoot (as illustrated in Fig. 5(b)) and such size relation remains constant across slopes and locomotor orientations due to anatomical variations between the fore- and hindfeet resulting from the smaller forefoot and shorter fore digits.

A complete A-D cycle is a necessary condition for the study of attachment-detachment movement, because the dynamic locomotion process cannot be separated from any stage of the cycle, therefore it is necessary to ensure that the footpads perform an entire A-D cycle. However, studies found that gecko toes keep everted when moving on the horizontal plane; therefore, we selected the experimental data on the horizontal plane where the movement speed was relatively slow, and the fore- and hindfoot had complete A-D cycles. To reduce the influence of speed, the experimental data of different moving surfaces having relatively close moving speeds were selected (see Supplementary material Table 2). Although the climbing speed of the vertical plane was higher than that of other motion cases ($p1 < 0.001$; $p2 = 0.033$; $p3 = 0.004$; $p4 < 0.001$), there was no correlation between the time proportion of adhesion, release, and speed. Therefore, the experimental results of the five motion cases can be compared and analysed together. Studies have shown that the time required for attachment (contact) and detachment (release) of geckos is fixed [19, 29]. Our findings also reveal that contact time ratios do not change with changes in locomotion demands (see Fig. 2(e)), however, the proportion of release time of fore- and hindfoot changes, and there is a correlation between the release time and velocity ($P = 0.471$). In addition, there were differences between the fore- and hindfeet in all circumstances ($p < 0.05$), except in the vertical-down locomotion ($p = 0.644$). The bending angle of the forefoot is smaller than that of the hindfoot when moving on different surfaces, whereas there was no significant difference between the contact time ratio of the fore- and hindfoot. The results support the theoretical calculation, with the bending angular velocity of the forefoot being smaller than that of the hindfoot.

There was no significant change in the bending angle of the forefoot on different moving surfaces; however, the bending angle of the hindfoot on the horizontal plane increased significantly (as shown in Fig. 5 (c)), whereas the bending angular velocity of the fore- and hindfoot is relatively minimal on the horizontal plane. This may be because the gecko can move on the horizontal plane without an adhesion force, and its toes evert when it moves rapidly on the horizontal plane. It can be speculated that there is no need for the gecko to press the toes quickly and completely to allow adhesion during the contact stage of the footpad in horizontal motion. The bending angle of the fore- and hind toes is likely to be limited by the physiological structure, and the proportion of contact time is not changed, which is required for

adhesion function. The change in the bending angular velocity is related to the change in the locomotion demands. Furthermore, whether the adhesion process is regulated actively or passively has long been a point of contention. A relationship between bending angle, angular velocity, and contact force may be one of the bases to verify the active/passive adhesion. In this study, because of our focus on the overall A-D cycle, we did not measure the contact force of a single toe, which will be tested and explored in a future study. The time proportion of each stage, the locomotion posture and its transition time, and the angle change in a gecko may guide the control strategy of a bionic robot with flexible adhesion ends.

4.2 Intercoordination between adhesion status and limb-foot locomotion

Adhesion locomotion relies on the A-D cycle of the attachment devices. Research has found that the posture and deployment of the footpads in the stance phase is related to the adhesion force which is critical to the adhesion status. As an A-D cycle also includes the swing, contact, and release stages, it is necessary to determine the relationship between these stages and the adhesion status. The direct way to measure this relationship is to use the force between the foot and base at the moment of contact. The initial contact force $F_{n_initial}$ comes from the movement of the fore- and hindlimbs in the contact stage, it changes significantly on different surfaces and moving directions (as shown in Fig. 6(b)). This is similar to the results on a vertical surface in different directions (upward, downward, left to right) [19]. Theoretically, the changes in foot-movement result in changes in force; however, the locomotion posture in the swing and contact stages of the fore- and hindfeet on various slopes and directions have no significant variation, specifically, the angle changing trend, the bending angle θ , and the contact time ratio. This indicates that $F_{n_initial}$ has little connection with the footpad's movement. $F_{n_initial}$ is generated instantly when the foot touches the base. Comparing the $F_{n_initial}$ of fore- and hindfoot (as shown in Fig. 6(b)) with the corresponding foot contact angle (as shown in Fig. 5(a)) on different slopes and motion directions, it was found that the contact angle of the fore- and hindfoot and the first contact force have the same magnitude relationship; that is, if the forefoot contact angle is greater than that of the hindfoot, the $F_{n_initial}$ of the forefoot is also larger than that of the hindfoot. Previous research by the author has shown that the contact angle changes significantly with inclination and motion direction changes. The relationship between the foot contact angle and functional requirements of the fore- and hindlimbs also changes. $F_{n_initial}$ measured in our experiments is similar to the forces obtained by Wang et al. [19]. Our results show that the magnitude-relationship between the $F_{n_initial}$ of the fore- and hindlimbs and contact angle on the vertical and 45° when climbing upward and downward is exactly the opposite. $F_{n_initial}$ adjusts as the inclination and direction change, however, the movement postures and angles of the fore- and hindfeet do not change. It can be deduced that the changes in the foot reaction force are primarily caused by the movements of the limbs and body, with little relation to fore- and hindfoot movement patterns. However, the physiological anatomy of the fore- and hindfeet, and the demands for adhesion, may account for some invariance.

