

## RESEARCH ARTICLE

# High-speed terrestrial substrate transitions: How a fleeing cursorial day gecko copes with compliance changes that are experienced in nature

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## Abstract

1. Animal movement is often largely determined by abiotic conditions of the environment, including substrate properties. While a large body of work has improved our understanding of how different substrate properties can impact locomotor performance and behaviour, few of these studies have investigated this relationship during transitions within a single locomotor event.
2. In nature, terrestrial animals frequently encounter substrate transitions, or changes in substrate level, incline, texture and/or compliance during a single bout of movement, which can be sudden for high-speed animals. These animals often adjust their posture and kinematics during transitions, and in some cases lose forward velocity.
3. We examined the occurrence and effect of non-elastic compliance transitions in *Rhoptropus afer*, a cursorial day gecko known for its ability to sprint rapidly for several metres at a time. We recorded substrate use during provoked escapes in the field and conducted locomotor trials on a trackway that mimicked natural structural habitat conditions with transitions from a rigid surface into sand and from sand back to a rigid surface.
4. During escapes, *R. afer* used substrates of different compliance (i.e. rock, gravel and sand) and transitioned to and from the more compliant surfaces with even frequency, which matched substrate and compliance availability estimates. In laboratory experiments, sprint speed was not significantly affected by acute changes in compliance, which was likely facilitated by an increased body angle and duty factor upon entering the sand, and potentially a high yield strength of the sand relative to applied forces.
5. We speculate that this species' ability to maintain speed during compliance transitions underlies their apparent indiscriminate substrate use during escapes, and that this behaviour may offer a selective advantage for evading larger terrestrial predators. Using field data to inform and contextualize laboratory experiments thus yields important insights as to how animals accommodate acute changes in substrate conditions encountered during critical locomotor events.

## KEYWORDS

biomechanics, gecko, locomotion, performance, substrate transitions

## 1 | INTRODUCTION

An organism's capacity to move is tied to the intrinsic properties of the media with which it interacts (Biewener & Patek, 2018; Urfi, 2016), such as water temperature (Fry & Hart, 1948), airflow (Combes & Dudley, 2009) or perch diameter (Losos & Sinervo, 1989). A multitude of studies have demonstrated the significance of substrate properties with respect to locomotor function, as well as ways in which animals respond to challenging conditions (Blob & Higham, 2014; Childress et al., 2012; Liao, 2007). However, much of this work has examined these relationships under discrete sets of structural substrate conditions, such as wide versus narrow (Sathe & Husak, 2015; Stevens, 2008), inclined versus declined (Birn-Jeffery & Higham, 2014; Full & Tullis, 1990; Lammers et al., 2006), rough versus smooth (Wheatley et al., 2018; Yanoviak et al., 2017) or some combination therein (Naylor & Higham, 2019; Redmann et al., 2020; Spezzano & Jayne, 2004); far fewer studies have examined how organisms respond to changes in substrate properties within a single locomotor event.

A perturbation, or sudden change in locomotor demands that may subsequently disturb stable movement (Jagnandan & Higham, 2018; Jindrich & Full, 2002; Koditschek et al., 2004), can be induced by a substrate transition, which we define broadly as a change in the material properties (namely physical and mechanical properties) of the substrate along the path of movement during a locomotor bout. This scenario presumably occurs frequently in nature, particularly for terrestrial animals, which are often found in structurally complex and heterogeneous habitats (Dickinson et al., 2000; Higham et al., 2019). Terrestrial substrate transitions by this definition include (but are not limited to) obstacles (i.e. physical barriers within the locomotor path) or other changes in substrate level, as well as changes in incline, texture (e.g. friction) and compliance (see Jagnandan & Higham, 2018).

The ability to maintain locomotor stability during such changes (i.e. dynamic stability), is particularly important for fast-moving animals, which must respond rapidly to avoid missteps or injury during critical activities, like prey capture, territory defence and predator evasion (Daley, 2008; Full et al., 2002; Irschick et al., 2008). Guinea fowl, for example, are able to continue their trajectory of motion and prevent themselves from falling after experiencing an unexpected drop in substrate height or friction during running by quickly altering their limb posture, angle of contact and centre of mass position (Clark & Higham, 2011; Daley et al., 2006). With regards to obstacle negotiation, many lizards elevate the head and trunk when sprinting towards a barrier, thus shifting their centre of mass over the hindlimbs (particularly in bipedal gaits), which allows them to generate higher propulsive forces for quickly clearing the obstacle (Kohlsdorf & Biewener, 2006; Parker & McBrayer, 2016; Tucker & McBrayer, 2012); this response is accompanied by a loss in forward velocity for some lizards (e.g. *Sceloporus malachiticus*, Kohlsdorf &

Biewener, 2006) but not others (e.g. *Aspidoscelis sexlineata*, Olberding et al., 2012; *S. woodi*, Parker & McBrayer, 2016).

Generally speaking, terrestrial locomotion on compliant (i.e. dampening) surfaces incurs a higher mechanical work requirement and metabolic energetic cost than that on solid surfaces (Lejeune et al., 1998; Li et al., 2012; Moritz & Farley, 2003). To compensate, some animals alter their body or limb posture or other limb properties, such as increasing limb stiffness on less rigid surfaces (Ferris & Farley, 1997; Ferris et al., 1998). As in obstacle negotiation, ground reaction forces (i.e. the equal and opposite forces exerted by the ground onto the contacting limb or body) can be maximized on compliant substrates by straightening and aligning the limb elements beneath the centre of mass (Biewener, 1989), as seen in basilisk lizards running on a fluid surface versus a solid one (Hsieh, 2003; Laerm, 1973); while it remains to be directly tested, rapid kinematic adjustments likely occur when these lizards transition between water and land.

Cockroaches (*Blaberus discoidalis*) conserve forward velocity when locomoting between artificial rigid and elastic compliant surfaces by assuming a lower body posture and thus shorter limb swing time, as well as keeping multi-limb contact, which helps to sustain total propulsive force (Spence et al., 2010). It is also likely that the elastic surface returns some energy to the animal and thereby reduces mechanical work to contribute to sprint speed maintenance, as has been demonstrated for humans on tuned compliant trackways (e.g. Ferris et al., 1998; Kerdok et al., 2002; McMahan & Greene, 1978) and for some animals moving on natural elastic substrates, such as Cuban tree frogs jumping from compliant perches (Astley et al., 2015; but see also Crandell et al., 2018; Gilman et al., 2012; Ribak et al., 2012 for examples where animals do not recover energy via elastic recoil).

Non-elastic compliant substrates are commonly experienced by ground-dwelling animals, such as mud, sand and other granular media, and their highly unique and dynamic properties can make them especially challenging to move on (Li et al., 2009, 2013). The extent to which a granular medium behaves more like a solid versus a fluid is dependent upon the depth of penetration and forces applied by the animal relative to the force required to deform it (i.e. yield stress; Jaeger et al., 1996; Mehta & Barker, 1994). When the yield stress is exceeded, the substrate fluidizes at the site of contact, but when it is compressed to an extent where the particles are 'jammed' together, it will solidify locally (Gravish et al., 2010; Qian et al., 2012). Solid-like conditions underfoot via a high yield stress and/or packing may allow an animal to move at speeds similar to those on a non-granular substrate (Mazouchova et al., 2010; Zhang et al., 2017).

While speed sensitivity (Irschick & Losos, 1999) has been observed for some lizard species (Bergmann et al., 2017; Brandt et al., 2015; Collins et al., 2013; Li et al., 2011; Vanhooydonck et al., 2015), others have shown more consistent performance across

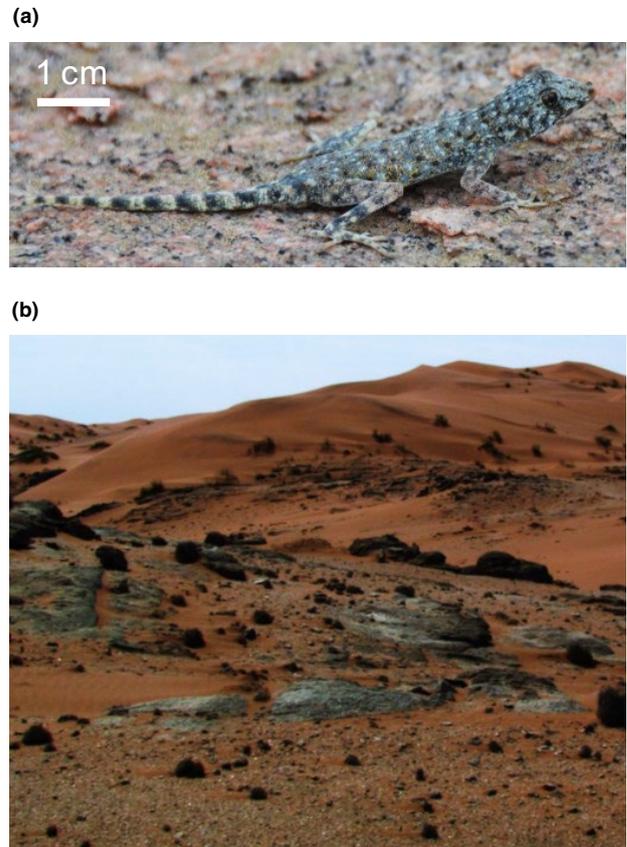
substrates of different compliance (e.g. *Acanthodactylus schreiberi*, Savvides et al., 2019; *A. sexlineata*, Sathe & Husak, 2018; *Callisaurus draconoides* and *Uma scoparia*, Korff & McHenry, 2011, but see Qian et al., 2015). These performance patterns might be explained by different substrates acting similarly and/or compensatory mechanisms exhibited by the animal. In the case of *C. draconoides*, for example, adopting a more flat-footed posture when running on sand appears to reduce penetration depth and thereby energy loss (Li et al., 2012). However, we know little about how and how often most lizards and other small-bodied terrestrial species accommodate compliance shifts in nature.

