Hexapods shift to increasingly stable gaits when climbing on inclined substrates

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Abstract

When terrestrial organisms locomote in natural settings, they must navigate complex surfaces that vary in incline angles and substrate roughness. Variable surface structures are common in arboreal environments and can be challenging to traverse. This study examines the walking gait of katydids (Tettigoniidae) as they traverse a custom-built platform with varying incline angles (30°, 45°, 60°, 75°, 90°) and substrate roughness (40, 120, and 320 grit sandpaper). Our results show that katydids walk more slowly as the incline angle increases,

with a decrease of around 0.39 BL/s for every 23° increase in incline, while substrate roughness has no effect on walking speed, even across different inclines. At steeper inclines, katydids are less likely to use an alternating tripod gait, opting instead to maintain more limbs in contact with the substrate during walking. However, rougher substrates reduce this effect, increasing the likelihood that katydids will employ a tripod gait even on steeper inclines. These findings provide insights into how environmental factors influence locomotor strategies in katydids and enhance our understanding of effective locomotor strategies in hexapods.

1 Introduction

Rainforests are ecosystems where substrates with varying incline and surface roughness are featured. For many species inhabiting these regions, mastering effective movement techniques on highly variable surfaces while combating gravity is vital for survival; otherwise they face the severe risks associated with falling from heights. Remarkably, both vertebrates and invertebrates have evolved strategies for successful arboreal movement including elongated limbs [1, 2], adhesive pads [3, 4, 5, 6, 7], balancing maneuvers [8, 9, 10], and cyclic movements where the center of mass accelerates periodically [11, 12]. Examining when and how organisms transition from a terrestrial gait to a climbing gait sheds light on their interactions with the environment and their ability to navigate complex and challenging environments. We aim to investigate gait transitions in arboreal katydids (family:Tettigoniidae) found in the Peruvian Amazon.

Insects are commonly observed using an alternating tripod gait while walking over a substrate. This movement pattern involves three limbs contacting the ground at any one moment: the front and hind limbs on one side, and the middle leg on the opposite side (Fig. 1a). This limb configuration creates a support polygon which typically contains the center of mass [13]. This gait is symmetrical, with each trio of limbs being highly coupled and functioning like a leg of a biped [14, 15] despite each limb uniquely and independently influencing the acceleration of the center of mass [16, 17]. The tripod gait is considered highly energy efficient [18] and is often regarded as one of the fastest methods for hexapod movement [19], apart from the intriguing bounding gaits observed in some arthropods [15].

Little is known about the specific gait mechanisms of katydids. Many species in this family are highly arboreal [20], navigating through diverse and complex terrain and orienting themselves using sensory cues from the environment [21]. A closely related species within the orthopteran family has been shown to use the tripod gait [22], which may be advantageous for the challenging terrains that katydids navigate. Cockroaches use the tripod gait on uneven terrain with slight alterations in their strides [23] induced by a mechanical feedback system that stabilizes the body when they run rapidly [24]. The stability of the tripod gait allows cockroaches to traverse a wide variety of challenging substrates [25] and, combined with adhesive footpads, perform acrobatic feats overcoming rapid changes in incline and hanging upside down [8]. Behavioral experiments [13] and computational models [19] have shown that the tripod gait remains stable on both horizontal and vertical surfaces [26], and indeed, the tripod gait has been observed in climbing cockroaches [11, 8]. In this situation, the front legs pull the head toward the wall while the hind legs push the abdomen away while all legs pull inward toward the midline which is like the force pattern produced by geckos suggesting that limbed animals use a common template for climbing and hexapods may fare well using a tripod gait [11].

On uneven terrain, factors such as incline angle and surface roughness can significantly impact an organism's speed and gait. For instance, in ants, rough surfaces can influence running speed by affecting adhesive and propulsive forces [27, 28]. An increase in surface incline generally reduces running speed and may alter the direction of the forces exerted by the limbs or modify the insect's gait [27, 29, 11]. In natural settings, incline and roughness often vary across different spatial and temporal scales, forcing organisms to navigate diverse, challenging substrates. Understanding how and when organisms adjust their kinematics and behavior in response to changes in substrate complexity can offer insights into how animals navigate and thrive in complex natural environments.