In addition to the relationship between the adhesion status and foot/limb locomotion, it is useful to establish the whole kinematic mode connecting the footpads, limbs and bodies that respond to various slopes. From the aforementioned results, it can be concluded that the fore- and hindfeet bending angle θ do not change, and θ of the forefoot is always smaller than that of the hindfoot, whereas the leg contact angle β changes with changing locomotion; when travelling on 45° slope, β of the limb above the centre of mass (COM) is smaller than that below the COM, while moving in a vertical plane β of the limbs above the COM is larger than that below the COM. Hence, the foot, leg, and body of the gecko are united to simplify the overall motion of the gecko when moving on diverse substrates (as shown in Fig. 6 (a)). Wang et al. proposed that the force patterns of the gecko's fore- and hindlimb alter when it travels on different inclined surfaces [22]. Therefore, although only the substrates of 45° and 90° angles were investigated, we may assume that there is a change threshold of the fore- and hindfeet's movement patterns. Research on the regulation principle of the gecko when it moves in varied slopes and directions is particularly critical for the adhesion climbing robot in engineering applications, as it can guide the control strategies for the robot climbing under varied circumstances.

4.3 Structure–function relationship across species

The attachment devices structure of geckos possesses dispersed and compliant digits, which is different from adhesion organs of many insects, and it also brings about a significant difference in their A-D cycle patterns, such as stick insects, beetles, and ants whose foot movements in the swing phase are closer to the non-adhesive foot, whereas the compliant footpads of geckos curl up and close together to minimise the resistance in the swing stage until the footpad is about to enter the stance phase. To ensure that all digits provide a greater contact area with the substrate, the distributed digits are re-opened. Furthermore, the A-D cycle takes advantage of the compliant properties of footpads. During the adhesion process, the phalanges, blood inside the digit, and other tissues work together to apply downward pressure and tangential force to the digit [17]; the combination of hyperextension driving the digit roll allows for easy and rapid detachment with a very small peeling force. In addition, the adhesion force is regulated by the direction of the dispersed compliant footpads and orientation of each digit. Because of the distributed footpads, geckos [11, 12] and tree frogs [2] adjust the deployment and direction to adapt to the force requirements of different slopes or environments, and to maintain stability in locomotion or static state.

Although the structures of the attachment devices of insects and geckos/tree frogs are different, the generation and maintenance of adhesion function during the adhesion stage have similar principles. Firstly, in the distributed arrangement of adhesive areas (as shown in Fig. 7(a)). The main adhesion areas of the compliant footpads of geckos and tree frogs are placed under each digit, similar to the insects like stick insects [30], ants [31], beetles[32], and others, which are distributed in the segmented tarsus. This distributed adhesion region plays a crucial function in the adhesion force management, and the adhesion area size is related to adhesion force. Geckos modify the adhesion area of their fore- and hindfeet greatly during the stance phase to accommodate varying adhesion requirements relative to the COM [11, 33]; the ants adjust the adhesion area on the tarsal segments to cope with the changing load [34]. Moreover, insects, geckos, and other animals on various environments are inseparable from the directional control

principle of adhesion, which is realized through the collaboration of micro and macro adhesion structure to achieve the change of adhesive area and adhesive strength [35]. Stable adhesion necessitates a small distance between the setae and the substrate [14], a certain shear force and normal force [16–18], which frequently necessitates the active and passive control of the digits. Beside, fast and easy detachment requires a certain angle [13, 36]. Gecko moves through the eversion of digit tip and the rotation of wrist/ankle joint, and insects push the adhesive pad outward to the body through leg movement and lift the adhesive joint. Furthermore, the feet of insects and geckos are often equipped with claws in addition to pads. The claw can be manipulated passively to create a mechanical interlocking with the substrate [37, 38]. Compared with the adhesive pad, the claw can satisfy the substrate with larger roughness [39, 40], improving the adaptability of the adhesive movement. The tree frog's foot, in the other hand, has no claws [41], hence its climbing adaptation range is limited (as shown in Fig. 7(c)). In addition, the A-D cycle of the different footpads of the adhesion animals share some similarities. Firstly, the fore- and hindfoot are capable of closed adhesion [9] due to the relatively similar adhesion structure system. The propulsive function of forefoot and hindfoot varies progressively on the substrates of 0-180 degrees, with the forefoot shifting from braking to driving and the hindfoot shifting in the opposite direction [22]; the feet above the COM play the main driving/braking function when the ant climbs up and down on the 30 and 60-degree slopes, [42]. Additionally, as the ends of the limbs, the feet should satisfy the overall movement requirements. Forelimbs often have some common functions like auxiliary vision and self-protection. As for geckos, fore-digits are brought together and actively close to the body during the swing phase (see Fig. 3(a)). This posture can reduce the foot volume and thus reduce the resistance of the swing process to a certain extent, and just as the forelimbs of many insects can explore the environment [43], the forefoot movement can help geckos better deal with challenging environments. Furthermore, the movement trends of the fore- and hindfeet have common features, such as the foot postures of a gecko, specifically, the fore- and hindfoot move “first backward (opposite to the direction of motion) and then forward (same direction of motion)” during the swing phase. But the “backward” is primarily represented in lateral view of forefoot, whereas the “backward” is primarily reflected in dorsal view of forefoot. The fore- and hindfoot structures are mechanically compliant; hence, the bearing force is low. The compliant and flaky footpad slides in the opposite direction during the prior time of swing, possibly due to air resistance and gravity on the vertical or inclined plane. To minimise resistance, all the forefoot digits are more collected and closer to the body. Because of the skeletal muscle structure of the hindlimbs, particularly the ankle musculoskeletal system limit, the yaw angle of the hindfoot varies dramatically (the foot rotates rearward). Furthermore, the bones and muscles of the gecko hindlimbs are heavier than that of the forelimbs [44]; and the hindlimbs have to bear more gravity and produce more propulsion, requiring more energy to move. There is limited energy consumption for other functions, such as the footpad locomotion in the swing stage, hence the hindfoot will adopt a labour-saving mode with the digits slightly gathered and distributed freely.

