

REVIEW

The bumpy road ahead: the role of substrate roughness on animal walking and a proposed comparative metric

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ABSTRACT

Outside laboratory conditions and human-made structures, animals rarely encounter flat surfaces. Instead, natural substrates are uneven surfaces with height variation that ranges from the microscopic scale to the macroscopic scale. For walking animals (which we define as encompassing any form of legged movement across the ground, such as walking, running, galloping, etc.), such substrate ‘roughness’ influences locomotion in a multitude of ways across scales, from roughness that influences how each toe or foot contacts the ground, to larger obstacles that animals must move over or navigate around. Historically, the unpredictability and variability of natural environments has limited the ability to collect data on animal walking biomechanics. However, recent technical advances, such as more sensitive and portable cameras, biologgers, laboratory tools to fabricate rough terrain, as well as the ability to efficiently store and analyze large variable datasets, have expanded the opportunity to study how animals move under naturalistic conditions. As more researchers endeavor to assess walking over rough terrain, we lack a consistent approach to quantifying roughness and contextualizing these findings. This Review summarizes existing literature that examines non-human animals walking on rough terrain and presents a metric for characterizing the relative substrate roughness compared with animal size. This framework can be applied across terrain and body scales, facilitating direct comparisons of walking over rough surfaces in animals ranging in size from ants to elephants.

KEY WORDS: Locomotion, Terrestrial, Legged, Adhesion, Friction, Running, Uneven, Obstacle traversal, Biomechanics

Introduction

The ground underfoot exhibits massive complexity, from micro-scale roughness that can affect claw and adhesive engagement, to macro-scale roughness that influences where feet are placed or how animals navigate (Fig. 1A). While there may not be a single universal example of roughness in nature, one thing is almost always true: substrates over which animals walk are not strictly flat. To understand locomotion in natural contexts, it is imperative to consider how roughness impacts locomotion biomechanics. With an ever-growing list of recent studies in comparative biomechanics that examine locomotion on rough substrates (Fig. 1B; Table S1), there is a need to review common concepts and standardize experimental approaches, terminology, and outlook (Cruse, 1976; Watson et al., 2002a,b; Blaesing and Cruse, 2004; Daley and Biewener, 2006; Daley et al., 2006; Kohlsdorf and

Biewener, 2006; Spagna et al., 2007; Endlein and Federle, 2008; Sponberg and Full, 2008; Harley et al., 2009; Perrot et al., 2011; Birm-Jeffery and Daley, 2012; Libby et al., 2012; Tucker and Mcbrayer, 2012; Olberding et al., 2012; Kress and Egelhaaf, 2012; Ritzmann et al., 2012; Sato et al., 2012; Collins et al., 2013; Theunissen and Dürr, 2013; Theunissen et al., 2014; Birm-Jeffery et al., 2014; Li et al., 2015; Parker and McBrayer, 2016; Yanoviak et al., 2017; Gart et al., 2018; Gart and Li, 2018; Stark and Yanoviak, 2020; Clifton et al., 2020a,b; Othayoth et al., 2020; Han et al., 2021; Othayoth et al., 2021; Wang et al., 2022; Othayoth et al., 2022; Green et al., 2022).

In this Review, we focus on comparative biomechanics studies of non-human animals that use limb-stepping terrestrial locomotion, which we imprecisely refer to as ‘walking’ for concision. We define walking as propulsive movement occurring through repeated, discrete contacts between limbs and a ground substrate, thus encompassing walking, running and other ground locomotion gaits (e.g. trotting, galloping, pacing, bounding, skipping). However, we do not include climbing, jumping, brachiation, or any movement that does not involve limbs or that involves substantial use of the trunk (e.g. slithering for example). Roughness is important in walking biomechanics because, as appendages lift from the ground and take a new step, the next stance height may be very different from the previous one. Thus, the force production capabilities are continually changing as footholds change during steps, inducing uncertainties in propulsion and stability as an animal steps over the surface.

The 3D shape of natural surfaces can exhibit features across a huge range of length scales, from micrometer and nanometer asperities up to multi-meter length protrusions and crevasses. Accordingly, scientists from many different disciplines have sought to quantify roughness over the years. At the smallest scales, the field of tribology, which is the study of surfaces in contact, focuses on microscopic, nanometer-scale surface structures (Bhushan, 2000). At the largest scales, geologists seek to map 3D surface structures over hundreds of meters (while still aiming for resolution in the millimeter–centimeter range) (Chorley, 2019). However, there is a lack of common terminology across these fields. For example, both geologists and tribologists define ‘roughness’ as the fine-scale features of surface unevenness (Bhushan, 2000; Chorley, 2019). However, ‘fine-scale’ to a tribologist is a nanometer, whereas to a geologist it is a decimeter (10^6 times larger!). The relevant scale of roughness also varies for animal movements: the substrate roughness that an animal experiences depends on its size, movements and sensory system. We assert that how an animal experiences roughness depends on the relative, and not absolute, size of substrate features.

Rough surfaces impact walking biomechanics through a variety of phenomena. (1) When the substrate roughness consists solely of structures much smaller than the animal, the influence of roughness occurs predominantly at the foot-ground contact mechanics which can enhance or degrade traction forces (Fig. 1A,B). (2) In comparison, substrate structures at approximately the scale of an animal’s leg length may disrupt foot placement, leg posture, body stability and the leg’s

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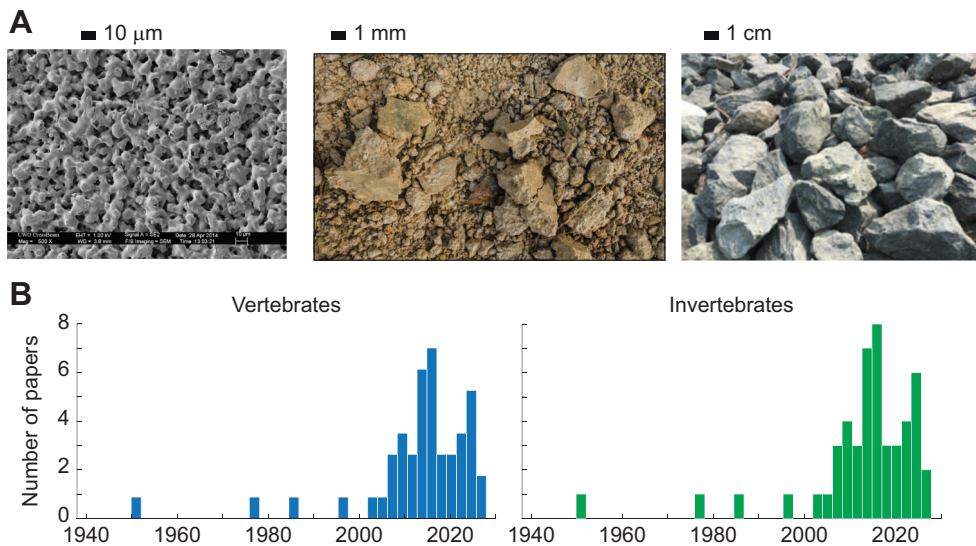


Fig. 1. Examples of substrate roughness in natural substrates and its importance in walking biomechanics studies. (A) Substrate roughness is present across all length scales in natural surfaces. From microscopic roughness (left), intermediate 'ground' scale roughness (middle) and larger scale roughness (right). (B) We reviewed 75 recent comparative biomechanics studies that focus on how roughness influences aspects of locomotion. Here, we plot the number of papers published across vertebrates (left) and invertebrates (right) that study locomotion in the 'ground roughness regime' showing a recent focus on this topic in the last decade. Data available in Table S1.

motion during swing. (3) Lastly, substrate features larger than an animal's body size may not be important from step to step but may instead induce navigational path planning. The behaviours that we mention for each regime are not strictly limited to only that regime. For example, small-scale roughness may destabilize the body, causing a shift in posture, and animals may choose to navigate around animal-scale structures or areas that challenge foot-ground contact (Clifton et al., 2020a). However, it is important to note that these three roughness regimes are not distinguished by an absolute scale and are instead all relative to the animal of study. A stone may be inconsequential to an elephant, but it may be a mountain to an ant. As such, we will advocate for the use of a relative metric of roughness with respect to an animal's size, as detailed in the section below on the 'roughness ratio'.