This study investigates how surface incline and roughness affect the climbing behavior of katydids. We conducted field research at the Finca Las Piedras research station in the Peruvian Amazon over a period of 10 days as part of the in-situ Jungle Biomechanics Lab stupski2024curiositydrivensciencesitujungle. During this time, we observed several katydid species climbing trees and positioned on inclined surfaces that varied from smooth to rough textures (Fig. 1b). This led

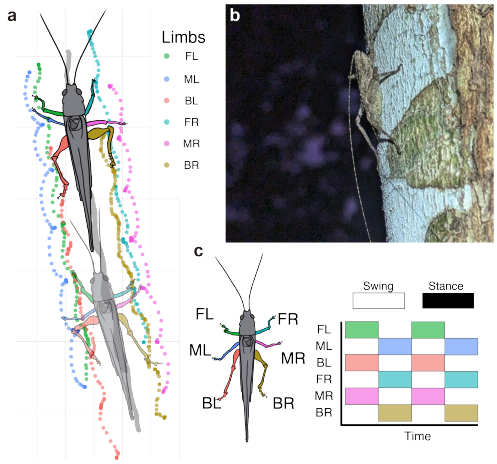

Figure 1: (A) A diagram of a katydid using an alternating tripod gait to traverse a substrate (S.Fig 1). (B) A katydid in the Peruvian Amazon Rainforest maneuvering across a tree trunk. (C) Katydids are hexapods; while moving in an alternating tripod gait, the front left, middle right, and back left limbs coordinate their movements. Colors represent individual limbs in the gait plot, indicating when they make contact with the substrate. The swing phase denotes when a limb is in motion, while the stance phase represents when the limb maintains contact with the substrate.

us to focus on this clade further. We hypothesize that steeper inclines and smoother surfaces will complicate climbing in katydids, resulting in reduced climbing speed, though they will maintain a tripod gait. This research aims to fill knowledge gaps related to the biomechanical and ecological aspects of gait transitions in insects within their natural environments.

2 Methods

2.1 Specimen Collection and Experimental Protocol

Over a period of 10 days in August 2024, we collected 24 katydids from the Peruvian Amazon Rainforest at the Finca Las Piedras Research

Station (Parcela 4, Sector Monterrey, Peru; -12.225718266152889, -69.11430715640181). Individuals were collected at night using a hand net and then transferred into foldable mesh insect containers. All katydids were imaged, underwent experimental trials and were kept in captivity for up to two days; they were then released at their collection site. Each individual was marked with white, non-toxic paint on their head to assist in video tracking and to ensure no recapture of individuals (Collection Permit: 1288-2022-GOREMAD-GRFYF).

We constructed a custom-designed walking platform measuring 22 cm by 28 cm from aluminum extrusion parts (Fig. 2A). The walking platform was adjustable and could be set to five different inclines: 30, 45, 60, 75, and 90 degrees. We could also adhere various slips of sandpaper to the surface to adjust the roughness that the katydid moved across. We used three different grit types of sandpaper from McMaster-Carr: 40, 120, and 320 (22 cm by 28 cm). A GoPro Hero 10 Black camera was mounted 36 cm away, positioned orthogonally to the walking surface to record the walking trials and filming at 60 Hz.

During each trial, an individual was positioned at the bottom of the inclined platform and allowed to climb upward. If no movement occurred, the individual was gently nudged from behind. If the katydid still did not ascend, the trial was restarted. Ideally, each individual would complete five sequential runs for every combination of incline and substrate, presented in random order. However, due to fatigue or lack of incentive, not all individuals were able to complete all trials. Trials in which the katydid failed to secure a grip or did not move were excluded. In total, the 24 individuals collectively completed 492 trials, with each individual contributing between 2 and 39 trials (Mean: 20.5 $\pm$ 11.4 trials). Each individual experienced between 1 and 9 distinct combinations of incline and surface roughness. A complete list of trial numbers, along with the grit and angle combinations for each individual, is available in the supplement.