The excellent adhesion and locomotion characteristics allow adhesion animals climb on various slopes and even ceilings (as shown in Fig. 7(c)). Studies found the role of the adhesion pads on different tarsus and the coordinated movement mechanism of insects[45], and explored whether the movement trajectory

of the foot during the whole movement cycle affects its adhesion function[42]. However, the A-D cycle of insects is far less complicated than that of geckos, and the release and contact processes are not visible in insect locomotion. The coordination mechanism between the different digits of geckos and the regulation of the adhesion force during the supporting phase have been proposed [12, 33]. This paper has carried out a comprehensive and systematic investigation of the A-D cycle of geckos' complex distributed footpads and found that the foot locomotion postures are consistent in the swing and contact stages, with the exception of the release stage, which is related to the speed of movement of different surfaces. This is similar to the drag behavior of the ant hindfoot. When the ant descends a slope, the hindfoot is obviously dragged in the swing phase to avoid abrupt braking.

The invariance in the locomotion postures of the A-D cycle of geckos fore- and hindfoot in response to changes in the locomotor environment. Nowadays, lots of adhesion robots have been devised, however, they do not work as effectively as that of real geckos. To improve the robot's climbing performance and adaptation to varied surroundings, the control mechanism should mimic the motion control technique of that of geckos, in addition to the optimal mechanism design. The position of the footpads during the swing process has little influence on the foot reaction force during the contact process, indicating that the motion control of the robot foot during the swing process may be reduced, and furthermore, implying that the best control is frequently the simplest. Additionally, although the structure and force patterns of the fore- and hindfoot differ, the invariance of the A-D cycle across motion settings reminds us that the A-D cycle control strategy for the foot of the gecko-inspired robot should be universal. The description of the fore- and hindlimb movement characteristics is helpful in better understanding the A-D cycle and locomotion function, and highlighting the intriguing functional variations of the gecko's different organs. Exploring the physiological mechanisms behind the differences in the fore- and hindfeet is also of great importance to fully understand how reptiles effectively realise adhesion function in various terrains, which is critical for the design and control strategy of bionic adhesion mechanisms.

Conclusion

Our work investigates the A-D cycle of the gecko's complex compliant footpads for level and up-down locomotion on 45° and vertical surfaces. The gecko's foot locomotion posture (angle extremes and changing trends) in the swing stage, and the bending angles (fore: 41°, hind: 51°) and contact time ratio (7.42 %) in the contact stage did not change with changes in the climbing demands. However, the forefoot's A-D cycle differs from that of the hindfoot; specifically, the variation range of the forefoot posture is larger than that of the hindfoot, and the forefoot angle changing trend is opposite to that of the hindfoot. Additionally, the leg contact angle and initial contact force changed with the changing substrates, whereas the foot bending angle remained the same, suggesting that the foot reaction force patterns are more related to limb/body movement than footpad movement during the swing or contact stage. The fore- and hindfoot of the gecko evolved different structures, reflecting different functions. The invariance in the swing and contact stages of the A-D cycle respond to changing locomotion demands, indicating that the adhesion function is unaffected by the regulations (locomotion postures and durations) in the swing and contact stages, even though it relates to the footpad deployment in the

stance phase. This represents a unified adaptation strategy that lowers the diversity and complexity of locomotion control. It advances the comprehension of the adhesive locomotion mechanism, reflects the structural evolution and adaptation strategy of attachment devices for functional requirements, and provides insight into the design and control of adhesion robots.

Abbreviations

A-D: attachment–detachment; R: release stage; S: swing stage; C: contact stage; A: adhesion stage; T_R , T_S , T_C , T_A : the duration of four stages; Df_R , Df_S , Df_C , Df_A : the duration percentage of each of one cycle; COM: centre of mass.

Declarations

Ethics approval

The tests done at NUAA were approved by Jiangsu Association for Laboratory Animal Science and the Jiangsu Forestry Department (Approved File No. 2019-152). No animals were injured in any experiments.

Consent for publication

Not applicable.

Availability of data and material

All data generated or analysed during this study are included in its supplementary information files.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

Zhouyi Wang and Zhendong Dai conceived the ideas and designed the methodology; Weijia Zong and Bingcheng Wang carried out the lab experiment; Weijia Zong wrote manuscript; Zhourong Zhang and

Chang Yin collected and analyzed the data. All authors contributed critically to the drafts and gave final approval for publication.