We explored terrestrial compliance transitions within *Rhoptropus afer*, the Namib Day Gecko (Peters, 1869), a species well-known among gekkonids for its unique cursorial morphology (i.e. elongated hindlimb elements, Bauer et al., 1996; Johnson et al., 2005) and high sprint-speed performance. Unlike its scansorial congeners, *R. afer* occupies open and relatively flat rocky habitats, and when provoked, can run continuously for several metres at a time at speeds upward of 3 m per second (Collins et al., 2015; Higham & Russell, 2010; Lamb & Bauer, 2006; Odendaal, 1979). Moreover, we know from previous work that *R. afer* habitats are structurally heterogeneous between and within populations in 'rockiness' and incline (Collins et al., 2015), the latter which not only impacts sprint speed performance, but also alters limb mechanics and relative contributions to forward velocity (Collins & Higham, 2017). We observed substrate use and compliance transitions during escapes in the field and conducted field-informed experiments in the laboratory to test the hypothesis that running performance and/or kinematics of *R. afer* are altered during rapid shifts between solid and sandy substrates. This species may avoid running from more solid to compliant surfaces when evading a threat if the transition results in a loss of speed. Alternatively, *R. afer* may be able to maintain speed during transitions via compensatory kinematic adjustments, such as increasing body pitch angle, to improve force production on a compliant substrate. Sustained performance may allow geckos to use various substrates within the habitat without preference. Understanding *R. afer*'s behaviour in nature and how they accommodate such abrupt changes along their locomotor paths allows us to better contextualize the function and evolution of their specialized running phenotype among geckos, as well as that of other high-speed lizards and terrestrial animals.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and field recordings

The study was conducted at the Gobabeb Research and Training Centre (Namib-Naukluft Park, Namibia) in January 2016. We collected data from wild *R. afer* at a single site south of the field station across the Kuiseb River (-23.565540, 15.039675 DD), a granitic outcrop interspersed with fine sand blown in from the adjacent dunes (see Figure 1). Preliminary observations of geckos moving on both rock and more deformable substrates were preceded by provoked

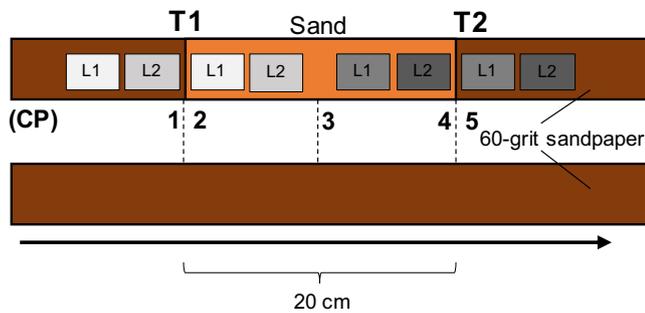


**FIGURE 1** (a) *Rhoptropus afer* individual; (b) Image from study site at Gobabeb Research & Training Centre showing granite rock interspersed with fine dune sand and gravel mixture

'escapes' (i.e. continuous running for at least 1 m), in which E.R.N. would directly approach an animal at a steady walking pace upon sighting while recording the gecko's trajectory using a GoPro Hero4 camera (120 fps). Geckos typically ran for a few metres before taking refuge within or under rock or resting, and so multiple escapes from the same animal were recorded if it could be induced to flee again. We recorded 56 total escape bouts from 15 animals over the course of 4 days. As we could not confidently distinguish geckos in the field, we cannot say if or how frequently observations were repeated on the same individual, but our intention was simply to document general patterns of substrate and transition use at the site.

### 2.2 | Locomotor trials and video processing

We constructed a 2-m horizontal trackway for locomotor trials that featured approximately 20 cm of unpacked level dune sand collected from the field site at its centre and solid trackway on either side, thus representing two compliance transitions (into sand and out of sand); the trackway could also be configured as a continuous solid surface (i.e. no transition; see Figure 2). The solid portions of the trackway were lined with 60-grit sandpaper, an artificial surface found to be fairly representative of the microtopographies of natural rock sampled within the biogeographical range of *Rhoptropus* (Russell &



**FIGURE 2** Schematic of locomotor trial experimental set-up showing the two trackway configurations (sand transition and non-transition) within the field of view; the five checkpoints (CPs) and the pairs of strides for limb one (L1) and two (L2) at transition one (T1) and two (T2) are shown

Johnson, 2014). A sample of the dune sand was retained for subsequent grain and surface strength analyses (see Appendix S1a for methodological details).

Ten individuals captured from the study site were induced to run down the trackway from the same starting point into a 'refuge' box while we recorded the centre of the trackway from lateral view using a Phantom Miro M110 high-speed camera (500 fps; approx. 60 cm field of view). We measured body temperature with an infrared thermal sensor aimed at the cloaca of the gecko immediately before placing it on the trackway; all body temperatures recorded fell within the normal field active temperature range of 30–35°C (Brain, 1962; Higham & Russell, 2010). While we attempted to elicit high-speed running down the trackway, obtaining maximum performance was not the objective of this study. Multiple trials per individual per trackway configuration were conducted, with individual order randomized; the time expense of changing the experimental set-up necessitated that multiple individuals be tested on each treatment at time. Geckos were kept in cloth bags after initial capture and between trials, which were conducted during daylight hours. We collected standard morphometric (i.e. snout–vent length, limb element lengths) and body mass data before returning individuals to their capture site (see Table S1 in Supporting Information and Higham & Russell, 2010 for methodological details). All handling and experimental procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of California, Riverside (AUP 20170039).

We digitized the frame-by-frame movement of lateral body points (i.e. snout tip, shoulder, wrist, hip, ankle) using DLTdv5 (Hedrick, 2008) in MATLAB (version R2015b; MathWorks Inc.) and documented the sequence and timing of ipsilateral strides (on the gecko's right side) for each trial. Stride sequences and entire trials where geckos did not run straight or deviated from typical quadrupedal and bipedal gait patterns (e.g. 'leaping' between strides; see Snyder, 1952) were excluded, leaving 26 sand transition trials and 29 non-transition trials; trials with bipedal strides were limited (7 sand and 3 non-transition). We used IGOR PRO (version 4.0; Wavemetrics, Inc.) to plot and smooth the raw 2D coordinate data from these trials with standard smoothing splines (smoothing factor = 3).

## 2.3 | Analysis

### 2.3.1 | Field recordings

Substrates were categorized as one of three types: solid rock (i.e. the least compliant), gravel or eroded rock pieces (pea to walnut-sized) mixed with dune sand, or 'pure' sand (i.e. the most compliant). From the GoPro videos, we documented the sequence of substrates that the gecko traversed during each recorded escape, as well as the sequences of three 'transects' (*sensu lato*) drawn onto a single frame (i.e. image) of the escape event; for consistency and to provide a wider field of view in most cases, we sampled the frame at the midpoint of the escape duration. For the first transect, a straight line was drawn from the gecko's snout to the edge of the image or visible habitat in the axial orientation of the body. The second and third transects were drawn perpendicular on either side of this line from the snout to the edge of the image or visible habitat. We tallied the number of times each of the three substrate types and six possible transition types (e.g. rock to gravel) were encountered by both the geckos and along the transects and pooled the data. Chi-square goodness-of-fit tests were used to first test the null hypothesis of equal use (i.e. even proportion) of substrate and transition types during escapes. We then tested if the geckos' substrate and transition use significantly deviated from expected proportions (i.e. availability) estimated from the transect data.

### 2.3.2 | Locomotor trials

#### *Checkpoint analysis for entire transition trial*

To capture potential responses in instantaneous velocity and body pitch angle (defined in Table S2) to compliance changes over the entirety of a locomotor bout, we averaged and compared coordinate data from five frames (0.01 s) at each of five trackway 'checkpoints': CP (1) immediately preceding sand contact, CP (2) immediately preceding sand contact, CP (3) the midpoint of sand contact, CP (4) immediately preceding secondary contact with solid trackway and CP (5) immediately preceding secondary contact with solid trackway; analogous points were approximated within the non-transition trials to contextualize patterns within the sand transition trials (Figure 2).

We ran linear mixed-effects (LME) models with the LME4 and LMERTEST packages (v1.1-23 and 3.1-2; Bates et al., 2015; Kuznetsova et al., 2017) in R (v4.0.2; R Foundation for Statistical Computing) via RStudio (v1.2.5001; RStudio, Inc.), which allows the incorporation of multiple fixed effects, including a main effect (i.e. checkpoint) and covariates (i.e. temperature, body size and/or velocity), and nested random effects to account for repeated measurements and uneven trial counts per gecko (Harrison et al., 2018; Lindstrom & Bates, 1990). Preliminary univariate ordinary least-squares (OLS) regressions and correlations of main variables and covariates from the sand transition dataset (five checkpoint observations per trial) further informed model assembly (OLS results summarized in Table S3a). After log-transforming all continuous variables for

normality, we ran saturated (i.e. all fixed effects included) and reduced nested models for both instantaneous velocity and body pitch angle within the two sets of trackway trials (see Table S4a for trial counts and S5 for model structure). We used corrected Akaike information criterion (AICc) scores, namely the difference between the lowest-scoring model and other models ( $\Delta\text{AICc}$ ) to select the best-fitting model. If  $\Delta\text{AICc}$  between the next lowest-scoring model was 4, we considered the lowest-scoring model to be the single best model, while  $\Delta\text{AICc} < 4$  meant that we could not reject the other model(s), and the model with the simplest structure was selected (Burnham & Anderson, 2002). The `LMERTEST` package was also used to obtain type III ANOVA tables (Satterthwaite approximation for degrees of freedom) to test the significance of each of the fixed effects and to extract variance components to calculate linear mixed model-based repeatability,  $R_M$  (i.e. estimated intraclass correlation coefficient; Nakagawa & Schielzeth, 2010). The `EMMEANS` package (v1.4.8, Lenth et al., 2020) was used to obtain estimated marginal means of models that showed a significant effect of checkpoint and to obtain contrasts (Satterthwaite approximation and Tukey adjustment), and the `PARTR2` package (v0.9.1, Stoffel et al., 2020) was used to obtain the marginal  $R^2$  (i.e. the variance of the fixed effects) and conditional  $R^2$  (i.e. the variance of both the fixed and random effects values; Nakagawa & Schielzeth, 2013).