2.2 Tracking and Gait Analysis

To measure body speed, the white paint marked on each katydid was automatically tracked using a custom written MATLAB code. This process involved isolating the katydid by subtracting median image pixels, binarizing the image, dilating and eroding to isolate the white dot. We then tracked its position over time to generate body position data and used the `peakVals` function in MATLAB to find the local

maxima of body velocity. Pixels from videos were calibrated to the millimeter scale using a ruler. We then averaged across the local maxima to obtain an average of the peak velocity during a walking trial for each individual. We then averaged trials within individuals for repeated measures on the same grit and angle combination and used those averages for statistical analysis (described below). All body speed was converted into body length per second (BL/s) using the combined length of the head, pronotum, and tegmen (Fig. 2B).

To look at gait transitions across grit and angle, we scored whether an individual used an alternating tripod gait (the front and hind legs on one side and the middle leg on the opposite side move simultaneously) or used a different gait (with 4 or more limbs in contact with the surface at one time) during their upward climb for each trial. Each trial was reviewed twice, once each by two separate observers (CAR and JSH). The trial was then marked with either a tripod or non-tripod gait. We averaged trials within individuals for repeated measures on the same grit and angle combination to determine a percent use of tripod gait for that individual on that particular incline and grit combination. We used those averages for statistical analysis (described below).

A random subset of videos (50 in total from 11 individuals) was manually tracked using `DLTDV8` in MATLAB [30]for a more detailed analysis of limb coordination, stride length, and stance duration. These were also used to validate the visual tripod gait determinations. For this manual tracking, the anterior-most point of the head, the posterior tip of the abdomen, and the distal tip of each limb were recorded across the entire trial. We used custom-written code in R (RStudio, v2024.09.1) to track and visualize the movement of limbs over time.

2.3 Statistical Analysis

To look at how the incline angle and substrate affected walking speed, we built a linear mixed-effects model (LMM) using the `lmer` function in R. As fixed effects, we included the incline angle, the sandpaper grit, and their interaction. Individual was included in the model as a random effect to account for repeated measures and inter-individual variation. We used the `MuMIn::dredge()` function in R to fit all subsets of the full factorial model and then compared the models using their AICc to select the one with the best fit (Table 1; S.Table 1).

To determine whether the incline angle or substrate affected the

usage of the tripod gait, we built a generalized linear mixed model (GLMM) using the `glmer` function in R. The response variable was the proportion of tripod gait usage, modeled as a binomial outcome. Similar to the body speed LMM, we used the incline angle, sandpaper grit, and their interaction as fixed effects, with the individual ID as a random effect. We fitted the full factorial model sets and identified the best fit using their AICc scores (Table 2; S.Table 2). To evaluate our best fit models, we examined the residual versus fitted plots.

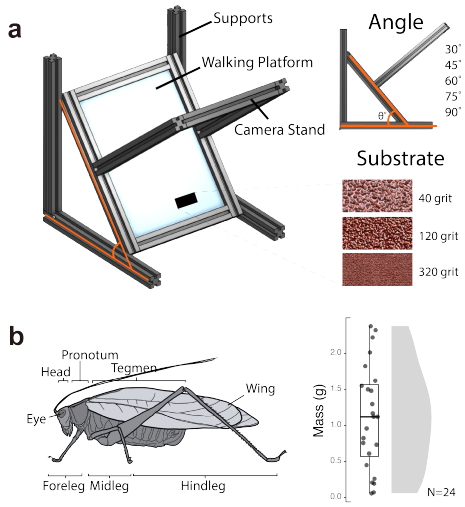

Figure 2: (A) A schematic of the experimental climbing wall. The wall was designed so that the incline and frictional substrate could be modified for different experimental trials (S.Video 1). (B) A drawing of the lateral view of a typical katydid with its limbs and body sections labeled. Katydids collected for this dataset weighed between 0.06 and 2.38 grams. Points represent individual katydids, while the shaded region illustrates the distribution.