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Figures

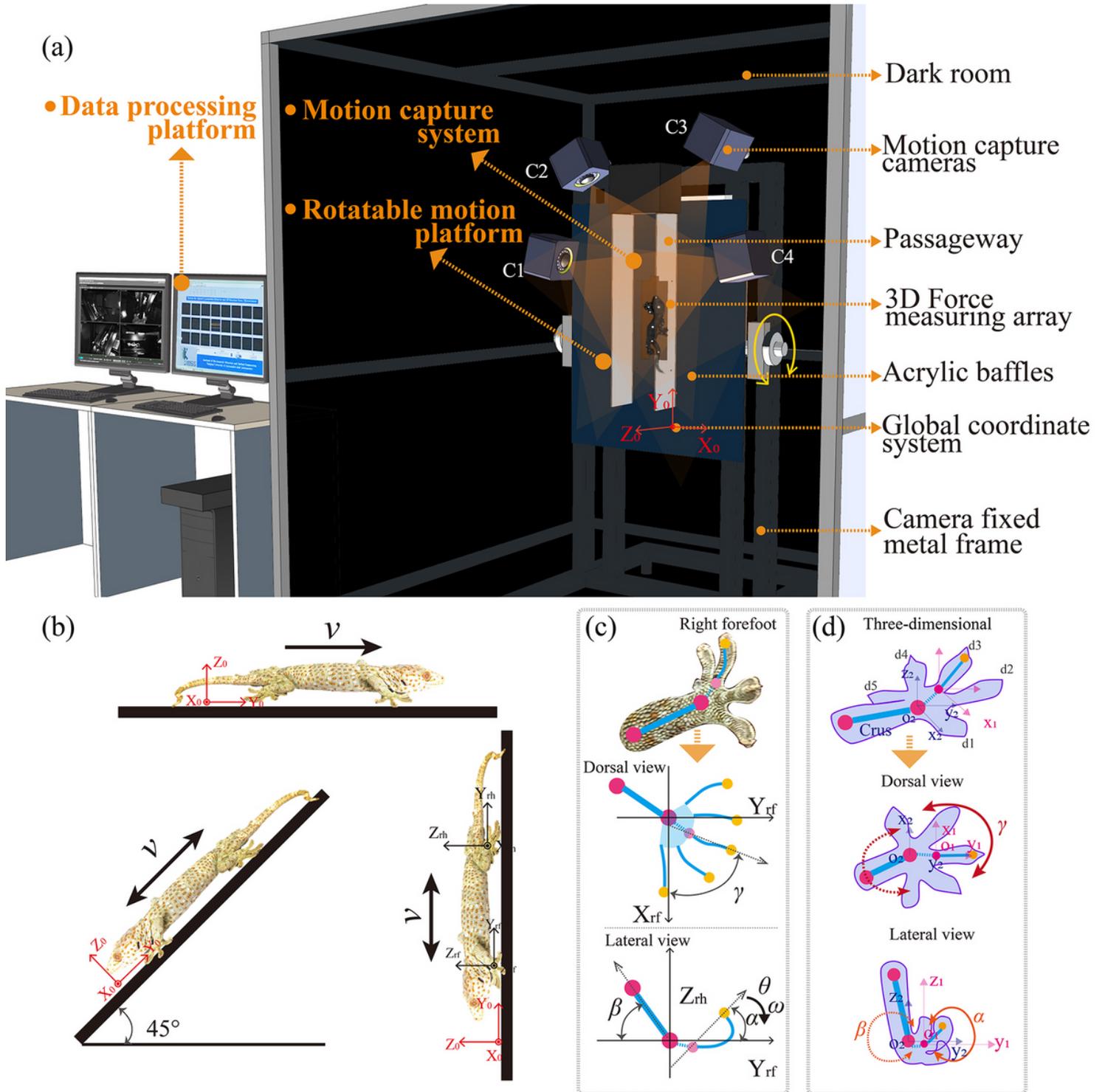


Figure 1

Experimental setup, protocol and variables definition. (a) Experimental setup; (b) Experiment process, gecko climbing on level, 45° and vertical surface upwards and downwards; (c–d) Definition of foot locomotion variables of the fore- and hind footpads.