*Between-stride analysis at transition sites*

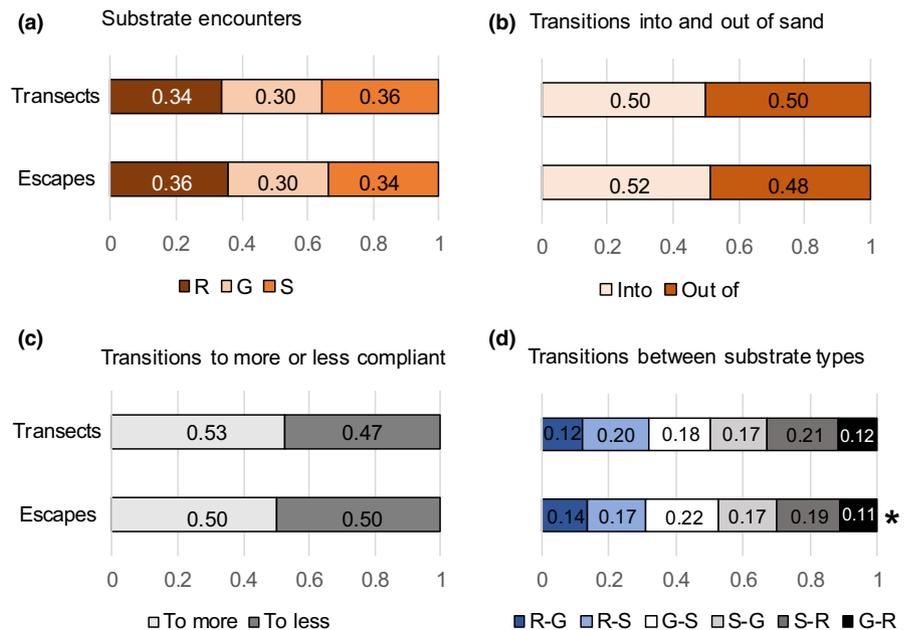
To focus in on potential locomotor responses at each of the two transition sites (T1 and T2), we conducted between-stride comparisons of stride velocity, duty factor, stride length, step length, body pitch angle and effective forelimb and hindlimb length (S2). At T1 (solid to sand), we designated 'limb one' as making the first sand stride and penultimate stride on solid trackway and 'limb two' as making the second sand stride and ultimate stride on solid trackway; we made the same designation at T2 (sand to solid), with limb one making the

first stride on solid trackway (and penultimate stride in sand), and limb two making the second stride on solid trackway (and ultimate stride in sand; see Figure 2). Thus, for each limb at each transition site, we compared the stride of new substrate contact with its predecessor (see Table S4b for stride counts). To test for this effect of stride position on our dependent variables, we used the same methods as in the checkpoint analysis to build, run and evaluate our LME models (see Table S3b for univariate OLS variable relationships).

**3 | RESULTS**

**3.1 | Field observations of substrate use**

We found that *R. afer* individuals used all three substrate types in 34 of our 56 recorded escape bouts, and that total encounters with rock, gravel and sand did not significantly deviate from even proportions ( $\chi^2_{(2)} = 2.07, p = 0.36$ ; Figure 3a). Moreover, these proportions of substrates used did not significantly deviate from those estimated from our transects ( $\chi^2_{(2)} = 0.98, p = 0.61$ ). In terms of movement between substrates during escapes, we observed 337 total transitions, 254 of which were transitions to or from sand. For these sand-specific transitions, geckos transitioned into and out of sand with statistically even frequency ( $\chi^2_{(1)} = 0.25, p = 0.62$ ), which also matched our transect estimates ( $\chi^2_{(1)} = 0.31, p = 0.58$ ; Figure 3b). We observed the same pattern for transitions to more versus less compliant substrata during escapes ( $\chi^2_{(1)} = 0.86, p = 0.35$ ), including the concurrence with transect estimates ( $\chi^2_{(1)} = 0.73, p = 0.39$ ; Figure 3c). The relative proportions of the six discrete transition types were not even ( $\chi^2_{(5)} = 14.7, p = 0.01$ ), with geckos transitioning between gravel and rock (and vice versa) less frequently than the other types, however, our transect estimates once again corroborated behavioural observations ( $\chi^2_{(5)} = 4.34, p = 0.50$ ; Figure 3d).



**FIGURE 3** Proportions of (a) substrate types encountered (rock, R; gravel, G; sand, S), (b) sand transitions, (c) transitions to more or less compliant substrates for recorded escapes and transect estimates, and (d) transitions between all substrate types (e.g. rock to gravel, R-G). The asterisk (\*) indicates a significant deviation from even proportions within escape trials ( $\alpha = 0.05$ ); there were no significant deviations between escape and transect proportions

## 3.2 | Locomotor trials

### 3.2.1 | Checkpoint analysis

We observed a significant effect of checkpoint on instantaneous velocity (Table 1), with post-hoc tests indicating that velocity decreased between the first two CPs and the later CPs in both the sand transition and non-transition trial sets (Figure 4a). Body pitch angle was significantly predicted by checkpoint and velocity within the sand transition trials, with geckos elevating the trunk between the first two CPs and CP3 (mid-sand; Figure 4b). The non-transition trials did not show a significant effect of checkpoint on body angle. We note, however, that linear mixed model-based repeatability was low for body pitch angle ( $0.15 \leq R_M \leq 0.25$ ). In contrast, velocity showed very high repeatability ( $R_M \geq 0.95$ ). Full LME model summaries with AICc scores and estimated marginal mean contrasts are provided in Tables S5 and S6.

### 3.2.2 | Between-stride analysis

We did not detect a significant effect of substrate change (i.e. stride position) for stride pairs about the two transition sites (T1 and T2) on between-stride velocity ( $R_M \geq 0.98$ ), but we did so for stride length, step length, duty factor and body pitch angle at T1 (solid to sand) and for body pitch angle and effective limb length ( $0.36 \leq R_M \leq 0.95$ ) at T2 (sand to solid; Table 2). Specifically, there was a significant decrease in stride length ( $R_M \geq 0.84$ ) for limb one at the transition into sand, where body size (i.e. SVL) was also a significant predictor (Figure 5a). Step length ( $0.46 \leq R_M \leq 0.62$ ), duty factor ( $0.31 \leq R_M \leq 0.65$ ) and body pitch angle ( $0.35 \leq R_M \leq 0.51$ ) significantly increased between the limb two strides at the transition into sand; SVL was a significant covariate for step length, and stride velocity was a significant covariate for duty factor (Figure 5b–d). At the transition out of sand, body

pitch angle decreased between both limb one and limb two strides (Figure 5e,f); effective forelimb length also decreased between limb two strides with total forelimb length and velocity as covariates, but we note that this result was marginally significant (Figure 5g). See Tables S7–S9 for complete LME model summaries, ANOVA tables and estimated marginal mean contrasts.

## 4 | DISCUSSION

We used field observations to both ground truth and contextualize laboratory examination of the locomotor impacts of substrate compliance transitions within the same population of a high-speed gecko, *R. afer*, which exhibits similar escape behaviour to many cursorial lizard species. Substrate type and transition use data suggest that *R. afer* moves frequently and fairly evenly between substrates of different compliance when fleeing a perceived terrestrial threat. Moreover, experimental trials indicate that these animals are able to maintain sprint speed during sand transitions while modifying some aspects of posture, namely body pitch angle, and kinematic timing. Despite our coarse categorization of natural substrate types, our results highlight the heterogeneity of landscapes traversed by many terrestrial animals. Collins et al. (2015) found variability in the structural composition of multiple *R. afer* localities, particularly with respect to incline; incline use during escapes in three of four populations in the study did not significantly differ from incline availability. We similarly saw no indication of preference for or avoidance of rock, gravel or sand, or transitions to more or less compliant surfaces during escapes in our study population (Figure 3).

Although we observed an overall decline in instantaneous velocity between the start and end of the sand transition trials, this pattern was also seen in the non-transition trials (Figure 4a). We therefore do not think that this is an actual effect of compliance changes, but rather a consequence of the geckos perceiving the end

Variable	Fixed effects	Sum Sq	NumDF	DenDF	F	p-value
Sand transition trials						
Velocity	Body temp	0.0010	1	21.50	1.88	0.185
	SVL	0.0005	1	7.34	0.91	0.371
	<b>Checkpoint</b>	0.0108	4	104.00	5.24	<b>6.89E-04</b>
Body pitch angle	Velocity	0.1868	1	17.59	7.20	<b>0.016</b>
	SVL	0.0071	1	6.42	0.27	0.620
	<b>Checkpoint</b>	1.0444	4	104.34	10.07	<b>6.25E-07</b>
Non-transition trials						
Velocity	Body temp	0.0001	1	134.33	0.13	0.719
	SVL	0.0003	1	9.86	0.49	0.502
	<b>Checkpoint</b>	0.0266	4	116.01	9.98	<b>5.63E-07</b>
Body pitch angle	Velocity	0.0086	1	31.37	0.81	0.376
	SVL	0.0013	1	6.79	0.13	0.735
	<b>Checkpoint</b>	0.0536	4	117.54	1.26	0.290