In this Review, we will summarize current knowledge of walking on rough substrates relating to non-human animals. To enable comparisons across biomechanics research, we seek to provide common terminology and standard metrics for biomechanists interested in studying walking over rough ground. In the first section, we will introduce a non-dimensional metric of roughness (normalized to animal size) to classify roughness into three regimes and facilitate comparison of walking biomechanics across systems and scales. We will then review the common methods and technologies used to quantify roughness. The following three sections review literature related to walking over rough terrain with surface features separated into three general regimes: (1) much smaller than the foot, (2) approximately body scale and (3) much larger than the body. Lastly, we conclude with a discussion of future opportunities and challenges in studying walking over rough substrates.

Understanding locomotion over rough substrates: tools and techniques

Studying walking on rough surfaces requires the ability to measure and quantify substrate roughness in natural environments and fabricate rough surfaces to use in laboratory settings. In this section, we will define a scale-independent metric for describing rough substrates, κ , and review common methods for measuring roughness across scales.

The roughness ratio: a metric for comparative biomechanics of walking on rough substrates

For an animal walking on non-flat terrain, the impact of substrate roughness depends at least on the body size, morphology,

physiology, and behavior. We propose that geometric scaling analysis can provide a quantitative characterization of the relative roughness, facilitating comparison among animals and conditions.

Two systems are geometrically similar if lengths a and b in systems 1 and 2 obey the equation, $\frac{a_1}{b_1} = \frac{a_2}{b_2}$ (Schmidt-Nielsen and Knut, 1984). Typically, comparisons of geometric ratios are made between two length/area/volume measurements of morphological features, for example, the ratio of leg length versus body length compared across different animals (Biewener, 2005; Pontzer, 2007). Geometric theories have been applied to 3D substrates such as the geometric self-similarity of surfaces (i.e. fractals) (Morse et al., 1985; Chakerian and Mandelbrot, 1984), and in the 'size-grain hypothesis', arguing that smaller invertebrates experience 'rougher' substrates (Kaspari and Weiser, 1999, 2007). In this Review, we advocate extrapolating this approach to studies of animal walking on non-flat terrain by calculating a scale-independent roughness ratio, κ .

For any animal, we can define a characteristic body dimension, l_{animal} , relevant for walking (Fig. 2A). We propose using standing hip-height because it provides the approximate scale of average step length and foot-ground contact size across a wide range of morphologies (see Box 1 for further discussion). Similarly, we can define a characteristic dimension of substrate roughness, $l_{\text{substrate}}$, which can be measured and quantified by the methods like those described in the sections below (see Box 2 for further discussion). To systematically study how animals contend with roughness, we introduce the roughness ratio, κ :

$$\kappa = \frac{l_{\text{substrate}}}{l_{\text{animal}}}. \quad (1)$$

This geometric ratio aims to provide a size-independent metric to classify the different regimes of how roughness influences animal walking across different terrains and within and across taxa.

Despite the confounding factors influencing a choice of l_{animal} (See Box 1), we present κ as a dimensionless number that primarily serves to segregate general roughness regimes, and so the value of l_{animal} is most important at an order of magnitude. Dimensionless numbers are useful heuristics in many fields that represent the broad contributions of two opposing factors. The use of dimensionless numbers has been applied to biomechanics numerous times, helping to quantify 'how diverse aspects of

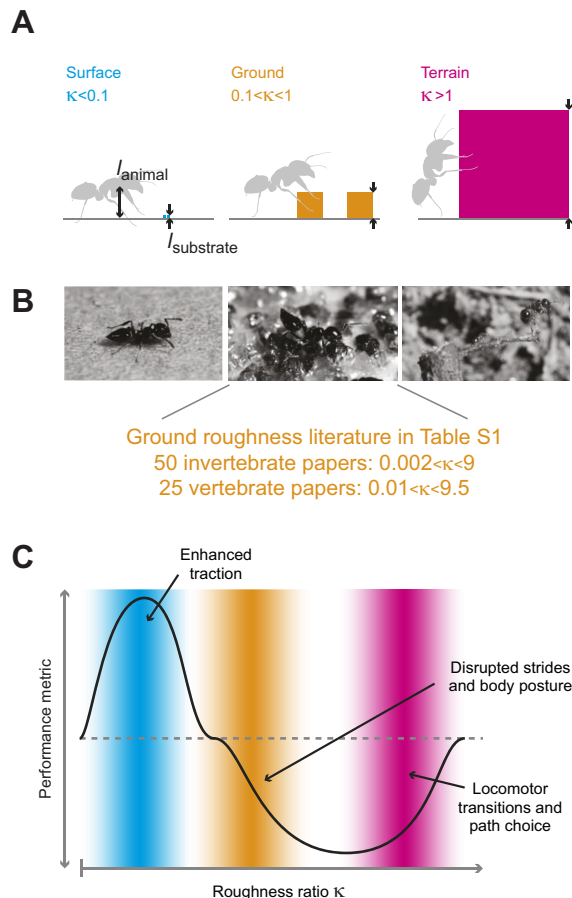


Fig. 2. The relative size of substrate roughness compared with animal size influences locomotion. (A) Substrate features impact walking based on their size relative to an animal. The roughness ratio compares a characteristic length of the substrate roughness to a measure of animal size, for which we suggest hip height. This ratio, κ , can separate the effect of unevenness into three relative regimes: surface, ground and terrain roughness. We examined 50 papers on invertebrates where $0.002 < \kappa < 9$ and 25 papers on vertebrates where $0.01 < \kappa < 9.5$ (see Table S1). (B) Ants change walking speed on sandpapers of different grit sizes, but they must transition to climbing for larger obstacles (left and center from Yanoviak et al., 2017). (C) An example prediction of how roughness might influence walking performance metrics such as speed, stability or energetic cost (inspired by Yanoviak et al., 2017).

distantly related organisms reflect the interplay of the same underlying physical factors' (Vogel, 1998). A key characteristic of dimensionless numbers is that they primarily serve as a general classification instead of a precise quantification. Swimming animals may experience drastically different flow conditions under low Reynolds regimes ($Re < 1$), versus moderate ($Re \sim 10$) or high, ($Re > 10^3$) conditions (Vogel, 2008). These classifications are helpful for contextualizing an animal's swimming behavior. It is within this context that we establish the roughness ratio, κ , and broadly classify the effect of roughness into three regimes. (1) $\kappa < \sim 0.1$, or 'surface roughness', represents ground asperities much smaller than an animal's foot size that influence an animal's capacity to generate adhesive or frictional ground reaction. (2) $\sim 0.1 < \kappa < \sim 1$, or 'ground roughness', may disrupt normal stepping kinematics and destabilize the body. (3) $\kappa > \sim 10$, or 'terrain roughness', cannot be accounted for within one or two steps and instead induces path planning.