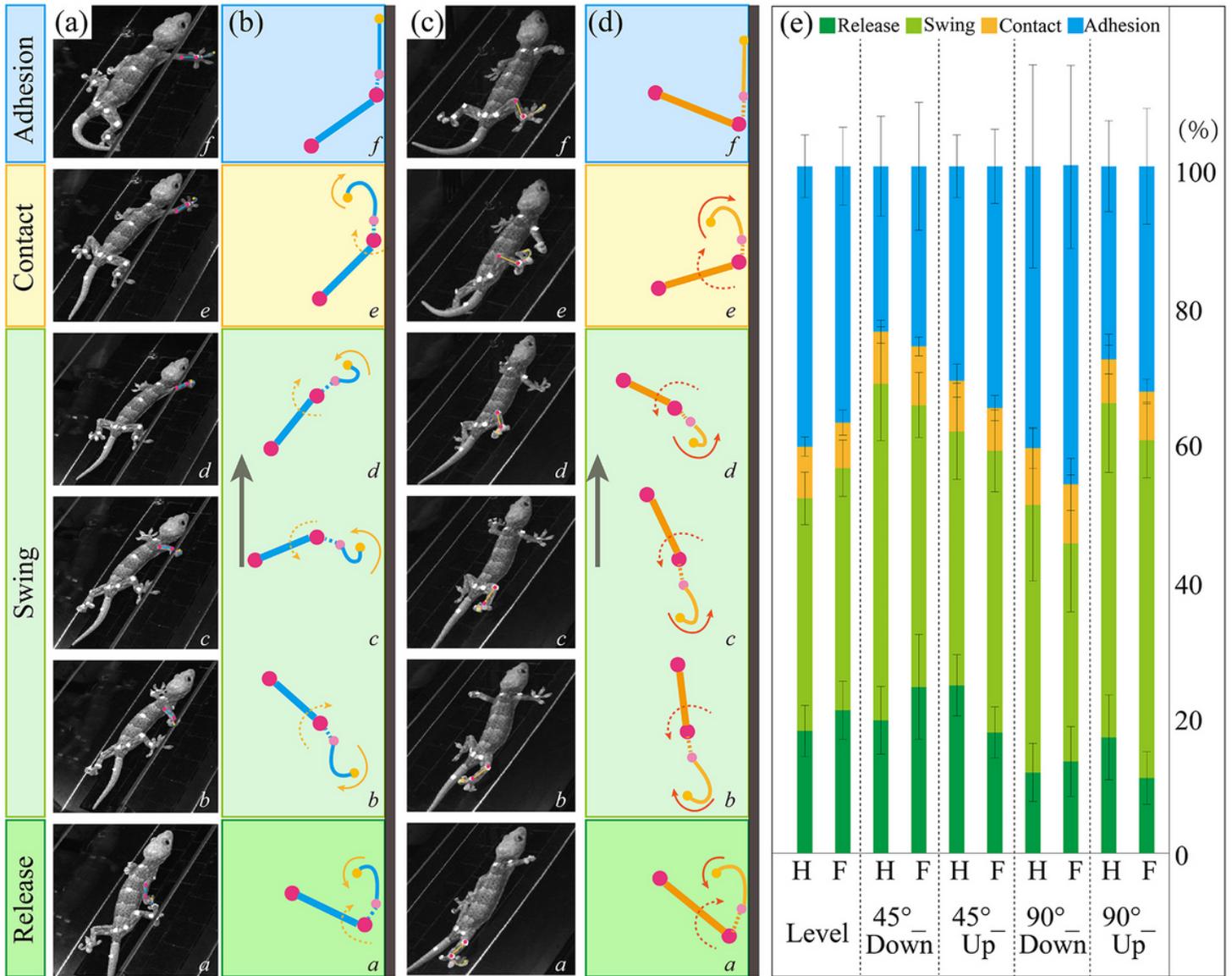


Figure 2

Time proportions of different stages of fore- and hindfoot locomotion in an A-D cycle. (a–b) Snapshots and the corresponding simplified schematic diagrams of gecko's forefoot locomotion in an A-D cycle (lateral view); (c–d) Snapshots and the corresponding simplified schematic diagrams of gecko's hindfoot locomotion in an A-D cycle (lateral view); (e) Time proportion in each stage of an A-D cycle of fore- and hindfoot in level and upward–downward locomotion on 45° and vertical surfaces (H represents hindfoot; F represents forefoot).