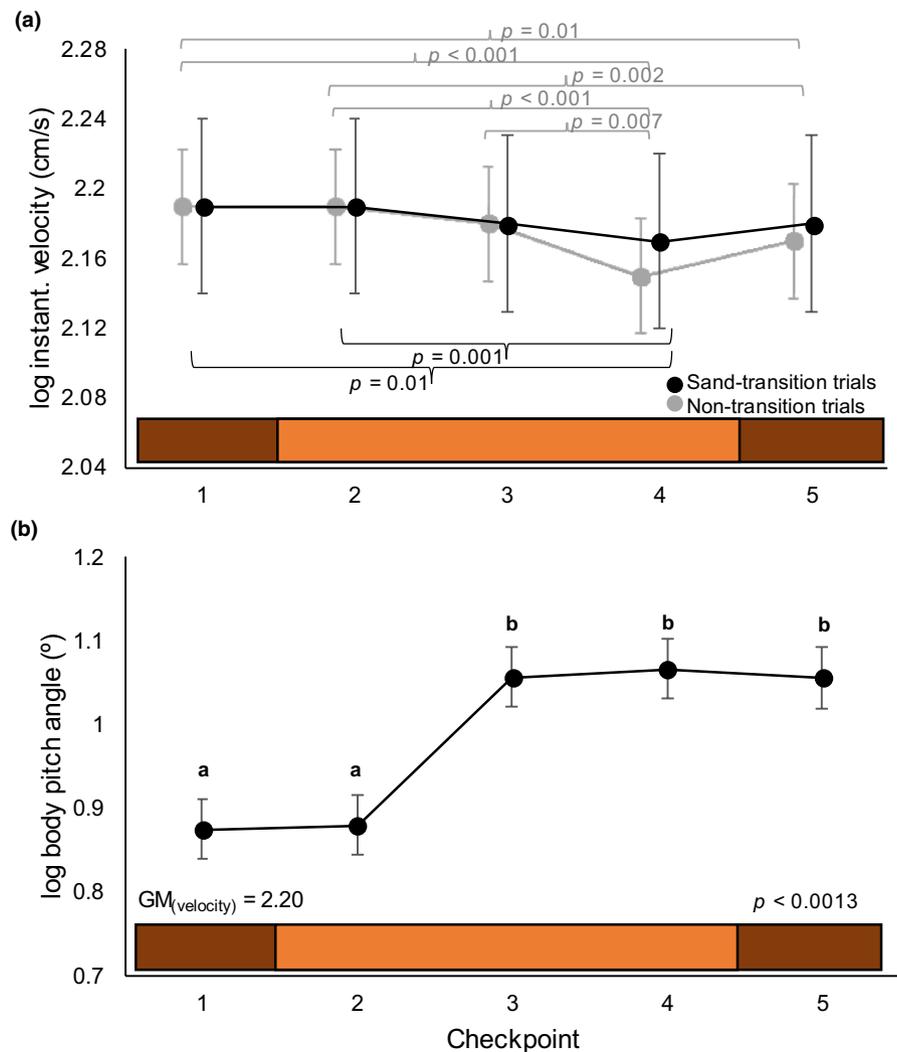
**TABLE 1** Type III ANOVA summary table for all fixed effects of saturated models in the checkpoint analysis, including sand and non-transition trials; the Satterthwaite approximation for degrees of freedom was used. The main effect (checkpoint), is bolded. Bolded p-values indicate significant fixed effects ( $\alpha = 0.05$ ); SVL, snout-vent length

of the trackway and/or decreased lighting within this region from the placement of the refuge box. Birn-Jeffery and Higham (2016) showed that *R. afer* (a diurnal gecko) does reduce its speed in lower light conditions, likely due to loss of visual acuity. While stride length did decrease between the strides of the first sand-contacting limb (Figure 5a), we did not detect between-stride changes in velocity at either of the two transition sites, further supporting the notion that sprint speed in *R. afer* is relatively insensitive to sudden changes in substrate deformability.

Given the consistent predictive relationship of velocity with respect to duty factor, we expected to see parallel changes in these variables, specifically decreased velocity and increased duty factor due to sinking into fine granular media (Bergmann et al., 2017). Increased relative contact time between the strides of the second sand-contacting limb (Figure 5c) without a loss of speed corresponds with increased step length for this limb (Figure 5b; McMahon & Greene, 1979). Applying push-off force for a longer period of time likely allows *R. afer* to travel a greater distance during stance, which may reflect a compensatory biomechanical response for maintaining forward velocity on a compliant substrate (Bergmann et al., 2017; McMahon & Greene, 1978). Alternatively, an animal could exert

higher push-off forces onto the substrate to compensate for a dampening effect (Demes et al., 1995). Adopting a more upright limb posture and elevating the trunk can both enhance an animal's vantage of the locomotor path and increase hindlimb loading for propulsion. Moreover, some animals exhibit the ability to adjust the effective length of their limbs (and therefore also limb stiffness) when running over uneven terrain, which allows them to maintain stability and velocity (e.g. Daley & Biewener, 2006; Druelle et al., 2019). We observed only a marginally significant increase in effective forelimb length during the second transition onto solid trackway (Figure 5g), which suggests that some limb compression may occur due to the increase in substrate stiffness (Ferris et al., 1999). More pronounced changes were seen in body pitch angle, which increased proceeding entry into sand and decreased between the last strides in sand and the first strides on solid substrate (Figures 4b and 5d-f).

However, it remains unclear the extent to which this postural change represents behaviour versus neuromechanical responses and how these systems coordinate during compliance transitions. Preserving dynamic stability in challenging terrestrial environments requires adjustments that are under the control of both passive-dynamic (i.e. intrinsic) mechanics and active neural control (Biewener



**FIGURE 4** Estimated marginal means plots for variables significantly predicted by the five trackway checkpoints: (a) instantaneous velocity for both sand transition (black) and non-transition trials (grey) and (b) body pitch angle for sand transition trials. Each plot shows the model-estimated means and standard error bars of the best-fitting model for that locomotor variable; grand means (GMs) of the covariates (as applicable) are shown, along with contrast *p*-values

**TABLE 2** Type III ANOVA summary table for all fixed effects of saturated models in the between-stride analysis where the main effect, stride position (i.e. first stride on new substrate vs. last stride on initial substrate; bolded), was a significant predictor of locomotor variables; the Satterthwaite approximation for degrees of freedom was used. Bolded  $p$ -values indicate significant fixed effects ( $\alpha = 0.05$ ); T1 = transition 1 (into sand), T2 = transition 2 (out of sand); L1 = limb one, L2 = limb two, SVL = snout-vent length, FLL = forelimb length (actual)

Variable	Stride pair	Fixed effects	Sum Sq	NumDF	DenDF	$F$	$p$ -value
Step length	T1, L2	Velocity	0.0005	1	30.86	0.10	0.759
		SVL	0.0798	1	30.00	16.77	<b>3.09E-04</b>
		<b>Stride position</b>	0.0413	1	29.84	8.68	<b>0.006</b>
Stride length	T1, L1	Velocity	0.2146	1	10.02	166.45	<b>1.47E-07</b>
		SVL	0.0280	1	6.16	21.71	<b>0.003</b>
		<b>Stride position</b>	0.0090	1	26.01	7.00	<b>0.014</b>
Duty factor	T1, L2	Velocity	0.2244	1	30.68	34.07	<b>2.20E-06</b>
		SVL	0.0112	1	30.06	1.70	0.202
		<b>Stride position</b>	0.0483	1	29.95	7.33	<b>0.011</b>
Body pitch angle	T1, L2	Velocity	0.0160	1	12.04	1.84	0.200
		SVL	0.0075	1	6.05	0.87	0.387
		<b>Stride position</b>	0.1191	1	30.00	13.75	<b>0.001</b>
	T2, L1	Velocity	0.0283	1	36.62	4.47	<b>0.042</b>
		SVL	0.0009	1	9.80	0.15	0.708
		<b>Stride position</b>	0.0649	1	43.46	10.24	<b>0.003</b>
	T2, L2	Velocity	0.0139	1	43.02	2.13	0.152
		SVL	0.0002	1	8.42	0.03	0.868
		<b>Stride position</b>	0.0647	1	38.28	9.88	<b>0.003</b>
Effective forelimb length	T2, L2	Velocity	0.0051	1	19.21	6.23	<b>0.022</b>
		FLL	0.0167	1	5.37	20.49	<b>0.006</b>
		<b>Stride position</b>	0.0038	1	23.97	4.67	<b>0.041</b>

& Daley, 2007; Full & Koditschek, 1999), but high-speed animals are likely to rely more heavily on the former for more rapid responses to perturbations (Grimmer et al., 2008; Moritz & Farley, 2004; Sponberg & Full, 2008).