The delineations of these classifications are, by necessity, vague. However, specific κ values may prove informative within a regime

Box 1. How to choose l_{animal}

The choice of any consistent l_{animal} poses challenges, although we propose that hip height best balances relevance and ease of calculation. The ideal l_{animal} would directly relate to how an animal contends with terrain asperities, including those much smaller than their foot size as well as obstacles that disrupt stepping. Across broad phylogenetic comparisons, leg length should scale approximately linearly with foot size, with relevance for small-scale ground asperities. However, varying proportions of the limb segments as well as postural variation (e.g. digitigrade vs. plantigrade, crouched vs. erect limbs) may dramatically alter stepping movements for limbs with the same total length (Daley and Birn-Jeffery, 2018). When considering stepping over obstacles, the peak height of the foot during swing phase may best relate to an animal's strategy for coping with disruptions. However, swing height is rarely reported in the literature and may be less informative for the impact of small-scale ground asperities. When considering the horizontal dimensions of an obstacle (such as stepping across gaps), step length or body length may best inform walking strategies, although, again, postural changes will confound these relationships. We encourage the use of hip height during a relevant behavior (e.g. standing, walking, running), as it likely relates to both swing height and leg length (and therefore foot size), plus has already been incorporated in a few studies (Birn-Jeffery and Daley, 2012; Blum et al., 2014). In studies that have already incorporated a version of this metric (such as Birn-Jeffery and Daley, 2012; Blum et al., 2014), step height was varied relative to the measured distance from the hip to the ground at the time of touchdown in running birds. We expect considerable variation in hip height between behaviors (e.g. walking while foraging vs. walking while vigilantly scanning for predators). This anticipated variability and the association of hip height with anatomical or kinematics parameters has not been empirically tested, and we hope that future work will directly explore how measures of body size and posture relate to the effect of roughness.

under controlled conditions, for example, in comparing how various hexapedal insect species shift walking strategies over vertical steps that range in height (Fig. 2A,B). Within these different κ regimes the challenges and affordances of roughness can benefit and hinder locomotion: small scale roughness can enhance foot traction while larger scale roughness can disrupt stance and swing motions (Fig. 2C). We would also like to note that, unlike most of the dimensionless numbers used in biomechanics, κ does not represent the contributions of two competing forces and instead is a ratio of lengths. Thus, two animals of different sizes that experience the same relative roughness (same κ) may have vastly different dynamical factors that influence how they respond.

As part of this Review, we have compiled a database of studies focusing on how roughness influences invertebrate and non-human vertebrate walking, including a report or estimation of κ (Table S1).

Statistical metrics of substrate roughness

In this section, we describe several metrics that can be used to measure $l_{\text{substrate}}$ value. In Box 2 we provide suggestions for best practices in quantifying and reporting statistics of height variation for rough surfaces. If we imagine the x and y axes of a Cartesian coordinate system aligned to lie on a flat plane, then 'roughness' is the variation of the height in the perpendicular direction which we call vertical, $z(x, y)$. Measurements of roughness use a sensor to produce a discretized representation of the surface height, $z(x_i, y_j)$, where the height has been sampled at the points x_1, \dots, x_N and y_1, \dots, y_N (Fig. 3A). Furthermore, it is often the case that a roughness measurement is only performed along a line or transect (Fig. 3B), which may not accurately reflect the full 3D surface. However, these

Box 2. How to choose $I_{\text{substrate}}$

We have provided four statistical metrics which each describe different aspects of a surface's height variation, two metrics for vertical height variation and two metrics for horizontal variation. We advise that as a best practice for biomechanics studies on rough substrates, authors should present information about both the vertical and horizontal height variation using standardized metrics such as provided here.

For vertical height variation we suggest that the RMS roughness metric (R_q) be used for substrates with random height variation, as is present in natural terrain. However, for experiments that focus on a single step/gap obstacle, the maximal height variation metric (R_z) would be appropriate as it captures the exact length scale of the obstacle height (i.e. R_z =the height of the perturbation; Fig. 4B).

For horizontal surface variation both the peak density (S_x) and zero crossing metric (S_0) are well suited for substrates with random height variation, as is present in natural terrain. However, for experiments that focus on single step/gap obstacles, the zero crossing density is more appropriate, as it represents the relative length of the perturbation (i.e. $1/S_0$ = length of the perturbation; Fig. 4D).

In all cases, it is up to the best judgement of each author to determine what are the appropriate metrics required to best convey the details of surface roughness. If additional roughness statistics are required, detailed formulas and their interpretation can be found in Bhushan (2000).

simplified transects enable quantification using relatively straightforward metrics (see below). It should be noted that there is not necessarily a 'best' metric; instead biomechanists interested in how roughness influences locomotion should choose and report multiple metrics that are the most relevant for their particular hypothesis or study.

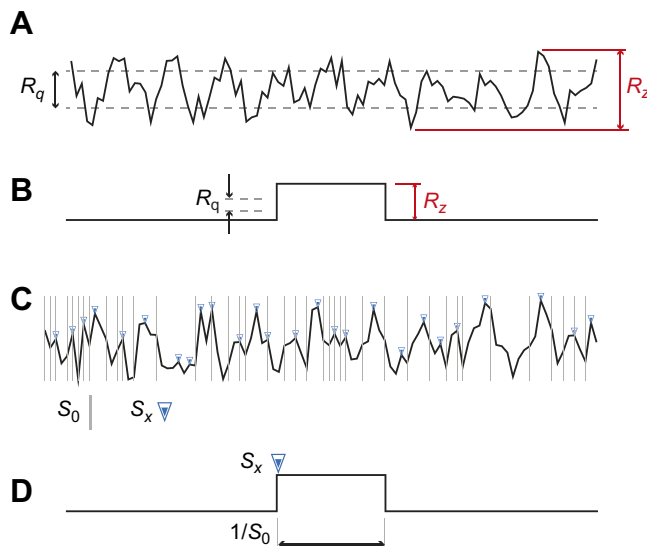


Fig. 3. Examples of the roughness metrics introduced. (A) A natural surface has random vertical height variation. The root-mean-square (RMS) height variation R_q is suitable for capturing the statistical variation in height. R_z measures the maximum absolute height. (B) The maximal height variation R_z is well suited to characterize single obstacles, while R_q is not as informative. (C) To quantify height variation along the horizontal direction, the peak density (S_x) and the zero crossing density (S_0) are both useful metrics. Arrows show locations of the 26 peaks for this surface. Gray lines show the 40 zero crossings. (D) The zero crossing density S_0 is well suited to characterize single obstacles or periodic patterns, whereas S_x may not be as informative. The inverse of the zero crossing density is the mean length between zero crossings of the surface.

Roughness measurements fall into two categories: (1) vertical variation in height and (2) horizontal spacing of height variation. Below we provide two recommended metrics for both vertical and horizontal roughness statistics (for more statistics of roughness, see Bhushan, 2000). For vertical height variation, we suggest using root-mean-square height (RMS) variation, R_q , and maximal height variation, R_z :

$$R_q = 2 \sqrt{\frac{1}{N} \sum_{i=0}^N (z(x_i) - \bar{z}(x_i))^2}, \quad (2)$$

$$R_z = \max(z(x_i)) - \min(z(x_i)), \quad (3)$$

where $\bar{z}(x_i)$ is the mean of the surface height. R_q describes the vertical variance of the surface, while R_z provides a direct measurement of the maximal roughness present (Fig. 3A). Both metrics together provide useful – and complementary – information about the surface profile (see Box 2).