3 Results

Species identification from the 24 katydids used in this study indicated that we had individuals from approximately six genera across three Supertribes of Tettigoniidae (Pleminiiti, Copophorini, and Agraeciini). Unfortunately, we were unable to export specimens or collect tissue samples, preventing us from identifying the species level, nonetheless individuals were identified at the genus level using dorsal images

and confirmed with assistance from a taxonomist specializing in Peruvian katydids, Dr. David Nickle (Smithsonian Natural History Museum). Individuals in the study ranged from 0.06 to 2.38 grams (mean: 1.11±0.72 g) and from 0.83 to 6.89 cm (mean: 4.3±1.9 cm; Fig. 2B). Body speeds varied from 0.2 BL/s (Grit:40, Incline Angle: 75) to 12.2 BL/s (Grit:320, Incline Angle:30), translating to absolute distances of 1.3 to 13.3 cm/s (mean: 6.6±3.0 cm/s; Fig 3). The percentage chance of using an alternating tripod gait among individuals ranged from 42.7 to 100 percent, although the likelihood of using this gait depends on multiple factors (see results below). Notably, we were unable to get any individuals to adhere and climb up the walking platform when it was set at 90 degrees with the smoothest sand paper grit (Fig. 4).

The best-performing model in our linear mixed-effects model (LMM) of walking speed included incline angle as the sole fixed effect, with a random intercept for the individual (Table 1). The LMM that incorporated sandpaper grit as a fixed effect, along with another model that included grit as a fixed effect and an interaction term with angle, performed nearly as well (based on AIC); however, they did not improve the model's fit. Consequently, this suggests that the roughness of the sandpaper grit had minimal impact on walking speed in our experiment. In the optimal model, peak speed decreased with increasing incline angle (Estimate $= -0.385$, $t = -4.00$), indicating a reduction of approximately 0.39 BL/s for each standard deviation increase in the incline. However, the variance for the random effect (Individual) was 3.33, suggesting substantial variation in baseline walking speed among individuals. It is important to note that the random intercept also reflects the mass of the individual, as each individual possesses a specific mass. We did not include mass as a separate covariate or random effect, as it was constant and collinear for each individual. Including both would increase model complexity without improving interpretability.

In our generalized linear mixed-effects model (GLMM), the best-performing model (based on AIC) included incline angle, sandpaper grit, and their interaction (Table 2). While several simpler models performed comparably, the inclusion of both fixed effects and their interaction provides the best explanatory power for predicting tripod gait usage. In the strongest model, incline angle had a considerable negative effect on tripod gait usage (Estimate $= -2.87$, z-statistic $= -6.76$), indicating that steeper slopes reduce tripod gait use. However, this effect was somewhat mitigated by substrate roughness; on

120-grit sandpaper, tripod gait usage increased (Estimate = 0.804). This suggests that steeper inclines reduce tripod gaits less severely on rougher substrates. As with the LMM of body speed, the GLMM revealed significant individual-level variance (Variance = 2.71), indicating individual differences in gait preference. Similar to the LMM, the fixed effects term includes individual information, including mass. Therefore, we did not include body mass as a separate random effect, as it was collinear with individual identity.