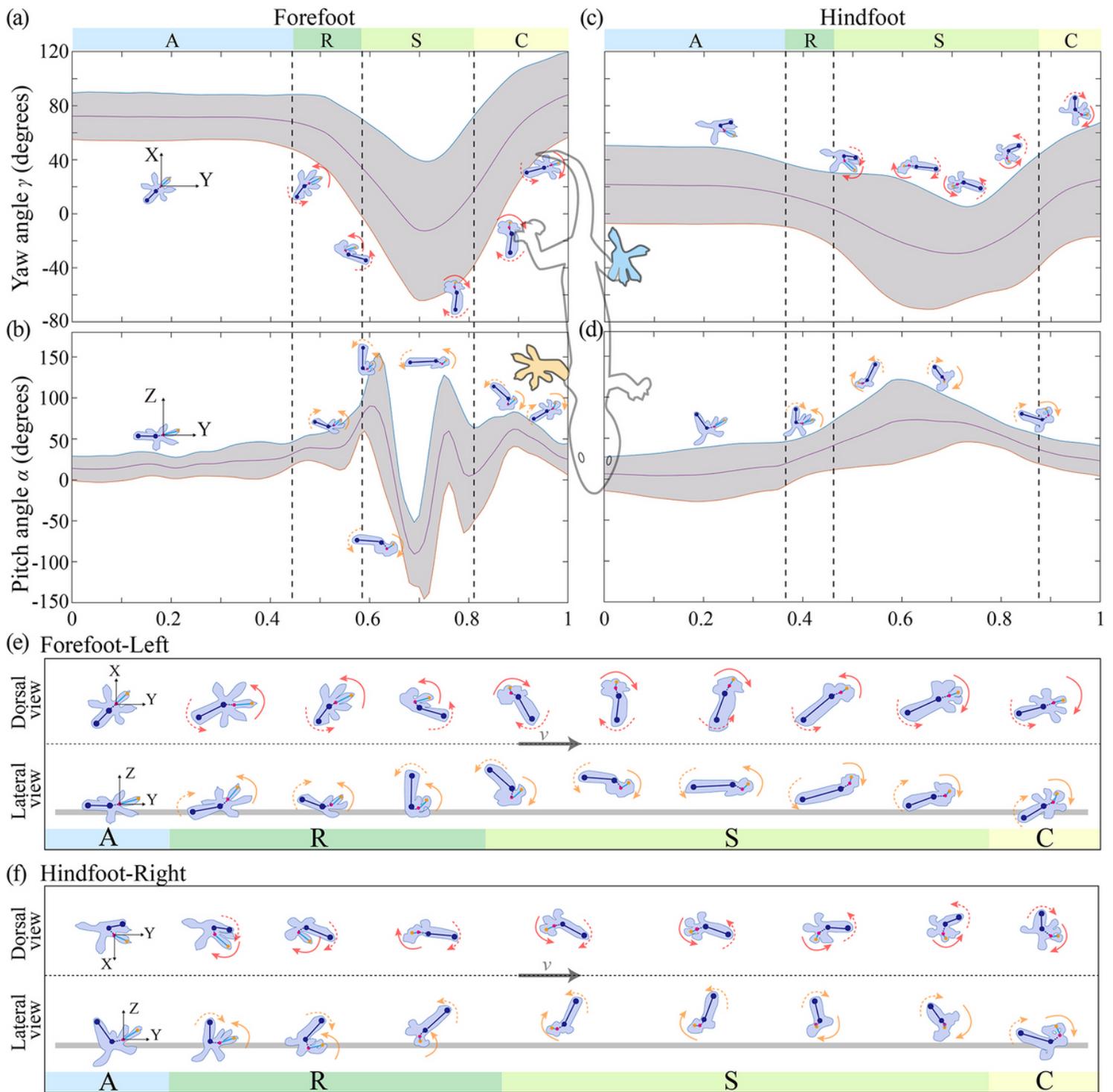


Figure 3

Locomotion postures and the changing trend of fore- and hindfoot. (a–d) Pitch and yaw angle changes during the four stages in the A-D cycle with schematic diagrams of foot motion postures above and below the curve ($n = 6$; Vertical-down climbing); (e–f) Schematic diagram of the A-D cycle postures of the (e) forefoot and (f) hindfoot in the dorsal and lateral view (Vertical-down climbing; Solid line arrow indicates digits rotation; Dotted arrow indicates the leg rotation).

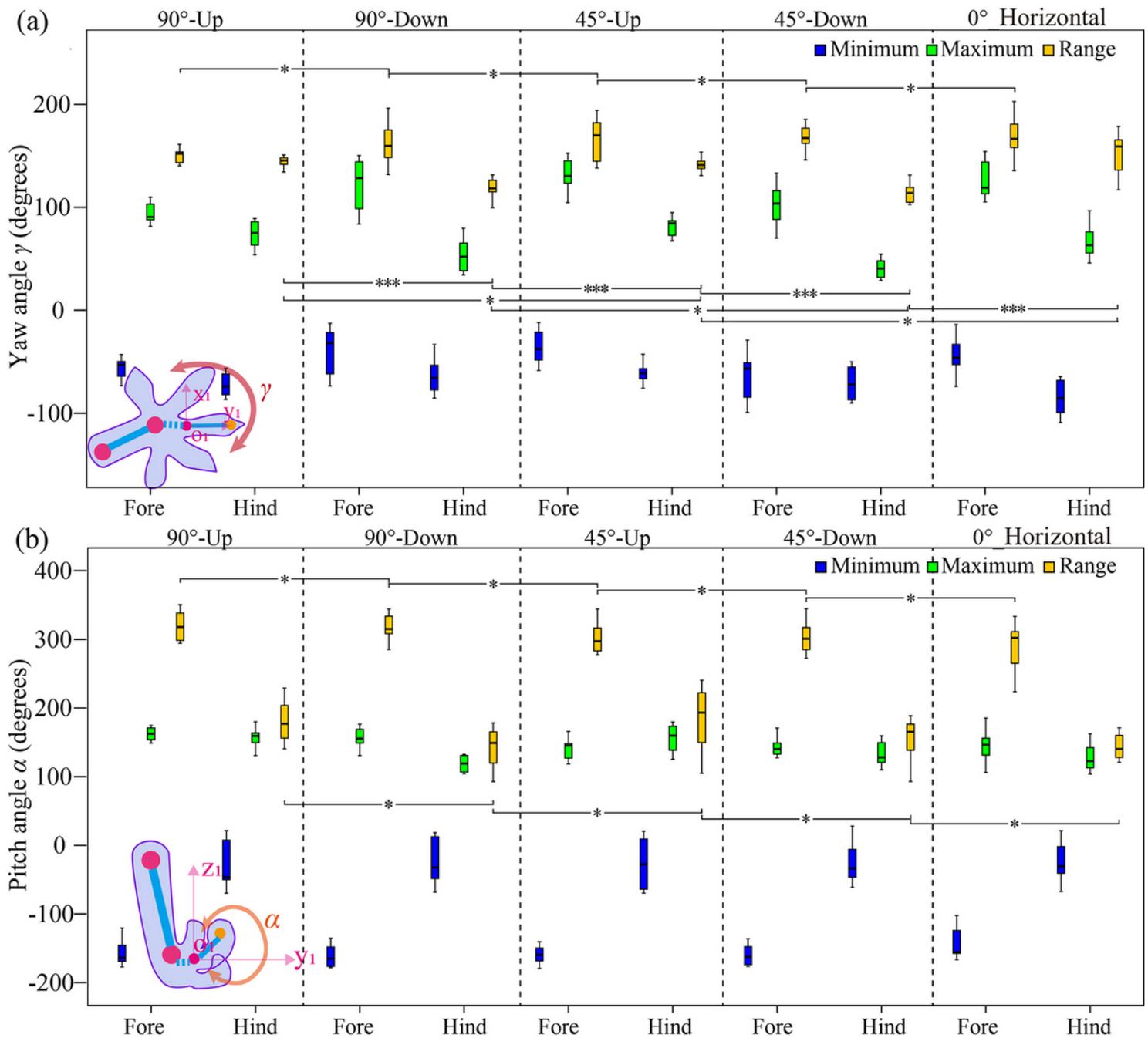


Figure 4

Maximum, minimum, and range of the fore- and hindfoot. (a) yaw angle and (b) pitch angle. (n = 10; Significance: * represents $p > 0.05$, ** represents $0.001 < p < 0.05$, *** represents $p < 0.001$)