Surfaces can have the same vertical height variation statistics, while having very different actual surface profiles. For example, the profiles $z(x)=\sin(x)$ and $z(x)=\sin(100x)$ have the same R_z and R_q , while having very different peak spacing properties. Thus, measurements of substrate roughness should also report horizontal spacing statistics of the surface profile. Here we present two roughness horizontal metrics. The peak density, S_x is the number of peaks per unit length (Fig. 3C). Surfaces with high peak density have many closely spaced peaks. The inverse of peak density, $\frac{1}{S_x}$, provides a characteristic horizontal length scale for substrate roughness. Next is the zero-crossing density, S_0 , the number of times the surface height crosses the average height line per unit length (Fig. 3C). While S_x gives information about typical peak spacing, many peaks can be adjacent to each other without deep valleys in between, therefore not representing a large change in the overall height profile.

Experimental methods to quantify substrate roughness

The experimental determination of roughness broadly falls into three categories. (1) Tactile-based sensing where an object is in contact with a surface to measure height deviation. (2) Passive imaging using multiple cameras and the surface profile is rendered from computer vision techniques. (3) Active imaging where a laser or some other light source is pointed at the surface, and the light reflected by the surface is used to calculate the surface profile. These approaches have different spatial resolutions, fields of view, and height resolutions.

Tactile-based sensors measure roughness with a 'stylus' in contact with the surface (much like the needle of a record player) to scan the area of interest (Bhushan, 2000; Hizioglu, 1996; Poon and Bhushan, 1995). The resolution of tactile approaches is affected by two main quantities: the range of vertical motion constrains the maximal height variation measurable, and the sharpness of the stylus limits the measurable gaps and therefore minimal height variation. Because of its small working range, this approach is only common for measuring the nano- and microscopic properties of surfaces. For larger distance tactile-based measurements geologists have used a contour gauge, which is a series of rods that conform to the profile of a surface (see Fig. 3C; Shepard et al., 2001). A limitation of tactile-based approaches is that the measurement is fundamentally one-dimensional since the stylus is moved along a path.

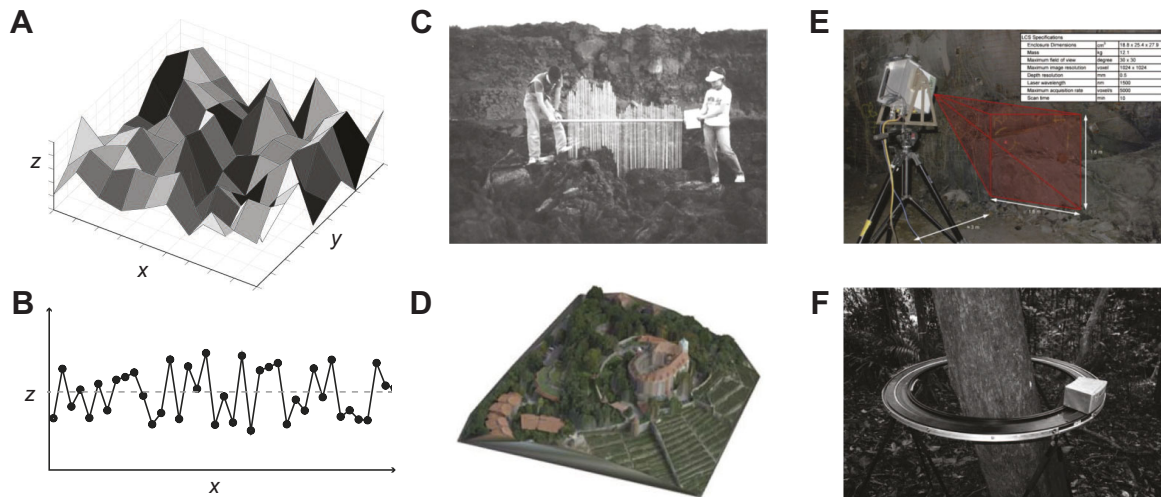


Fig. 4. Methods for measuring roughness of natural substrates. (A) A computer rendering of a 2D scan of surface height $z(x,y)$. (B) A surface height profile constructed by plotting the surface height along a specified (x) direction of the 2D surface. Gray dashed line is the mean value of the surface, $\bar{z}(x)$. Points represent the discrete locations that the surface height is sampled. (C) Geological measurement of roughness using a simple, tactile based profilometer device (reproduced from Shepard et al., 2001). (D) Reconstruction of surface profiles through photogrammetry (Rothermel et al., 2012). (E) Laser scanning of surfaces can directly measure roughness parameters (reproduced from Mah et al., 2013). (F) Measurements of the surface profile of tree bark by a laser profilometer for ant climbing biomechanics study (Yanoviak et al., 2017).

Passive imaging methods rely on using camera images of the surface to reconstruct the 3D profile (Rothermel et al., 2012). Here, we focus on techniques that attempt to directly reconstruct the 3D surface. There are also imaging methods that provide statistical properties of the surface (e.g. specular reflection Bennett and Porteus, 1961), but without quantifying the surface profile.

Images from two or more calibrated cameras can be used to determine the (x,y,z) spatial location of an object (Hedrick, 2008). These methods have been extended to the reconstruction of entire surfaces in a process often referred to as photogrammetry (Mikhail et al., 2001). Surface reconstruction from photogrammetry (referred to as structure-from-motion; Westoby et al., 2012; Smith et al., 2016; Fonstad et al., 2013) can involve images captured from multiple cameras simultaneously or from a single moving camera. A photogrammetry algorithm matches features of the surface across the images to estimate the 3D surface shape (Fig. 3D). These methods have been predominantly used to reconstruct surface profiles at the centimeter to meter scale, typically in geological studies (Rieke-Zapp et al., 2001; Rothermel et al., 2012; Butler et al., 1998; Westoby et al., 2012; Smith et al., 2016; Fonstad et al., 2013). Surface reconstruction from photogrammetry is popular owing to the accessibility of using only a single camera and open-source software (Falkingham, 2012).

Photogrammetry struggles to reconstruct smaller scale surface profiles (e.g. $\approx 1 \mu\text{m}$) since small lenses limit depth of field and light levels. The more common approaches for passive imaging of microscale features include scanning electron microscope (SEM) imaging and confocal microscopy. However, SEM imaging cannot be directly used to reconstruct the height profile of a surface much like a single overhead picture cannot generate a height profile (Marinello et al., 2008). Confocal microscopy can directly measure the height profile by scanning the focal plane of the microscope along the vertical direction (z -axis) and observing the features in focus (Lange et al., 1993; Udupa et al., 2000).

Active imaging methods use special light sources, sensors, and non-optical methods for surface measurement. The most common active imaging method for surface reconstruction uses a laser line

swept across a surface (Fig. 3E,F) and recorded by a camera from an oblique angle. This method has been used in geological research to reconstruct surfaces from the millimeter to meter range (Mah et al., 2013; Buckley et al., 2008; Roman et al., 2010; Fardin et al., 2004; Mills and Fotopoulos, 2013; Van Stan et al., 2010). One such example in the context of biomechanics is the use of a laser scanner (Van Stan et al., 2010) to characterize tree bark roughness (Fig. 3F) in a study of ant walking over natural and artificial roughness substrates (Stark et al., 2018).

Laser-scanning-based surface measurements have several limitations. First, the surface must reflect the laser light and the surface features of interest must be wider than the laser width. Second, concave surface features may shadow the laser from the camera's view. Similarly, if the vertical direction of the surface being imaged is at a right angle to the camera's line of sight, the reflected light cannot be imaged.

For centimeter- to meter-scale surfaces, another common method is LIDAR or 'light detection and ranging'. This method uses measurements of reflected light to construct surface profiles. However, LIDAR differs from the previously described laser scanning systems because LIDAR systems measure reflectance and time-of-flight properties of the reflected light to generate a surface profile. LIDAR systems have also been used in geology to reconstruct large-scale surfaces (Pollyea and Fairley, 2011; Glenn et al., 2006; Puente et al., 2013).