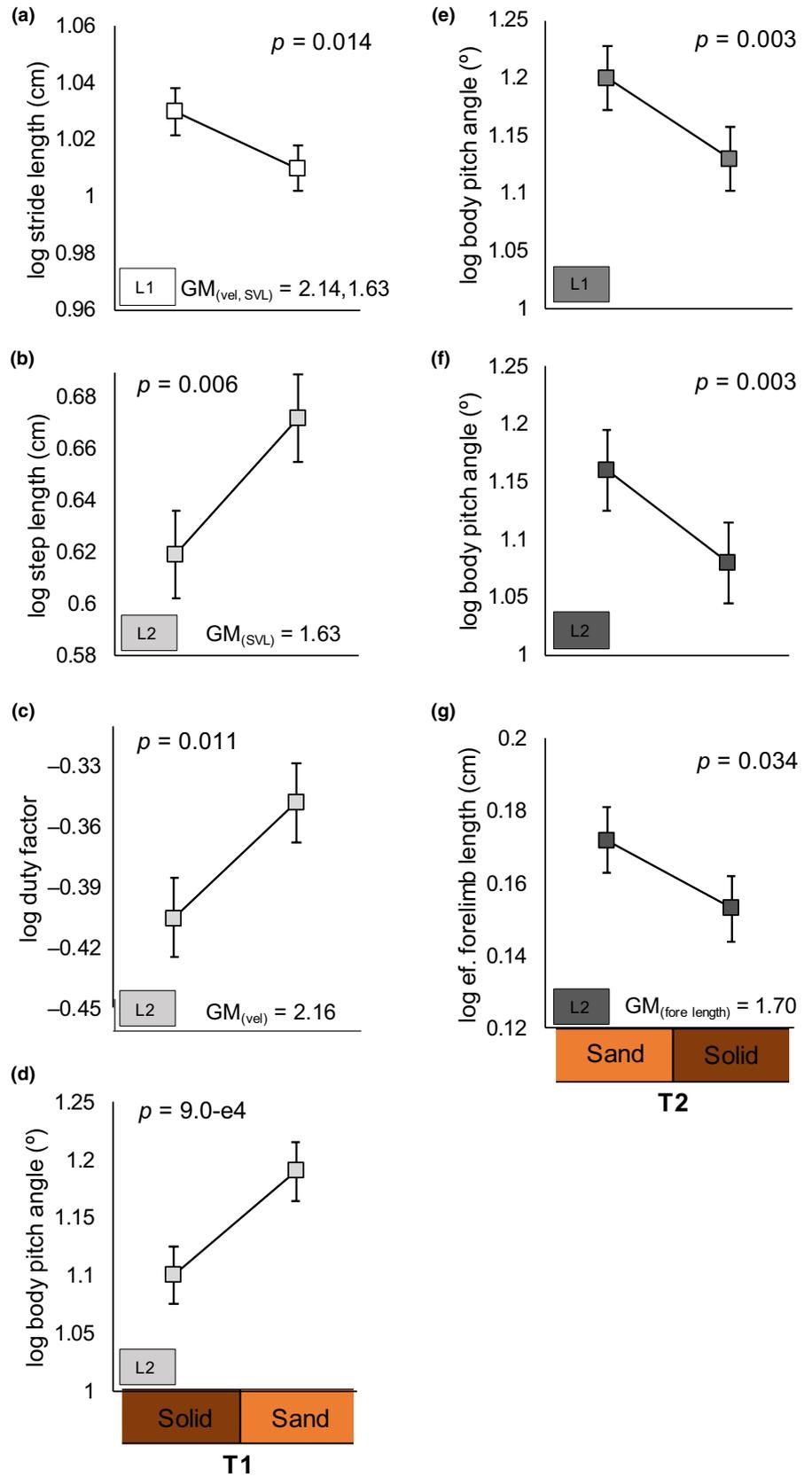
With respect to lizards running on difficult terrain, it has been hypothesized that increased trunk elevation represents a mechanical by-product of a rapid caudal shift of the centre of mass onto the hindlimbs during accelerative bursts (Aerts et al., 2003; Clemente et al., 2008; Clemente & Wu, 2018; Irschick & Jayne, 1999; Van Wassenbergh & Aerts, 2013), and alternatively that it is an active, adaptive behaviour (Kohlsdorf & Biewener, 2006; Parker & McBrayer, 2016; Tucker & McBrayer, 2012). Within our study, significant changes in velocity between checkpoints or between-stride pairs at transition sites were not detected alongside changes in body pitch angle. Although our observations are limited, we did see that *R. afer* ran bipedally under both sand and non-transition conditions. Further investigation of tail kinematics and of motor patterns during high-speed pitched and bipedal locomotion in this species and across lizards is pertinent for resolving this question. Regardless of the nature of the response for changes in body pitch angle, pitching likely contributes to *R. afer*'s ability to sustain high-speed locomotion during shifts in substrate compliance.

There may be additional aspects of timing and kinematics that contribute to sprint speed maintenance on a level, deformable

substrate that we did not consider in this study, such as *R. afer*'s ankle movement or digit position. Notably, *R. afer* can often be observed with its reduced frictional adhesive toe pads down (i.e. toes slightly flexed) rather than up (i.e. toes hyperextended) during level running on a solid substrate, which is more mechanically advantageous (Collins & Higham, 2017). If and how *R. afer* and other toe pad-bearing geckos modulate toe length on a granular substrate remains to be assessed. Qian et al. (2015) noted that total foot area doubles when the toes are flexed versus hyperextended in the gecko *Chondrodactylus bibronii*, which reduces their estimated static 'foot pressure' (see their figure 9). Like the flatter foot posture observed in *C. draconoides* running on sand (Li et al., 2012), longer digits should reduce penetration depth; this would be potentially analogous to the toe fringes seen in many sand-dwelling lizards, including some geckos (Luke, 1986), although further study is needed to clarify their species and context-specific locomotor function(s), including burrowing (Carothers, 1986; Higham, 2015; Pianka & Vitt, 2003; Zheng et al., 2020).

It is essential to point out that the efficacy of such kinematic and morphological 'strategies' is dependent upon the specific granular media with which the animal is interacting. Grain size (including grain size variation) and packing density influence yield stress, which along with penetration depth determine when and

**FIGURE 5** Estimated marginal means plots from the between-stride analysis for locomotor variables significantly predicted by stride position (i.e. initial stride on new substrate vs. previous stride on former substrate) per limb (L1, L2) and transition, either into sand (T1) or out of sand (T2) (see Figure 2): (a) stride length for L1 at T1, (b) step length for L2 at T1, (c) duty factor for L2 at T1, (d) body pitch angle for L2 at T1, (e) body pitch angle for L1 at T2, (f) body pitch angle for L2 at T2, and (g) effective forelimb length for L2 at T2. Plots show the model-estimated means and standard error bars from the best-fitting models; grand means (GMs) of the covariates (as applicable) are shown, along with contrast *p*-values; SVL = snout-vent length, vel = velocity, fore length = forelimb length (actual)



how a granular medium fluidizes or solidifies under and around the foot (Bergmann et al., 2017; Gravish et al., 2012; Jaeger et al., 1996; Li et al., 2013). Korff and McHenry (2011) concluded from consistent performance results in *C. draconoides* and *U. scoparia* that the surface strength of the dune sand ( $4.7 \pm 2.1$  kPa;  $0.25 \leq$  grain size  $< 1.0$  mm) used in their study was likely high enough to withstand the applied forces and penetration of these species. Qian et al. (2015) similarly found that decreasing substrate penetration resistance for glass spheres ( $250 \pm 30$   $\mu$ m) did not reduce speed in *C. draconoides* but did so in *U. scoparia* and *C. bibronii*. They also calculated the lowest static foot pressure for *C. draconoides* relative to these species ( $0.75 \pm 0.25$  kPa) and observed that its relatively large hind foot penetrates to a shallow depth and actually 'paddles' through the surrounding fluid-like material via ankle rotation until jamming (i.e. solidification) occurs (Aguilar & Goldman, 2016), as originally posited by Li et al. (2012; see also Qian et al., 2012; Zhang et al., 2013).

We do not know if *R. afer* interacts similarly with the dune sand within its habitat, but we did find comparable grain sizes to that in Korff and McHenry (2011) at our study site (average of  $0.33 \pm 0.03$  mm; 49% of grains between 0.25 and 0.5 mm), and a surface strength of  $3.07 \pm 0.76$  kPa from our sample (see Appendix S1a). While this substrate may be less resistant to penetration than the dune sand used by *C. draconoides*, *R. afer* has a much smaller body size (1.5–3.5 g in our study vs. 8.3–16.7 g in Korff & McHenry, 2011) and smaller foot pressure of  $0.48 \pm 0.04$  kPa (calculated sensu Qian et al., 2015; see Appendix S1b for details), meaning that limb penetration would likely be limited simply based on static properties of the organism. Moreover, *R. afer* appears to run in the laboratory at similar speeds to *C. draconoides* on a field trackway (average maximum velocity on dune sand =  $2.2 \pm 0.2$  m/s, Korff & McHenry, 2011); mean stride velocity in our study was  $2.12 \pm 0.17$  m/s (also consistent with Higham & Russell, 2010). Given these attributes of both the substrate and the animal, it is plausible that *R. afer* does not apply enough force or penetrate the sand deep enough during running to prevent it from maintaining forward velocity with pitching. This is further supported by the fact that we did not detect a reduction in limb compression when the animals transitioned from the solid trackway into the sand. Nonetheless, finer kinematic study of the limbs and actual measurements of dynamic force production on compliant media are needed to formally test these hypotheses in *R. afer* and other animals (Sweeney, 2019; Zhang et al., 2017).

Such measurements would also better contextualize behavioural observations. If *R. afer* does not experience a drop in sprint speed performance or a high cost of transport during compliance transitions in nature, then selection acting on substrate preference during escapes may be relaxed; this would potentially result in the observed match between transition use and availability. Alternatively, indiscriminate transition use during escapes could provide a selective advantage for terrestrial predator evasion. Extensive work in multiple animal systems has documented habitat selection as a key type of 'anti-predator' behavioural strategy, where prey species can

maximize their ability to avoid and flee from threats (see Lima, 1992 and Wirsing et al., 2010). For example, Sathe and Husak (2018) found that *A. sexlineata* was more likely to occupy substrates in which their sprint speed performance was highest (e.g. rock). However, they also noted that lizards tended to flee to grass, where they exhibited diminished performance, potentially because prey detection and locomotor performance of predators might also be impaired in these conditions.

It is possible that larger, heavier diurnal terrestrial predators, such as *Psammophis leightoni* (*namibensis*), a lizard-specializing snake species found at the field site, may experience decreased locomotor performance during pursuit over a heterogeneous landscape of variably compliant surfaces. Assessing predator sprint speed performance, as well as predator and prey manoeuvrability during escapes will be essential first steps for making adaptive inferences (Moore & Biewener, 2015), but we hypothesize that *R. afer*'s speed insensitivity underlies its escape behaviour, which are both under positive selection as linked, survival-enhancing traits (Arnold, 1983; Garland Jr. & Losos, 1994). Testing this idea will improve our understanding of how and under what conditions this and other high-speed locomotor systems have evolved. We hope that our study further illustrates the importance of integrating field data with biomechanical analyses (i.e. 'mechanical ecology', Bauer et al., 2020) in the quest to elucidate how organisms move successfully within their environments.