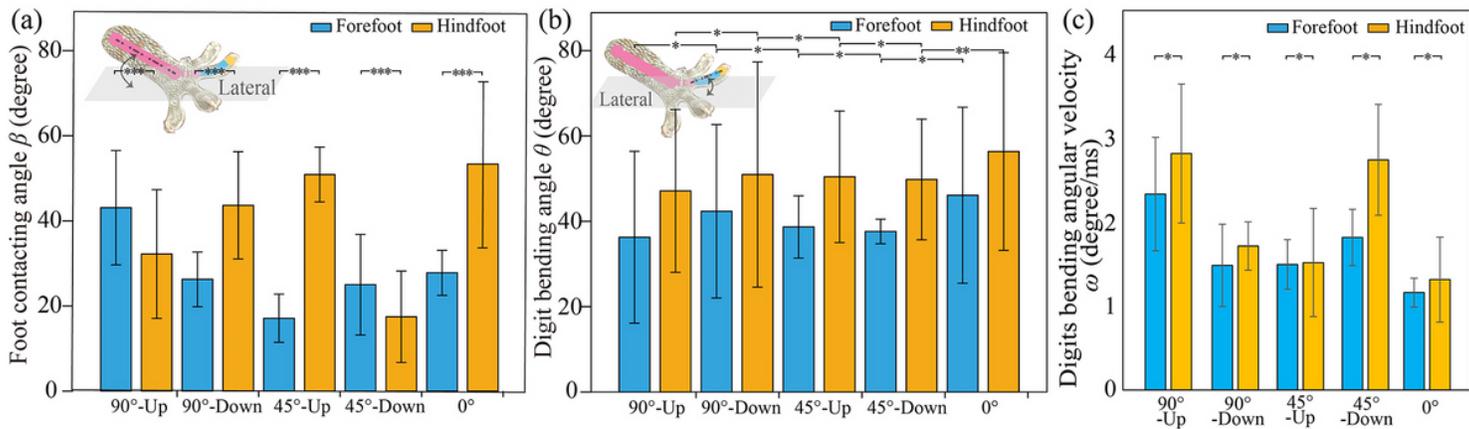


Figure 5

Contact angle, digit bending angle and the bending angular velocity. (a) Average contact angle of the fore- and hindfoot when moving in the vertical plane (up and down), 45° inclined plane (up and down) and horizontal plane; (b) Fore- and hindfoot bending angles in five locomotion conditions; (c) Fore- and hindfoot bending angular velocity in five locomotion conditions. (n = 10; Significance: * represents $p > 0.05$, ** represents $0.001 < p < 0.05$, *** represents $p < 0.001$)

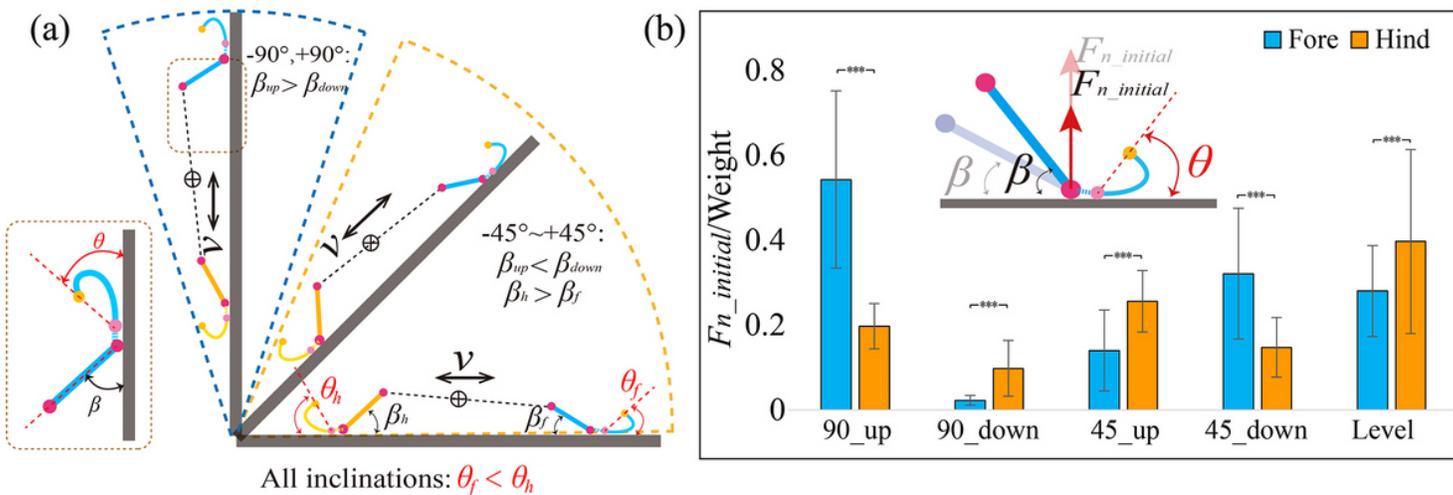


Figure 6

The comparison of the contact angle, bending angles and F_{n_intial} of fore- and hindfoot. (a) Schematic diagrams of the contact and bending angles of the fore- and hindlimbs and feet of the gecko on different inclinations and motion directions (Blue lines: foreleg/foot; Orange lines: hindleg/foot; \oplus represents the COM; black dotted line indicates the body); (b) Initial contact force between the fore- and hindfoot and the substrates in five locomotion conditions (for details on F_{n_intial} of level locomotion, refer to [22]).