'Surface roughness' regime ($\kappa \sim 0.1$)

When walking organisms experience roughness at the small scale (i.e. horizontal lengths smaller than foot size), variation in surface asperity size directly impacts foot-ground contact mechanics (Fig. 5A). However, not all feet are equal. Many organisms employ attachment and adhesive systems to maintain secure contact with the rough substrates they walk across (Gorb, 2008; Ji et al., 2011; Chan and Carlson, 2019). While there are many types of adhesive and attachment mechanisms used by animals, walking organisms must detach their feet each step, so we will only focus on systems that are temporary (i.e. not permanent or transitory; Gorb, 2008).

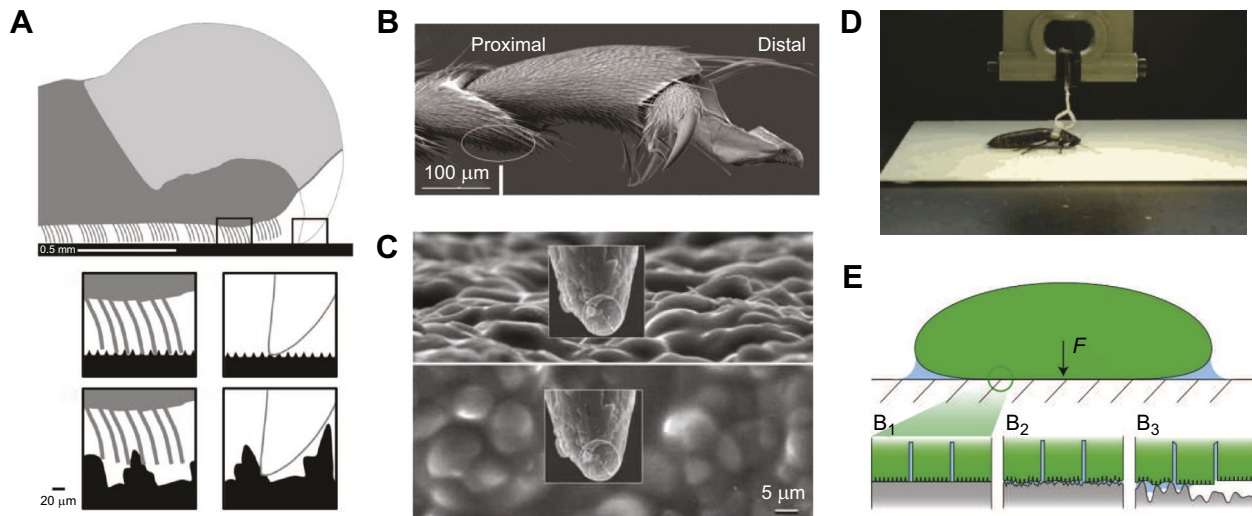


Fig. 5. Surfaces with roughness at small scale ($\kappa < 1$) influence the traction force animals can exert on the ground. (A) An overview of how different elements of the lizard (geckos, anoles) foot engage with different sized roughness features (reproduced from Naylor and Higham, 2019). (B) Tarsus and hairs on the underside of the tarsus are used to generate high friction in Weaver ants (*Oecophylla smaragdina*) (reproduced from Endlein and Federle, 2015). (C) Scanning electron micrograph images of rough surfaces with the claw tip of the beetle *Pachnoda marginata* overlaid at scale for comparison (reproduced from Dai et al., 2002). (D) Measurement of surface adhesion by the Madagascan hissing cockroach, *Gromphadorhina portentosa* (reproduced from van Casteren and Codd, 2010). (E) Schematic of proposed role of substrate friction (F) on capillary adhesion in tree frogs. As surface roughness increases (B_1 – B_3), the fluid wetting properties change from full coverage contact (left) to intermittent capillary bridging (right) (reproduced from Langowski et al., 2018).

Most studies testing adhesive or attachment on rough surfaces measure the forces produced when an organism is pulled perpendicular from a substrate (i.e. normal pull-off force) or slid tangentially across a substrate (i.e. shear sliding force). These investigations are most directly related to organisms clinging to a substrate as observed during predator-prey interactions or territorial disputes. A much smaller subset of studies explore how small-scale roughness impacts attachment and detachment while moving. All attachment and detachment forces depend on the type of contact made by the feet or smaller structures on the feet (e.g. wrinkles, claws), the directionality of these anatomical features, and the length-scale of substrate roughness. Here we focus on foot-ground contact mechanics on rough substrates by categorizing the ways feet can generate traction against a substrate. These include: (1) continuous frictional contact; (2) non-continuous contact via projections on the feet (e.g. wrinkles, claws, fibrils); (3) continuous fluid contact; and (4) a combination of some or all of the above (Gorb, 2008; Ji et al., 2011; Chan and Carlson, 2019). We will highlight relevant examples of both the adhesive and/or attachment performance and walking performance on small-scale rough substrates. We define attachment as mechanical interlocking, and adhesion as non-mechanical interlocking mechanisms (e.g. glue, attractive forces, friction).

Continuous friction contact

When walking with a flat foot or structure on the foot (e.g. the relatively smooth sole of a human foot), foot-ground contact mechanics are driven by friction. When walking, an organism applies force to the ground and force is returned in both the vertical and tangential directions (Cooper et al., 2008). The ratio of the force resisting the movement between two solid objects and the normal force applied to press them together is the coefficient of friction (μ ; where $\mu = \text{frictional force} / \text{normal force}$).

The coefficient of friction is related to a variety of properties specific to the two solids in contact (e.g. material structure and composition, compliance and viscoelasticity, and surface roughness

Tramsen et al., 2018). On natural surfaces with roughness, the coefficient of friction is higher than smooth surfaces, and walking becomes more stable. This is why when roughness decreases, organisms tend to slip and even fall (i.e. coefficient of friction falls below the minimum required to maintain stable limb-ground contact; Clark and Higham, 2011). Some animals possess special foot structures, like the soft pads of Weaver ants, to increase friction (as well as adhesion) on smooth surfaces (Fig. 5B). However, there is a limit to the frictional benefits of roughness, and this is reached when asperity size approaches either very small (i.e. nearing smooth surface contact mechanics that lead to slipping) or very large scales (i.e. creating gaps that disrupt foot-ground contact).

When locomoting on smooth substrate surfaces, organisms such as birds risk reaching the minimal slip distance to induce falling (Clark and Higham, 2011); for example, helmeted guinea fowl that slip for ≈ 10 cm are highly likely to fall (Clark and Higham, 2011). The frequency of slips on the smooth substrate depends on locomotor kinematics such as limb angle and speed when encountering the low-friction substrate, where higher angles and speeds prevent more slips (Clark and Higham, 2011). Although it is not fully understood, it is likely that increased speed and limb angle changes the critical interplay between center of mass (COM) and base of support (BOS). Specifically, falls occur when COM does not cross BOS during ground contact. At higher speeds, COM may move faster during the stance phase to move past the BOS and either maintain or quickly regain balance on low friction substrates. Similarly, changing the limb angle can help with the interplay between COM and BOS. Thus, larger-scale processes like kinematics (e.g. changes in speed, limb angle) may serve an important compensatory function when using continuous frictional contact on substrate surfaces with small-scale roughness.