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## CONFLICT OF INTEREST

The authors declare no conflicting interests. T.E.H. is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making process for this paper.

## AUTHORS' CONTRIBUTIONS

E.R.N. and T.E.H. conceived the ideas and designed the study; E.R.N. collected, processed, and analysed the data and wrote the manuscript. Both authors revised the manuscript and approved the final version.

## DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository <https://doi.org/10.6086/D1GQ3S> (Naylor & Higham, 2021).

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## REFERENCES

- Aerts, P., Aerts, P., Damme, R. V., D'Août, K., & Hooydonck, B. V. (2003). Bipedalism in lizards: Whole-body modelling reveals a possible spandrel. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 358(1437), 1525–1533. <https://doi.org/10.1098/rstb.2003.1342>
- Aguilar, J., & Goldman, D. I. (2016). Robophysical study of jumping dynamics on granular media. *Nature Physics*, 12(3), 278–283. <https://doi.org/10.1038/nphys3568>
- Arnold, S. J. (1983). Morphology, performance and fitness. *American Zoologist*, 23(2), 347–361. <https://doi.org/10.1093/icb/23.2.347>
- Astley, H. C., Haruta, A., & Roberts, T. J. (2015). Robust jumping performance and elastic energy recovery from compliant perches in tree frogs. *Journal of Experimental Biology*, 218(21), 3360–3363. <https://doi.org/10.1242/jeb.121715>
- Bates, D. M., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bauer, A. M., Russell, A. P., & Powell, G. L. (1996). The evolution of locomotor morphology in *Rhoptropus* (Squamata: Gekkonidae): Functional and phylogenetic considerations. *African Journal of Herpetology*, 45(1), 8–30. <https://doi.org/10.1080/21564574.1996.9649959>
- Bauer, U., Poppinga, S., & Müller, U. K. (2020). Mechanical ecology—Taking biomechanics to the field. *Integrative and Comparative Biology*, 60(4), 820–828. <https://doi.org/10.1093/icb/icaa018>
- Bergmann, P. J., Pettinelli, K. J., Crockett, M. E., & Schaper, E. G. (2017). It's just sand between the toes: How particle size and shape variation affect running performance and kinematics in a generalist lizard. *The Journal of Experimental Biology*, 220(20), 3706–3716. <https://doi.org/10.1242/jeb.161109>
- Biewener, A. A. (1989). Scaling body support in mammals: Limb posture and muscle mechanics. *Science*, 245(4913), 45–48. JSTOR.
- Biewener, A. A., & Daley, M. A. (2007). Unsteady locomotion: Integrating muscle function with whole body dynamics and neuromuscular control. *Journal of Experimental Biology*, 210(17), 2949–2960. <https://doi.org/10.1242/jeb.005801>
- Biewener, A. A., & Patek, S. (2018). *Animal Locomotion* (Second). Oxford University Press.
- Birn-Jeffery, A. V., & Higham, T. E. (2014). The scaling of uphill and downhill locomotion in legged animals. *Integrative and Comparative Biology*, 54(6), 1159–1172. <https://doi.org/10.1093/icb/icu015>
- Birn-Jeffery, A. V., & Higham, T. E. (2016). Light level impacts locomotor biomechanics in a secondarily diurnal gecko, *Rhoptropus afer*. *Journal of Experimental Biology*, 219(22), 3649–3655. <https://doi.org/10.1242/jeb.143719>
- Blob, R. W., & Higham, T. E. (2014). Terrestrial locomotion—Where do we stand, where are we going? An introduction to the symposium. *Integrative and Comparative Biology*, 54(6), 1051–1057. <https://doi.org/10.1093/icb/icu105>
- Brain, C. K. (1962). Observations on the temperature tolerance of lizards in the central Namib Desert, South West Africa. *Cimbebasia*, 4, 1–5.
- Brandt, R., Galvani, F., & Kohlsdorf, T. (2015). Sprint performance of a generalist lizard running on different substrates: Grip matters. *Journal of Zoology*, 297(1), 15–21. <https://doi.org/10.1111/jzo.12253>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd ed.). Springer.
- Carothers, J. H. (1986). An experimental confirmation of morphological adaptation: Toe fringes in the sand-dwelling lizard *Uma scoparia*. *Evolution*, 40(4), 871–874. JSTOR. <https://doi.org/10.2307/2408475>
- Childress, S., Hosoi, A., Schultz, W. W., & Wang, J. (Eds.). (2012). *Natural locomotion in fluids and on surfaces: Swimming, flying, and sliding*. Springer-Verlag. <https://doi.org/10.1007/978-1-4614-3997-4>
- Clark, A. J., & Higham, T. E. (2011). Slipping, sliding and stability: Locomotor strategies for overcoming low-friction surfaces. *Journal of Experimental Biology*, 214(8), 1369–1378. <https://doi.org/10.1242/jeb.051136>
- Clemente, C. J., Withers, P. C., Thompson, G., & Lloyd, D. (2008). Why go bipedal? Locomotion and morphology in Australian agamid lizards. *Journal of Experimental Biology*, 211(13), 2058–2065. <https://doi.org/10.1242/jeb.018044>
- Clemente, C. J., & Wu, N. C. (2018). Body and tail-assisted pitch control facilitates bipedal locomotion in Australian agamid lizards. *Journal of the Royal Society Interface*, 15(146), 20180276. <https://doi.org/10.1098/rsif.2018.0276>
- Collins, C. E., & Higham, T. E. (2017). Individuals of the common Namib Day Gecko vary in how adaptive simplification alters sprint biomechanics. *Scientific Reports*, 7(1), 15595. <https://doi.org/10.1038/s41598-017-15459-6>
- Collins, C. E., Russell, A. P., & Higham, T. E. (2015). Subdigital adhesive pad morphology varies in relation to structural habitat use in the Namib Day Gecko. *Functional Ecology*, 29(1), 66–77. <https://doi.org/10.1111/1365-2435.12312>
- Collins, C. E., Self, J. D., Anderson, R. A., & McBrayer, L. D. (2013). Rock-dwelling lizards exhibit less sensitivity of sprint speed to increases in substrate rugosity. *Zoology*, 116(3), 151–158. <https://doi.org/10.1016/j.zool.2013.01.001>
- Combes, S. A., & Dudley, R. (2009). Turbulence-driven instabilities limit insect flight performance. *Proceedings of the National Academy of Sciences of the United States of America*, 106(22), 9105–9108. <https://doi.org/10.1073/pnas.0902186106>
- Crandell, K. E., Smith, A. F., Crino, O. L., & Tobalske, B. W. (2018). Coping with compliance during take-off and landing in the diamond dove (*Geopelia cuneata*). *PLoS One*, 13(7), e0199662. <https://doi.org/10.1371/journal.pone.0199662>
- Daley, M. A. (2008). Biomechanics: Running over uneven terrain is a no-brainer. *Current Biology*, 18(22), R1064–R1066. <https://doi.org/10.1016/j.cub.2008.09.050>
- Daley, M. A., & Biewener, A. A. (2006). Running over rough terrain reveals limb control for intrinsic stability. *Proceedings of the National Academy of Sciences of the United States of America*, 103(42), 15681–15686. <https://doi.org/10.1073/pnas.0601473103>
- Daley, M. A., Usherwood, J. R., Felix, G., & Biewener, A. A. (2006). Running over rough terrain: Guinea fowl maintain dynamic stability despite a large unexpected change in substrate height. *Journal of Experimental Biology*, 209(1), 171–187. <https://doi.org/10.1242/jeb.01986>
- Demes, B., Jungers, W. L., Gross, T. S., & Fleagle, J. G. (1995). Kinetics of leaping primates: Influence of substrate orientation and compliance. *American Journal of Physical Anthropology*, 96(4), 419–429. <https://doi.org/10.1002/ajpa.1330960407>
- Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R., & Lehman, S. (2000). How animals move: An integrative view. *Science*, 288(5463), 100–106. <https://doi.org/10.1126/science.288.5463.100>
- Druelle, F., Goyens, J., Vasilopoulou-Kampitsi, M., & Aerts, P. (2019). Compliant legs enable lizards to maintain high running speeds on complex terrains. *Journal of Experimental Biology*, 222(6). <https://doi.org/10.1242/jeb.195511>