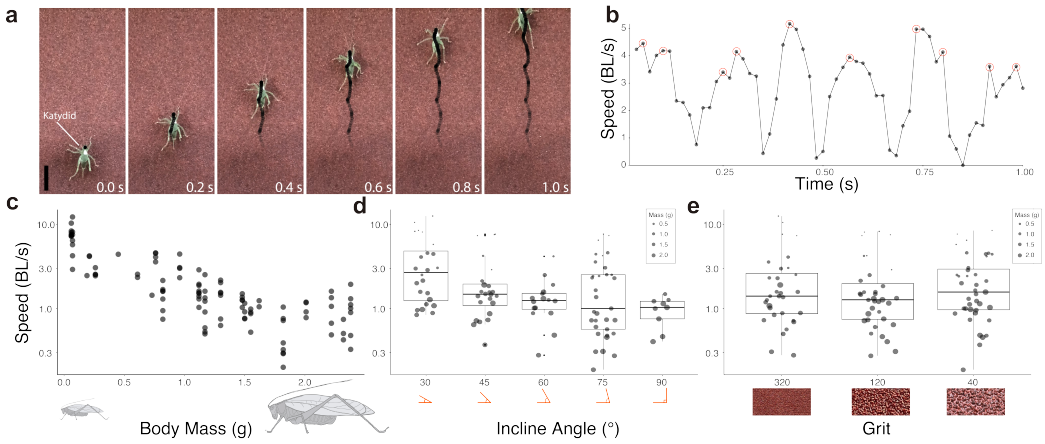

Figure 3: (A) Image sequence from GoPro footage showing a katydid traversing the climbing wall over time. The black points represent the tracked points used to calculate body speed. The vertical black line serves as a scale bar of 2 cm. (B) Body speed for a characteristic trial of a katydid walking experiment. Points indicate the tracked body speed between frames. Red circles highlight instantaneous peak speeds used to calculate the average peak speeds of katydid locomotion. (C) Average peak speed (BL/s) relative to body size. Each point represents the average speed of an individual within a specific incline angle and grit combination. (D) Average peak speed (BL/s) with respect to incline angle. (E) Average peak speed (BL/s) with respect to substrate roughness. For panels D and E, points represent the average speed of an individual within a specific incline angle and grit combination, and point size indicates the mass of the individual.

Table 1: Comparison of linear mixed models (LMMs) predicting average peak speed (BL/s) with different fixed effects.

Fixed Effects	**logLik**	**AICc**	**ΔAICc**	**Weight**
Angle	-172.213	**352.8**	0.00	**0.648**
Angle + Grit	-170.876	354.6	1.78	0.267
Angle + Grit + Angle:Grit	-169.720	356.9	4.10	0.083
(Intercept only)	-179.600	365.4	12.61	0.001
Grit	-178.348	367.3	14.47	0.000

4 Discussion

This research investigated the walking behavior of katydids (Tettigoniidae) on a platform with varying incline angles and substrate roughness. Our results show that katydids walk more slowly when climbing steeper inclines, while substrate roughness had no detectable effect on their walking speed. In contrast, gait patterns were affected by both incline and substrate. When traversing steeper inclines, katydids were more likely to shift away from using the alternating tripod gait toward a more stable gait, where more limbs maintained contact with the substrate. However, rougher substrates increased the likelihood of maintaining a tripod gait even at higher inclines. Notably, the individual effect on body speed and gait was significant in our experiment, suggesting that intrinsic traits within an individual, such as body size, play an important role in locomotion. Nevertheless, despite the strong individual effects, our models demonstrate that incline and substrate properties have a significant impact on locomotor strategies. Below, we discuss these findings and the limitations of this study in more detail.

Some creatures, including geckos and cockroaches, adeptly navigate inclined and vertical substrates and are capable of rapidly climbing with minimal difficulty [3, 11, 31]. However, in some cases, increasing incline results in significant variation in body speed and/or movement patterns, particularly when additional challenges like granular surfaces are present. For example, *Componotus* ants alter their movement from a tripod gait to a metachronal gait (where one limb moves at a time) when ascending a slippery, granular slope, reminiscent of an ant lion pit [32].

Climbing offers significant ecological advantages, whether by locating resources or escaping predators. Mathematical models addressing

attachment mechanics in climbing animals suggest that attachment performance to a vertical substrate may be size-independent [33]. Phylogenetic studies have demonstrated extreme allometry in the footpad area for vertebrates and arthropods, supporting the mathematical models but indicating a potential limit that could complicate adhesion-based climbing for organisms larger than geckos [34]. In that study, it was also found that hemimetabolous insects, such as katydids, possess smaller relative foot pads than their holometabolous counterparts or vertebrates, which may explain why incline angle influences katydid climbing so strongly.