Non-continuous projection contact

While continuous frictional contact is nearly universal, some organisms ‘fill the gaps’ that small-scale surface asperities leave, by using foot structures that functionally increase the size of the foot,

change foot–ground contact mechanics on rough surfaces (Arzt et al., 2003), or increase attachment forces via mechanical interlocking (Fig. 5B). Some organisms use non-continuous contact between small foot projections that take advantage of the increased surface area that asperities provide (i.e. they contact the sides and/or tops of surface asperities). These structures are generally fibrillar in nature (though there are some examples of wrinkles; Williams and Peterson, 1982). Performance of fibrillar projections on rough substrates is dependent on size and compliance of the fibrils (Spolenak et al., 2005; Persson and Gorb, 2003; Persson, 2007a). Organisms such as geckos and spiders use dry fibrillar contact to adhere to rough substrates (Arzt et al., 2003; Kesel et al., 2003). In geckos, adhesive performance is significantly related to small-scale roughness that is near the size of the tips of their fibrillar contacts (i.e. spatulae on the tips of setae). Here, roughness asperities that are near the size of the ≈ 200 nm wide spatulae produce the lowest adhesive pull-off force because only partial contact is formed, whereas on near smooth substrate surfaces, there is more contact with the spatulae and on rougher substrates the spatulae can conform to the sides of the asperities (Huber et al., 2007). The same result was found in spiders (Wolff and Gorb, 2012). Unfortunately, walking performance of geckos or spiders on small-scale rough substrates has not been tested, although see Palecek et al. (2022) for more detailed exploration of small-scale roughness and gecko attachment.

Larger foot projections (e.g. claws, claw-like structures, stiff tarsal hairs on ant feet Endlein and Federle, 2015) are commonly used for climbing (which we will not focus on in this Review); however, they also interlock with horizontal surface asperities (Chan and Carlson, 2019) (Fig. 5D) to increase traction. Performance of claws and claw-like structures is dependent on curvature and tip size (Patrick et al., 2018; Zani, 2000). Specifically, claws must be curved to reach the substrate surface and tapered enough to interlock with surface asperities. For example, in beetles, friction force during walking depends on surface asperity size and the diameter of the claw tip (Dai et al., 2002). Specifically, when substrate surface asperities were larger than the claw tip, interlocking occurred. However, when surface asperities were smaller than the claw tip diameter, friction between the claw and substrate dominated (Dai et al., 2002).

Continuous fluid contact

Some organisms (including beetles, ants, frogs) use fluid to fill the gaps between surface asperities to increase the surface contact area (Fig. 5E). These animals may either secrete a liquid or take advantage of a moist environment to create a capillary-like bridge (Chan and Carlson, 2019). A key component of continuous fluid contact is substrate wettability. Specifically, the more the fluid wets or spreads across a substrate (e.g. water spreading across a hydrophilic substrate), the more capillary-like pressure, and thus adhesion, is produced (Chan and Carlson, 2019). Wettability of the substrate is also important when the substrate is rough, where more wettable substrates will help fluid spread across and fill gaps within surface asperities (Chan and Carlson, 2019). The fluid itself is not necessarily water in these systems, and thus surface tension of the fluid also impacts the capillary pressure (Chan and Carlson, 2019). For tree frogs contacting small-scale roughness with fluid-based adhesive pads, adhesion is significantly better on substrates with small surface asperities than on those with larger asperities (e.g. 5 μm vs. 500 μm ; Crawford et al., 2016). This difference is likely due to limits on fluid production, as insufficient fluid will produce adhesion-disrupting air pockets on large surface asperities.

Studies have used artificial frog-inspired materials and theoretical predictions to understand the ability to self-clean and preserve adhesive fluid and/or remove excess fluid in channels (Persson, 2007b; Langowski et al., 2018; Crawford et al., 2012). However, there has been no direct work comparing adhesion results on rough substrates and walking performance.

Mixed contact

Most organisms use a combination of two or more of the aforementioned contact structures to interact with rough substrates. Most commonly, frictional, fibrillar or fluid-flooded foot pads are used along with hooked claws. Depending on the size of these structures, we would expect this foot structure diversity to enable secure walking across a broader range in small-scale surface roughness (e.g. nanometer, micrometer and/or millimeter asperities). Work directly comparing adhesive/attachment performance with locomotor performance on rough substrates is rarely done. However, for ants that use smooth adhesive pads coated in a glue-like secretion paired with interlocking claws, adhesive and attachment performance does not predict performance metrics such as speed (Stark and Yanoviak, 2020). Specifically, when measured statically, shear and normal adhesive and attachment forces produced by ants were low and even zero on very fine grit sandpaper substrates (e.g. $l_{\text{substrate}} < 0.1$ mm asperity size, $\kappa < 0.1$) and smooth glass. But, observed running speeds were only significantly reduced on smooth glass and slightly reduced on rougher sandpaper substrates (e.g. $l_{\text{substrate}} > 0.5$ mm asperity size, $\kappa \approx 0.3$; Stark and Yanoviak, 2020). Similar results were found in geckos, where claw removal significantly impacts adhesion but not running speed on substrates that varied in small-scale surface roughness (Naylor and Higham, 2019). Results from these studies suggest that adhesive and attachment performance does not accurately predict locomotor performance on rough substrates. Unfortunately, most studies only report static clinging performance. We suggest that clarifying work is necessary across all foot–ground contact mechanisms to determine how adhesion and attachment relates to locomotor performance on rough substrates.

'Ground roughness' regime ($\sim 0.1 < \kappa < \sim 1$)

When terrain complexity arises from ground roughness at scales between approximately foot size and body size, it challenges walking animals to: (1) actively or passively secure good footholds; (2) avoid, accommodate, or leverage limb and body collisions with the ground to maintain propulsion and stability and reduce resistance; or (3) use instability from limb/body–terrain interaction, or even deliberately adjust the limbs and body, to transition to other locomotor modes. Although there is no exact delineation of what corresponds to ground (versus surface or terrain) roughness, we posit that this range generally corresponds to terrain features that influence walking within one or a few strides.

Ground roughness has been examined mainly by exposing walking animals to individual obstacles, often gaps or steps (Fig. 6A–C). These individual obstacles help reveal the neuromechanical control principles underlying locomotion, by incorporating localized disruptions of steady walking patterns. A few studies have incorporated continuously rough substrates more reminiscent of natural terrain (e.g. a boulder field, Collins et al., 2013; rough large blocks, Sponberg and Full, 2008; dense vegetation, Li et al., 2015; Fig. 6C,D). A growing body of work addresses roughness at the upper edge of medium scale by incorporating cluttered large obstacles (e.g. grass-like vertical beams; Li et al., 2015; Othayoth et al., 2020; Wang et al., 2022)