- Ferris, D. P., & Farley, C. T. (1997). Interaction of leg stiffness and surface stiffness during human hopping. *Journal of Applied Physiology*, 82(1), 15–22. <https://doi.org/10.1152/jappl.1997.82.1.15>
- Ferris, D. P., Liang, K., & Farley, C. T. (1999). Runners adjust leg stiffness for their first step on a new running surface. *Journal of Biomechanics*, 32(8), 787–794. [https://doi.org/10.1016/S0021-9290\(99\)00078-0](https://doi.org/10.1016/S0021-9290(99)00078-0)
- Ferris, D. P., Louie, M., & Farley, C. T. (1998). Running in the real world: Adjusting leg stiffness for different surfaces. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1400), 989–994. <https://doi.org/10.1098/rspb.1998.0388>
- Fry, F. E. J., & Hart, J. S. (1948). Cruising speed of goldfish in relation to water temperature. *Journal of the Fisheries Research Board of Canada*, 7b(4), 169–175. <https://doi.org/10.1139/f47-018>
- Full, R. J., & Koditschek, D. E. (1999). Templates and anchors: Neuromechanical hypotheses of legged locomotion on land. *Journal of Experimental Biology*, 202(23), 3325–3332. <https://doi.org/10.1242/jeb.202.23.3325>
- Full, R. J., Kubow, T., Schmitt, J., Holmes, P., & Koditschek, D. (2002). Quantifying dynamic stability and maneuverability in legged locomotion. *Integrative and Comparative Biology*, 42(1), 149–157. <https://doi.org/10.1093/icb/42.1.149>
- Full, R. J., & Tullis, A. (1990). Energetics of ascent: Insects on inclines. *Journal of Experimental Biology*, 149(1), 307–317. <https://doi.org/10.1242/jeb.149.1.307>
- Garland Jr., T., & Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In P. C. Wainwright, & S. M. Reilly (Eds.), *Ecological Morphology: Integrative Organismal Biology* (pp. 240–302). University of Chicago Press.
- Gilman, C. A., Bartlett, M. D., Gillis, G. B., & Irschick, D. J. (2012). Total recoil: Perch compliance alters jumping performance and kinematics in green anole lizards (*Anolis carolinensis*). *Journal of Experimental Biology*, 215(2), 220–226. <https://doi.org/10.1242/jeb.061838>
- Gravish, N., Franklin, S. V., Hu, D. L., & Goldman, D. I. (2012). Entangled granular media. *Physical Review Letters*, 108(20), 208001. <https://doi.org/10.1103/PhysRevLett.108.208001>
- Gravish, N., Umbanhowar, P. B., & Goldman, D. I. (2010). Force and flow transition in plowed granular media. *Physical Review Letters*, 105(12), 128301. <https://doi.org/10.1103/PhysRevLett.105.128301>
- Grimmer, S., Ernst, M., Günther, M., & Blickhan, R. (2008). Running on uneven ground: Leg adjustment to vertical steps and self-stability. *Journal of Experimental Biology*, 211(18), 2989–3000. <https://doi.org/10.1242/jeb.014357>
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 6, e4794. <https://doi.org/10.7717/peerj.4794>
- Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspiration & Biomimetics*, 3(3), 034001. <https://doi.org/10.1088/1748-3182/3/3/034001>
- Higham, T. E. (2015). Bolting, bouldering, and burrowing: Functional morphology and biomechanics of pedal specialisations in desert-dwelling lizards. In O. R. P. Bininda-Emonds, & A. P. Russell (Eds.), *All animals are interesting: A festschrift in honour of Anthony P. Russell* (pp. 279–302). BIS-Verlag der Carl von Ossietzky Universität Oldenburg. <https://d-nb.info/1073318168>
- Higham, T. E., & Russell, A. P. (2010). Divergence in locomotor performance, ecology, and morphology between two sympatric sister species of desert-dwelling gecko. *Biological Journal of the Linnean Society*, 101(4), 860–869. <https://doi.org/10.1111/j.1095-8312.2010.01539.x>
- Higham, T. E., Russell, A. P., Niewiarowski, P. H., Wright, A., & Speck, T. (2019). The ecomechanics of gecko adhesion: Natural surface topography, evolution, and biomimetics. *Integrative and Comparative Biology*, 59(1), 148–167. <https://doi.org/10.1093/icb/icz013>
- Hsieh, S. T. (2003). Three-dimensional hindlimb kinematics of water running in the plumed basilisk lizard (*Basiliscus plumifrons*). *Journal of Experimental Biology*, 206(23), 4363–4377. <https://doi.org/10.1242/jeb.00679>
- Irschick, D. J., & Jayne, B. C. (1999). Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *Journal of Experimental Biology*, 202(9), 1047–1065. <https://doi.org/10.1242/jeb.202.9.1047>
- Irschick, D. J., & Losos, J. B. (1999). Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean Anoles. *The American Naturalist*, 154(3), 293–305. <https://doi.org/10.1086/303239>
- Irschick, D. J., Meyers, J. J., Husak, J. F., & Le Galliard, J. F. (2008). How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research*, 10(2), 177–196.
- Jaeger, H. M., Nagel, S. R., & Behringer, R. P. (1996). Granular solids, liquids, and gases. *Reviews of Modern Physics*, 68(4), 1259–1273. <https://doi.org/10.1103/RevModPhys.68.1259>
- Jagnandan, K., & Higham, T. E. (2018). How rapid changes in body mass affect the locomotion of terrestrial vertebrates: Ecology, evolution and biomechanics of a natural perturbation. *Biological Journal of the Linnean Society*, 124(3), 279–293. <https://doi.org/10.1093/biolinean/bly056>
- Jindrich, D. L., & Full, R. J. (2002). Dynamic stabilization of rapid hexapedal locomotion. *Journal of Experimental Biology*, 205(18), 2803–2823. <https://doi.org/10.1242/jeb.205.18.2803>
- Johnson, M. K., Russell, A. P., & Bauer, A. M. (2005). Locomotor morphology of the *Pachydactylus* radiation of lizards (Gekkota: Gekkonidae): A phylogenetically and ecologically informed analysis. *Canadian Journal of Zoology*, 83(12), 1511–1524. <https://doi.org/10.1139/z05-112>
- Kerdok, A. E., Biewener, A. A., McMahon, T. A., Weyand, P. G., & Herr, H. M. (2002). Energetics and mechanics of human running on surfaces of different stiffnesses. *Journal of Applied Physiology*, 92(2), 469–478. <https://doi.org/10.1152/japplphysiol.01164.2000>
- Koditschek, D. E., Full, R. J., & Buehler, M. (2004). Mechanical aspects of legged locomotion control. *Arthropod Structure & Development*, 33(3), 251–272. <https://doi.org/10.1016/j.asd.2004.06.003>
- Kohlsdorf, T., & Biewener, A. A. (2006). Negotiating obstacles: Running kinematics of the lizard *Sceloporus malachiticus*. *Journal of Zoology*, 270(2), 359–371. <https://doi.org/10.1111/j.1469-7998.2006.00150.x>
- Korff, W. L., & McHenry, M. J. (2011). Environmental differences in substrate mechanics do not affect sprinting performance in sand lizards (*Uma scoparia* and *Callisaurus draconoides*). *Journal of Experimental Biology*, 214(1), 122–130. <https://doi.org/10.1242/jeb.045682>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(1), 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Laerm, J. (1973). Aquatic bipedalism in the basilisk lizard: The analysis of an adaptive strategy. *The American Midland Naturalist*, 89(2), 314–333. JSTOR. <https://doi.org/10.2307/2424037>
- Lamb, T., & Bauer, A. M. (2006). Footprints in the sand: Independent reduction of subdigital lamellae in the Namib-Kalahari burrowing geckos. *Proceedings of the Royal Society B: Biological Sciences*, 273(1588), 855–864. <https://doi.org/10.1098/rspb.2005.3390>
- Lammers, A. R., Earls, K. D., & Biknevicius, A. R. (2006). Locomotor kinetics and kinematics on inclines and declines in the gray short-tailed opossum *Monodelphis domestica*. *Journal of Experimental Biology*, 209(20), 4154–4166. <https://doi.org/10.1242/jeb.02493>
- Lejeune, T. M., Willems, P. A., & Heglund, N. C. (1998). Mechanics and energetics of human locomotion on sand. *Journal of Experimental*