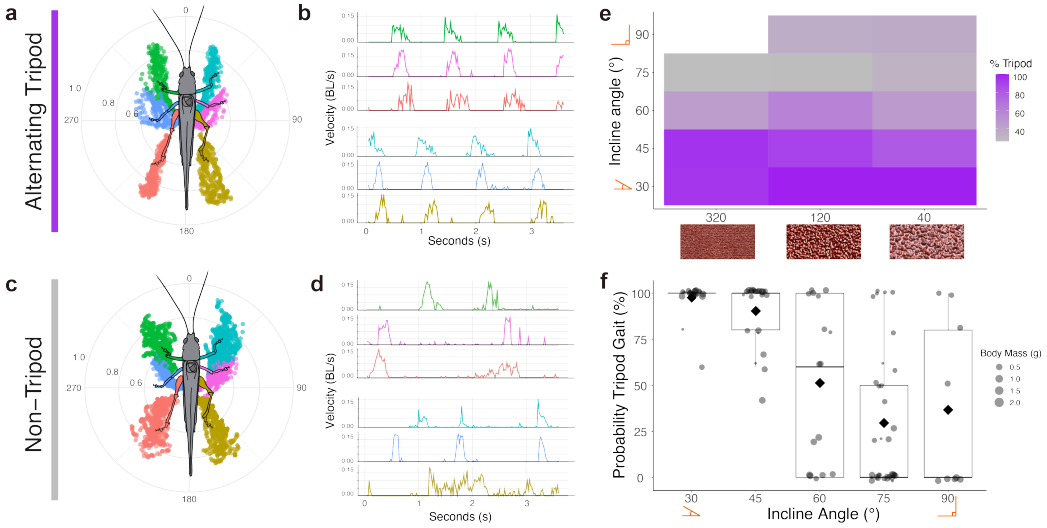

Figure 4: (A) a circular plot of a katydid's walk using an alternating tripod gait. (B) Speed of each limb in BL/s from panel A. (C) A circular plot of a katydid not using a tripod gait. (D) Speed of limbs from panel C. In panels A-D, colors represent different limbs. In panels A and C, distances and angles are relative to the body's centroid. (E) Heatmap showing tripod gait usage percentage across inclines and grits, with color indicating percent change in trials. (F) Probability of tripod gait across incline angles, with point size indicating individual mass. The black diamond represents the average percentage of individuals using a tripod gait at each incline angle.

Surface texture in our experiments did not significantly affect the movement speed of katydids, indicating that substrate frictional forces play a relatively minor role. Instead, katydids likely rely on the ad-

Table 2: Comparisons of generalized linear mixed models (GLMMs) predicting gait choice (Percent tripod gait) with different fixed effects

Fixed Effects	**logLik**	**AICc**	**ΔAICc**	**Weight**
Angle + Grit + Angle:Grit	-145.136	**305.4**	0.00	**0.632**
Angle + Grit	-148.328	307.3	1.84	0.252
Angle	-151.290	308.8	3.40	0.116
Grit	-239.299	487.0	181.58	0.000
(Intercept only)	-242.447	489.0	183.60	0.000

hesive properties of their tarsi, which enable them to cling to various textured surfaces. The tarsi enhance locomotion upon contact with the ground due to specialized microstructures that improve adhesion. Some insects possess hair-like structures (setae) that conform to small surface irregularities [35, 36, 37], creating numerous independent contacts through van der Waals forces [38]. However, other insects, like katydids, feature smooth pads with embedded fibers that deform around surface features, increasing contact area and enhancing adhesive and frictional forces [36, 7, 39]. Adhesion is further supported by secretions; insects with setae use internal tubes for fluid delivery, while those with smooth pads secrete it through pores. This secretion boosts pad contact area, adds viscosity, and facilitates capillary adhesion [40]. Although the composition of the secretion remains unclear, similar lipid-like substances are found in footprint droplets. While the secretion is vital for adhesion, structural adhesion is equally important [41].

Few studies have quantified how much weight an orthopteran's tarsus can support. In some species, the tarsus divides into four segments (tarsomeres), with different combinations engaging based on surface orientation [41, 42]. Jiao et al. (2000) [41] measured the adhesive force of a tarsomere in *Tettigonia viridissima* (Great Green Bush-cricket), which plateaued at 1.1 mN with loads exceeding 0.8 mN. Since a typical *T. viridissima* weighs about 1 g (9.8 mN), each leg must exert approximately 1.6 mN to support the insect, such as when hanging upside down. The adhesive force from a single tarsomere is inadequate, but engaging multiple tarsomeres can increase adhesion [41]. In another taxonomic group, Labonte and Federle (2013) [6] demonstrated that stick insects with adhesive pads increase their adhesion by pulling tangentially, generating greater attachment. If more legs contact the surface, the force requirements for each individual leg de-

crease reducing the need for tangential forces [6]. Our results suggest that as the incline angle increases, katydids move more slowly and shift away from the tripod gait, presumably to keep more feet in contact with the substrate and increase the support force they can generate. Future studies could measure the grip strength of Tettigoniidae and determine the angles and masses at which a tripod gait is insufficient for supporting a given mass and whether they use other behaviors, like stick insects, to assist in supporting body mass.