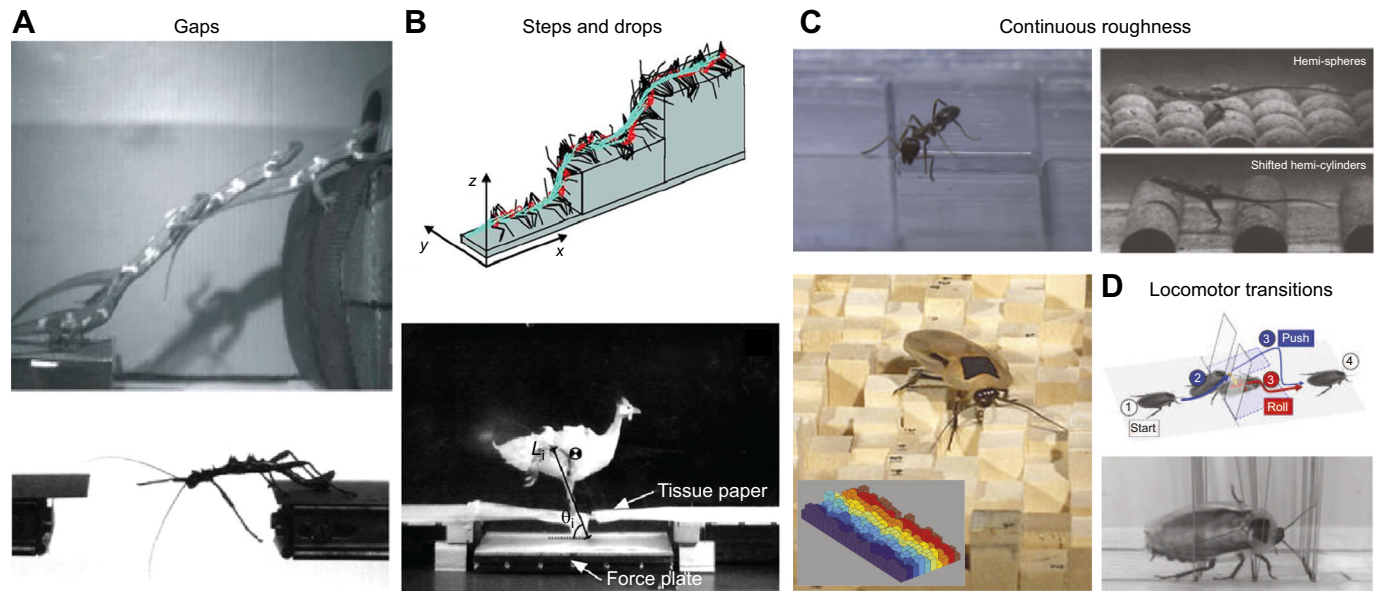


Fig. 6. Medium-scale ground roughness influences walking within one or a few steps. (A) To cross gaps, some animals use jumping or inertia (top) (Libby et al., 2012), while others cantilever their body and target the limbs to find a secure foothold (bottom) (Blaesing and Cruse, 2004). (B) Step climbing can include visual perception and tactile exploration in stick insects (top) (Theunissen et al., 2014). Surprise drops can reveal neuromechanical control principles in guinea fowl (bottom) (Daley et al., 2007). (C) Continuously rough terrain has been tested more broadly in invertebrates than in vertebrates. Manufactured checkerboards constrain ant walking speeds (top left) (Clifton et al., 2020a). Wooden blocks challenge cockroach running (bottom left) (Sponberg and Full, 2008). Spherical obstacles require bipedal lizards to use upright hindlimb postures (right) (Druelle et al., 2019a). (D) When confronted with large obstacles, cockroaches may choose to transition among locomotor modes (Li et al., 2015; Othayoth et al., 2020).

that force animals to transition among locomotor modes (e.g. from running to pushing across and climbing over obstacles or rolling through gaps between obstacles; Li et al., 2015; Othayoth et al., 2020; Wang et al., 2022). Numerous studies have observed animals on a ‘flat’ but inclined surface (including vertical and inverted surfaces). While these surfaces may destabilize the body and induce kinematic changes, slopes do not variably restrict foot placement or induce limb collisions in the same manner as more discrete or undulant changes in ground height. Thus, we will not consider inclined walking further in this review.

Walking animals move through a 3D world, which can generally be separated into upward, z , and longitudinal (fore–aft, x , and lateral, y) directions in an animal’s instantaneous body frame. For simplicity, here, we focus on straight walking in cephalized animals, and we define upward and longitudinal components of roughness relative to an animal’s neutral standing position.

With these definitions, all ground roughness involves variation in the substrate along the upward axis of the body frame. Some studies on medium-scale roughness focus only on this upward component (e.g. a single step of varying height; Ritzmann et al., 2012; Gart et al., 2019; Yuan et al., 2022), while others also incorporate a forward dimension (e.g. gap length; Blaesing and Cruse, 2004; Gart et al., 2018). However, natural terrain has structures that vary in upward, forward and lateral axes. Upward components of ground roughness induce body pitching and rolling, as well as requiring shifts in relative foot placement and, in some cases, swing phase kinematics. Ground roughness in the forward and lateral directions also influence foot placement, with the forward component especially disrupting step length and both the forward and lateral components disrupting step stability. The complexity of non-flat terrain and the behavioral variability of animals can easily eclipse this simplified conceptual approach. Indeed, in many natural environments, it is difficult to even identify an animal’s neutral standing position. Despite these

complexities, we encourage studies, especially those using engineered uneven substrates, to explicitly consider, control, vary, and communicate the relevant directional components of roughness.

In the remainder of this section, we will review the literature known to date that study animals walking across gaps, steps, or on continuously rough terrain.

Gap crossing

Gaps represent discontinuities in terrain with a vertical drop greater than an animal’s limb or body length. Crossing gaps plays a crucial role in arboreal locomotion, with animals reaching, jumping or flying among support structures (Graham and Socha, 2020). For terrestrial locomotion, most studies on vertebrates use gaps with horizontal distances greater than several step lengths, which induce jumping (Hunt et al., 2021; Astley et al., 2015; Green et al., 2022; Libby et al., 2012). Crossing gaps with horizontal scales less than the body length has primarily been studied in invertebrates. These studies can be broadly separated into two categories: (1) animals walking at relatively slow speeds using limbs or antennae that collect sensory information for pre-planning, and (2) faster animals without distinct stages of sensory planning.

When confronted with a gap, slower moving invertebrates may visually determine if the gap is traversable (Pick and Strauss, 2005) or induce searching movements with the antennae and limbs (Pearson and Franklin, 1984; Dürr, 2001; Bläsing and Cruse, 2004; Blaesing and Cruse, 2004) (Fig. 6A). Some locust species may visually target their limbs to secure footholds across the gap (Niven et al., 2012; Bell and Niven, 2016). Several studies measure limb coordination during gap crossing to reveal neural control patterns, such as in fruit flies and stick insects (Triphan et al., 2010; Bläsing, 2006). In contrast to slower, sensory-driven gap crossers, rapidly running cockroaches use kinetic energy to bridge large gaps without pre-planning (Gart et al., 2018). While research

surrounding fast traversal of gaps remains limited, studies that limit foothold locations may provide complementary insight. Spiders, cockroaches, and crabs successfully run across substrates providing only sparse foothold locations (e.g. a wire mesh) by altering limb kinematics to exploit distributed structures on the limbs (e.g. hairs, spines) that passively ensure secure foot–substrate contact (Spagna et al., 2007). These studies suggest that fast running animals may successfully cross gaps without planning by relying on embodied strategies and specialized anatomical structures. However, it should be noted that all of the animals studied above: are relatively small, making them less susceptible to damage from falling (Haldane, 1928) and typically contact the ground with more than two limbs at any time, providing a statically stable support polygon.

Step climbing

A discrete vertical change in terrain height may represent a step (up or down) or a bump (one step up then down), with multiple changes acting as a ‘staircase’. Step obstacles are easily manufactured and provide a predictable change in terrain relative to the direction of animal movement, therefore serving as a convenient method for introducing terrain complexity. Also, because steps are common in the engineered world, understanding step climbing provides inspiration for robotics and human rehabilitation (Bouman et al., 2020; Kannape and Herr, 2014). Most studies focus on rectangular steps, though some involve log-like circular steps. In this review, we will discuss step traversal for invertebrates and vertebrates separately.

How insects climb steps has mostly been studied in slow, sensory-dominated locomotion. These insects often adjust kinematics only after direct contact with the obstacle. Argentine ants do not decelerate until their antennae touch a step (Clifton et al., 2020b). In cockroaches, the distance at which they begin ‘high-stepping’ with the forelimbs depends on antennae length (Harley et al., 2009). Once an obstacle has been detected, cockroaches and stick insects investigate the new surface using their forelimbs (Theunissen et al., 2015) or antennae (Ritzmann et al., 2012). The decision to climb a step may depend on environmental cues, such as light level (Ritzmann et al., 2012), as well as body posture and antenna position right before contact. To climb a staircase, stick insects coordinate foot touchdown placement (Theunissen et al., 2014) and take shorter steps (Theunissen and Dürr, 2013) (Fig. 6B). Experiments across several insect species (including stick insects, cockroaches and caterpillars) show that step climbing success depends on proprioceptive hairs on the limbs (van Griethuijsen and Trimmer, 2010; Theunissen et al., 2014) and is modulated by localized brain regions (Harley and Ritzmann, 2010).