- Biology*, 201(13), 2071–2080. <https://doi.org/10.1242/jeb.201.13.2071>
- Lenth, R. V., Buerkner, P., Herve, M., Love, J., Riebl, H., & Singmann, H. (2020). *emmeans: Estimated marginal means, aka least-squares means* (1.5.3) [Computer software]. <https://CRAN.R-project.org/package=emmeans>
- Li, C., Hsieh, S. T., & Goldman, D. I. (2012). Multi-functional foot use during running in the zebra-tailed lizard (*Callisaurus draconoides*). *Journal of Experimental Biology*, 215(18), 3293–3308. <https://doi.org/10.1242/jeb.061937>
- Li, C., Lian, X., Bi, J., Fang, H., Maul, T. L., & Jiang, Z. (2011). Effects of sand grain size and morphological traits on running speed of toad-headed lizard *Phrynocephalus frontalis*. *Journal of Arid Environments*, 75(11), 1038–1042. <https://doi.org/10.1016/j.jaridenv.2011.06.015>
- Li, C., Umbanhowar, P. B., Komsuoglu, H., Koditschek, D. E., & Goldman, D. I. (2009). Sensitive dependence of the motion of a legged robot on granular media. *Proceedings of the National Academy of Sciences of the United States of America*, 106(9), 3029–3034. <https://doi.org/10.1073/pnas.0809095106>
- Li, C., Zhang, T., & Goldman, D. I. (2013). A terradynamics of legged locomotion on granular media. *Science*, 339(6126), 1408–1412. <https://doi.org/10.1126/science.1229163>
- Liao, J. C. (2007). A review of fish swimming mechanics and behaviour in altered flows. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1487), 1973–1993. <https://doi.org/10.1098/rstb.2007.2082>
- Lima, S. L. (1992). Strong preferences for apparently dangerous habitats? A consequence of differential escape from predators. *Oikos*, 64(3), 597–600. <https://doi.org/10.2307/3545181>
- Lindstrom, M. J., & Bates, D. M. (1990). Nonlinear mixed effects models for repeated measures data. *Biometrics*, 46(3), 673–687. <https://doi.org/10.2307/2532087>
- Losos, J. B., & Sinervo, B. (1989). The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *Journal of Experimental Biology*, 145(1), 23–30. <https://doi.org/10.1242/jeb.145.1.23>
- Luke, C. (1986). Convergent evolution of lizard toe fringes. *Biological Journal of the Linnean Society*, 27(1), 1–16. <https://doi.org/10.1111/j.1095-8312.1986.tb01723.x>
- Mazouchova, N., Gravish, N., Savu, A., & Goldman, D. I. (2010). Utilization of granular solidification during terrestrial locomotion of hatchling sea turtles. *Biology Letters*, 6, 398–401. <https://doi.org/10.1098/rsbl.2009.1041>
- McMahon, T. A., & Greene, P. R. (1978). Fast running tracks. *Scientific American*, 239(6), 148–163. <https://doi.org/10.1038/scientificamerican1278-148>
- McMahon, T. A., & Greene, P. R. (1979). The influence of track compliance on running. *Journal of Biomechanics*, 12(12), 893–904. [https://doi.org/10.1016/0021-9290\(79\)90057-5](https://doi.org/10.1016/0021-9290(79)90057-5)
- Mehta, A., & Barker, G. C. (1994). The dynamics of sand. *Reports on Progress in Physics*, 57(4), 383. <https://doi.org/10.1088/0034-4885/57/4/002>
- Moore, T. Y., & Biewener, A. A. (2015). Outrun or outmaneuver: Predator–prey interactions as a model system for integrating biomechanical studies in a broader ecological and evolutionary context. *Integrative and Comparative Biology*, 55(6), 1188–1197. <https://doi.org/10.1093/icb/icz074>
- Moritz, C. T., & Farley, C. T. (2003). Human hopping on damped surfaces: Strategies for adjusting leg mechanics. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1525), 1741–1746. <https://doi.org/10.1098/rspb.2003.2435>
- Moritz, C. T., & Farley, C. T. (2004). Passive dynamics change leg mechanics for an unexpected surface during human hopping. *Journal of Applied Physiology*, 97(4), 1313–1322. <https://doi.org/10.1152/jappphysiol.00393.2004>
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85(4), 935–956. <https://doi.org/10.1111/j.1469-185X.2010.00141.x>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Naylor, E. R., & Higham, T. E. (2019). Attachment beyond the adhesive system: The contribution of claws to gecko clinging and locomotion. *Integrative and Comparative Biology*, 59(1), 168–181. <https://doi.org/10.1093/icb/icz027>
- Naylor, E. R., & Higham, T. E. (2021). Data from: High-speed terrestrial substrate transitions: How a fleeing cursorial day gecko copes with compliance changes that are experienced in nature. *Dryad Digital Repository*, <https://doi.org/10.6086/D1GQ3S>
- Odendaal, F. J. (1979). Notes on the adaptive ecology and behaviour of four species of *Rhoptropus* (Gekkonidae) from the Namib Desert with special reference to a thermoregulatory mechanism employed by *Rhoptropus afer*. *Madoqua*, 1979(v11i3), 255–260.
- Olberding, J. P., McBrayer, L. D., & Higham, T. E. (2012). Performance and three-dimensional kinematics of bipedal lizards during obstacle negotiation. *Journal of Experimental Biology*, 215(2), 247–255. <https://doi.org/10.1242/jeb.061135>
- Parker, S. E., & McBrayer, L. D. (2016). The effects of multiple obstacles on the locomotor behavior and performance of a terrestrial lizard. *Journal of Experimental Biology*, 219(7), 1004–1013. <https://doi.org/10.1242/jeb.120451>
- Peters, W. C. H. (1869). Eine Mittheilung über neue Gattungen und Arten von Eidechsen. *Monatsberichte Der Königlichen Preussische Akademie Des Wissenschaften Zu Berlin*, 57–66.
- Pianka, E. R., & Vitt, L. J. (2003). *Lizards: Windows to the evolution of diversity* (1st ed.) University of California Press.
- Qian, F., Zhang, T., Korff, W., Umbanhowar, P. B., Full, R. J., & Goldman, D. I. (2015). Principles of appendage design in robots and animals determining terradynamic performance on flowable ground. *Bioinspiration & Biomimetics*, 10(5), 056014. <https://doi.org/10.1088/1748-3190/10/5/056014>
- Qian, F., Zhang, T., Li, C., Masarati, P., Hoover, A., Birkmeyer, P., Pullin, A., Fearing, R., & Goldman, D. (2012). Walking and running on yielding and fluidizing ground. *RSS Proceedings. Robotics: Science & Systems*, 8, 345–352.
- Redmann, E., Sheikh, A., Alqahtani, A., McCarty-Glenn, M., Syed, S., Mehta, R. S., & Ward, A. B. (2020). Terrestrial locomotion in American eels (*Anguilla rostrata*): How substrate and incline affect movement patterns. *Integrative and Comparative Biology*, 60(1), 180–189. <https://doi.org/10.1093/icb/icaa016>
- Ribak, G., Reingold, S., & Weihs, D. (2012). The effect of natural substrates on jump height in click-beetles. *Functional Ecology*, 26(2), 493–499. <https://doi.org/10.1111/j.1365-2435.2011.01943.x>
- Russell, A. P., & Johnson, M. K. (2014). Between a rock and a soft place: Microtopography of the locomotor substrate and the morphology of the setal fields of Namibian day geckos (Gekkota: Gekkonidae: *Rhoptropus*). *Acta Zoologica*, 95(3), 299–318. <https://doi.org/10.1111/azo.12028>
- Sathe, E. A., & Husak, J. F. (2015). Sprint sensitivity and locomotor trade-offs in green anole (*Anolis carolinensis*) lizards. *Journal of Experimental Biology*, 218(14), 2174–2179. <https://doi.org/10.1242/jeb.116053>
- Sathe, E. A., & Husak, J. F. (2018). Substrate-specific locomotor performance is associated with habitat use in six-lined racerunners (*Aspidoscelis sexlineata*). *Biological Journal of the Linnean Society*, 124(2), 165–173. <https://doi.org/10.1093/biolinnean/bly039>
- Savvides, P., Georgiou, E., Pafilis, P., & Sfenthourakis, S. (2019). Substrate type has a limited impact on the sprint performance of a

- Mediterranean lizard. *Acta Herpetologica*. [https://doi.org/10.13128/Acta\\_Herpetol-24153](https://doi.org/10.13128/Acta_Herpetol-24153)
- Snyder, R. C. (1952). Quadrupedal and bipedal locomotion of lizards. *Copeia*, 1952(2), 64–70. <https://doi.org/10.2307/1438533>
- Spence, A. J., Revzen, S., Seipel, J., Mullens, C., & Full, R. J. (2010). Insects running on elastic surfaces. *Journal of Experimental Biology*, 213(11), 1907–1920. <https://doi.org/10.1242/jeb.042515>
- Spezzano, L. C., & Jayne, B. C. (2004). The effects of surface diameter and incline on the hindlimb kinematics of an arboreal lizard (*Anolis sagrei*). *Journal of Experimental Biology*, 207(12), 2115–2131. <https://doi.org/10.1242/jeb.00995>
- Sponberg, S., & Full, R. J. (2008). Neuromechanical response of musculo-skeletal structures in cockroaches during rapid running on rough terrain. *Journal of Experimental Biology*, 211(3), 433–446. <https://doi.org/10.1242/jeb.012385>
- Stevens, N. J. (2008). The effect of branch diameter on primate gait sequence pattern. *American Journal of Primatology*, 70(4), 356–362. <https://doi.org/10.1002/ajp.20499>
- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2020). partR2: Partitioning R<sup>2</sup> in generalized linear mixed models. *BioRxiv*, 2020.07.26.221168. <https://doi.org/10.1101/2020.07.26.221168>
- Sweeney, A. (2019). *Force measurement of basilisk lizard running on water*. Arizona State University. <https://hdl.handle.net/2286/R.I.53856>
- Tucker, D. B., & McBrayer, L. D. (2012). Overcoming obstacles: The effect of obstacles on locomotor performance and behaviour. *Biological Journal of the Linnean Society*, 107(4), 813–823. <https://doi.org/10.1111/j.1095-8312.2012.01993.x>
- Urfi, A. J. (2016). Animal locomotion in different mediums. *Resonance*, 21(6), 545–556. <https://doi.org/10.1007/s12045-016-0359-8>
- Van Wassenbergh, S., & Aerts, P. (2013). In search of the pitching momentum that enables some lizards to sustain bipedal running at constant speeds. *Journal of the Royal Society Interface*, 10(84), 20130241. <https://doi.org/10.1098/rsif.2013.0241>
- Vanhooydonck, B., Measey, J., Edwards, S., Makhubo, B., Tolley, K. A., & Herrel, A. (2015). The effects of substratum on locomotor performance in lacertid lizards: Substrate and Locomotor Performance. *Biological Journal of the Linnean Society*, 115(4), 869–881. <https://doi.org/10.1111/bij.12542>
- Wheatley, R., Clemente, C. J., Niehaus, A. C., Fisher, D. O., & Wilson, R. S. (2018). Surface friction alters the agility of a small Australian marsupial. *Journal of Experimental Biology*, 221(8). <https://doi.org/10.1242/jeb.172544>
- Wirsing, A. J., Cameron, K. E., & Heithaus, M. R. (2010). Spatial responses to predators vary with prey escape mode. *Animal Behaviour*, 79(3), 531–537. <https://doi.org/10.1016/j.anbehav.2009.12.014>
- Yanoviak, S. P., Silveri, C., Stark, A. Y., Stan, J. T. V., & Levia, D. F. (2017). Surface roughness affects the running speed of tropical canopy ants. *Biotropica*, 49(1), 92–100. <https://doi.org/10.1111/btp.12349>
- Zhang, R., Han, D., Ma, S., Luo, G., Ji, Q., Xue, S., Yang, M., & Li, J. (2017). Plantar pressure distribution of ostrich during locomotion on loose sand and solid ground. *PeerJ*, 5, e3613. <https://doi.org/10.7717/peerj.3613>
- Zhang, T., Qian, F., Li, C., Masarati, P., Hoover, A. M., Birkmeyer, P., Pullin, A., Fearing, R. S., & Goldman, D. I. (2013). Ground fluidization promotes rapid running of a lightweight robot. *The International Journal of Robotics Research*, 32(7), 859–869. <https://doi.org/10.1177/0278364913481690>
- Zheng, P., Liang, T., An, J., & Shi, L. (2020). Morphological function of toe fringe in the sand lizard *Phrynocephalus mystaceus*. *Scientific Reports*, 10(1), 22068. <https://doi.org/10.1038/s41598-020-79113-4>

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