A key limitation of our study is that we could not focus our data collection on a single katydid species or developmental stage. Preferably, our study would use specimens from within a single species. This limitation stems from the logistical challenges of researching in a remote field environment under time constraints, as well as the relative abundance of katydids. We could not export specimens from the field station, making precise species-level identification impossible. Additionally, managing the motivation of an organism across so many trials is difficult. Although the order of grit and angle combinations was randomly selected for each individual, we could not run each katydid on every grit and incline angle combination. Consequently, variations in morphology and behavior across different species and developmental stages introduce additional variability into our model. This is evident in the large variance in the random intercept for our mixed models. However, our data still indicate that there are constraints on katydid climbing and gait. Even after accounting for individual variance in the models, we observe that incline angle negatively impacts movement speed, and both incline angle and substrate roughness influence overall gait. Future research could explore the allometric scaling of Tettigoniidae foot pads, calculate the safety factor of the katydid during adhesion, and investigate climbing behavior within a single species to better understand precisely why this transition in gait occurs and whether it relates to the need to support body mass while climbing.

This study and related follow-up studies aid in the design and improvement of hexapod and climbing robots. Hexapod robots, like RHex, enable comparative studies of limb compliance, gaits, and locomotion on varied surfaces [43, 44]. Compliant pads, similar to those that allow adhesion in katydids, help robots scale steeper surfaces. Our results suggest that to climb successfully, the robot's gait may need to be adjusted based on the adhesion capabilities of its appendages. When designing adhesive pads, size is crucial. Allometric scaling necessitates large pads for significant mass support, which

limits their use in larger devices beyond geckos [34]. A template for climbing in both hexapods and quadrupeds—where mass is accelerated and anchored periodically—has already inspired robot models for climbing [11]. The hexapedal robot RiSE mimics the splayed stance of climbing geckos and squirrels and follows a similar force pattern through its legs [45]. Like insects, this robot's foot structure interlocks with surface features to create adhesive forces, enabling it to scale various rough vertical surfaces such as brick, stucco, and tree bark. RiSE also employs sticky pads for smooth surfaces but can only climb slopes of up to 65°. Additionally, it ascends vertical surfaces at a speed of about 0.1 body lengths per second, using a wave gait with five limbs always in contact with the substrate [45]. Stickybot is an example of a climbing robot that is capable of scaling smooth, 90°inclines at a speed similar to RiSE. This robot uses dry adhesive pads reminiscent of gecko feet and is able to use a gait where only two of its four limbs contact the substrate at a time [46]. Future research into how katydids and other hexapods shift their gaits at varying inclines could enhance the design or programmed gait in robots.

5 Conclusion

Our research indicates that steeper slopes negatively impact katydid walking speed and the katydids shift away from a rapid, alternating tripod gaits. Moreover, we found that there can be interactive effects among substrate variables, which can influence the organisms' responses. Nonetheless, the substantial individual influences highlighted in our models suggest that body mass and species-specific morphology are crucial for locomotor performance. This study offers novel insights into Katydid locomotion in the Peruvian Amazon, enhances our understanding of insect biomechanics in natural environments, and may inform the design of bio-inspired robotic systems.

6 Supplementary data

Supplementary data available at TBD.

7 Competing interests

No competing interest is declared.

8 Author contributions statement

C.A.R., J.S.H, and J.M.R. conceived the experiments. C.A.R., J.S.H., J.Q.N., and G.R.G. assisted in specimen collection and field research. C.A.R. conducted the experiments, and C.A.R., J.S.H., and R.D.T. analyzed the results. J.M.R. and S.B. supervised this research. S.B. secured funding. All authors contributed to writing, discussion, and revising the manuscript.

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