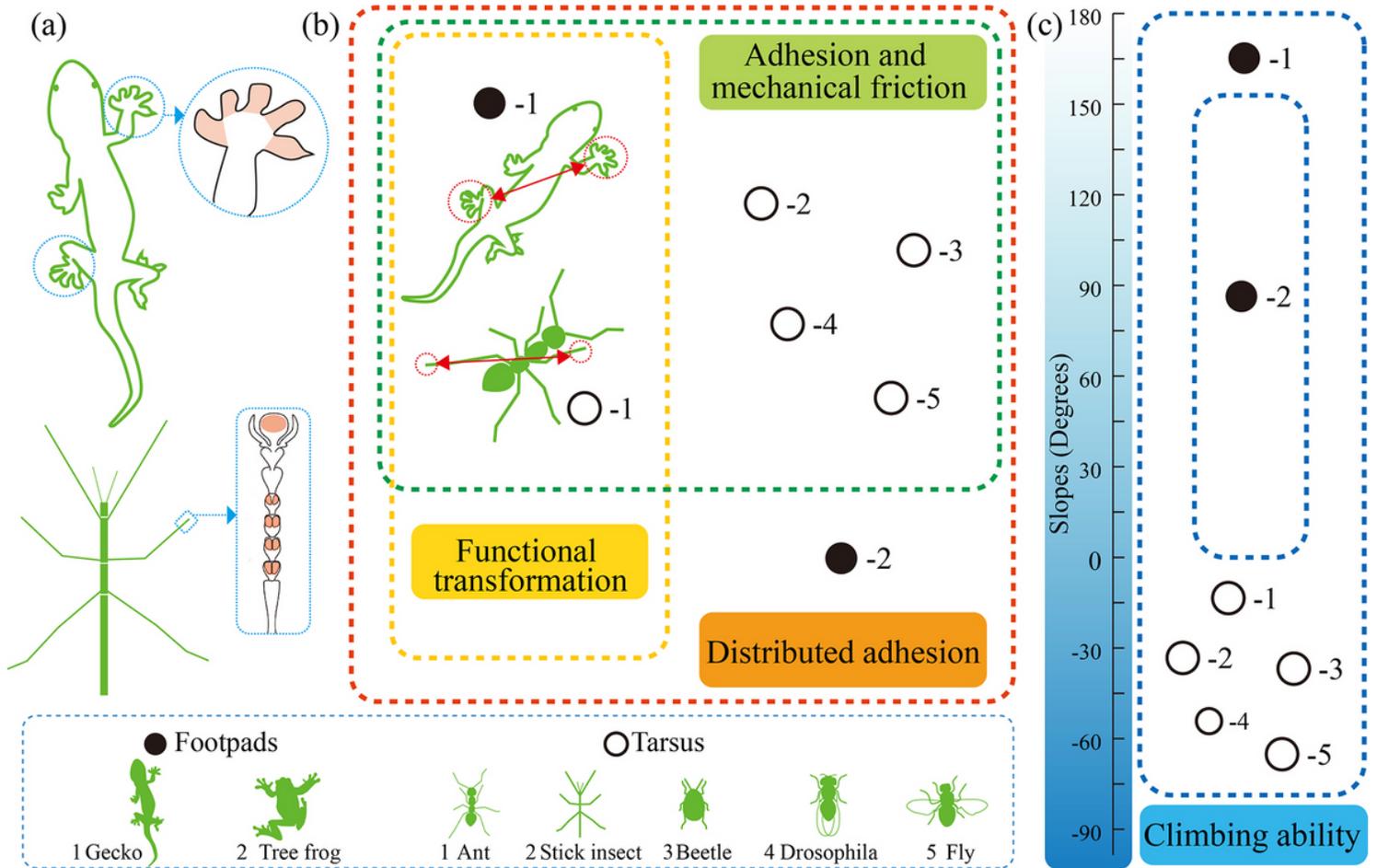


Figure 7

The comparison of the adhesion animals with different foot structures (a) Distributed adhesion area of gecko's footpad and insect's tarsus (light pink regions is the adhesion areas; take the stick insect as example, upper-right figure is modified from [46]); (b) The characteristics of different adhesion animals include the distribution of adhesion area, the synergy of adhesion and friction, and limb/foot function transformation; (c) The movement ability of different adhesion animals facing different inclinations. (●-1[22, 23, 33, 47]; ●-2 [2, 48]; ●-1[34, 42]; ●-2[46, 49]; ●-3[32, 38]; ●-4[50]; ●-5[1])

Supplementary Files

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- [SupplementaryMaterialsTable2Timeproportion.xls](#)
- [SupplementaryMaterialsTable3pvaluescontacttimes.xls](#)
- [SupplementaryMaterialsTable4pvaluesofthereleasetime.xls](#)
- [SupplementaryMaterialsTable5Theextremeandrangevalue.xls](#)
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