Fewer insect studies have investigated climbing steps at high speeds. Rapidly running tiger beetles hold their antennae rigidly forward to detect steps and quickly pitch up the body in response (Zurek and Gilbert, 2014). Running cockroaches can use kinetic energy to overcome a step’s potential energy barrier by transitioning from running to climbing (Gart and Li, 2018). However, as the step becomes higher, cockroaches become increasingly unstable in the yaw direction, making it more likely to fall off the step (Gart and Li, 2018).

Altogether, these insect studies have examined relatively few species. Because even closely related species may vary in step-climbing tactics (Theunissen et al., 2015), there is ample opportunity for comparative investigation of step climbing across invertebrates.

The great majority of research on step obstacles in vertebrates focuses on birds and bipedal lizards, which, unlike insects, lack

static stability and proprioceptive antennae. For a review of how birds adjust kinematics and muscle function when approaching, traversing and recovering from a step, see (Daley, 2018). These studies on birds incorporate both perceived steps, through visible detection (Birn-Jeffery and Daley, 2012) or training (Daley and Biewener, 2011) and unexpected sudden drops to a lower surface (Daley and Biewener, 2006; Daley et al., 2006, 2007). To summarize briefly, guineafowl adjust for stepping down based on the hindlimb’s orientation at the time of touchdown (Daley and Biewener, 2006), shifting limb kinematics to reduce limb loading even though it disrupts the center of mass dynamics (Blum et al., 2014) (Fig. 6B). The changes in limb behavior while crossing a step obstacle are controlled by shifts in the function of distal limb muscles, which both react to unexpected step perturbations (Daley et al., 2009) and pre-activate in advance of a known obstacle (Daley and Biewener, 2011). While most of these papers focus on guinea fowls, other tested species include quail (Andrada et al., 2022), pheasants (Birn-Jeffery and Daley, 2012) and ostriches (Birn-Jeffery et al., 2014). Despite ranging in size and limb posture, all species vault over steps to prioritize energetic efficiency (Birn-Jeffery et al., 2014). These studies are relevant for understanding human walking, especially as some directly measure muscle function (e.g. sonomicrometry) and manipulate innervation (Gordon et al., 2020).

Lizards running over step obstacles benefit from a bipedal hindlimb posture, which enables greater hip range of motion and, consequently, only a minor reduction in running speed (Olberding et al., 2012; Parker and McBrayer, 2016). Quadrupedal lizards are more impacted by step obstacles, using their forelimbs as levers to hoist themselves on to taller obstacles (Kohlsdorf and Biewener, 2006). However, as step obstacles get taller, lizards transition from running to vertical climbing by jumping, which enables the lizards to maintain faster approach speeds (Tucker and Mcbrayer, 2012; Yuan et al., 2022). Outside birds and lizards, the only vertebrates analyzed while walking over step obstacles are a rat species (Sato et al., 2012), which shift the preceding step placement and timing and then increase swing height to avoid the obstacle.

Negotiating continuous roughness

Natural terrain rarely consists of near flat ground with interspersed, discrete asperities. Instead, substrates in the wild often include continuous fluctuation in ground height. Most walking studies that incorporate continuous roughness expose animals to qualitatively different materials (e.g. various sandpapers, sand vs. gravel), with some quantification of these substrates (e.g. particle diameter). However, relatively few studies directly manufacture and vary 3D terrain features.

Most vertebrate studies of walking on substrates with qualitatively different roughness tested animals in the field. Lizard species that live in rocky terrain are less influenced by roughness compared with sand-dwellers (Collins et al., 2013). Dogs running on different fields (mowed, tall and cow-trodden grass) shift towards trotting gaits, which increase stability, but otherwise do not increase limb phasing variability (Wilshin et al., 2017, 2021). In contrast, studies in vertebrates that directly control and quantify roughness have only been performed in lizards using cylinders or hemispheres (Fig. 6C). Lizards running on more complex terrain assume upright limb postures (Druelle et al., 2019a; Crockett, 2017), which is better achieved by species that are running specialists (Druelle et al., 2019b). These studies show that naturalistic terrain with continuous roughness significantly influences walking patterns across species, shifting control to favor greater range of motion or increased stability.

Compared with vertebrates, far more studies have been conducted on invertebrates walking over continuously rough terrain, probably because of their easier upkeep in labs and relatively lenient institutional care. Many of these studies measure average speeds in ants walking on qualitatively different terrains, by varying sand/gravel particle size (Bernadou and Fourcassié, 2008; Bernadou et al., 2011; Grevé et al., 2019) and using engineered materials (Czaczkes et al., 2018; Yanoviak et al., 2017; Stark and Yanoviak, 2020; Oettler et al., 2013). It is no surprise that ants slow down on rougher terrain, but these substrates also reduce seed harvesting efficiency (Crist and Wiens, 1994; Bernadou et al., 2011) and induce higher pheromone deposition rates (Czaczkes et al., 2018). Importantly, several field studies directly associate roughness-induced speed restrictions to path planning. Ants use branches as detours over leaf litter (Loreto et al., 2013), detect food sources sooner on vines compared with bark (Clay et al., 2010) and prefer setting up foraging trails on engineered flat versus checkerboard substrates (Clifton et al., 2020a). These studies directly connect walking biomechanics on rough terrain to ecological patterns, animal behavior and species distributions.

A growing body of work on invertebrates uses manufactured terrain with specified roughness parameters (Fig. 6C). Some of these studies focus on vertical variations in ground height (Sponberg and Full, 2008; Diaz et al., 2023), others vary the horizontal spacing of terrain features (Kress and Egelhaaf, 2012; Clifton et al., 2020b) and yet another couples the vertical and horizontal components by randomly distributing spheres of varying sizes (Li et al., 2013). Most of these papers track instantaneous speed, and in some cases, 3D limb kinematics. However, diversity in test species (cockroaches, ants, crabs and centipedes) and terrain type limits the identification of conserved patterns. Cockroaches running on blocks that have Gaussian-distributed heights do not adjust limb phasing or foot placement on a step-to-step basis (Sponberg and Full, 2008), although centipedes on a similar substrate reverse the wave-like coordination of their limbs (Diaz et al., 2023). Crabs walking on rough terrain shift from a coordinated alternating-tetrapod gait to random limb coordination (Li et al., 2013), but ants walking on checkerboards mostly maintain regular stepping (Clifton et al., 2020a). Yet, across several species and terrain types, the limbs were observed to passively maneuver past collisions with substrate structures (Diaz et al., 2023; Sponberg and Full, 2008; Clifton et al., 2020a), suggesting a potentially conserved strategy for invertebrates to successfully navigate over continuously rough terrain.

Transitioning among locomotion modes

Obstacles at sizes between medium and large scales of roughness may induce animals to transition among locomotor modes (Li et al., 2015) (Fig. 6D). Recent research established a potential energy landscape approach (Othayoth et al., 2021) for modeling and understanding how locomotor transitions emerge from controlled physical interaction with gaps (Gart et al., 2018), steps (Gart and Li, 2018), flexible beams (Othayoth et al., 2020; Wang et al., 2022) and rigid pillars (Han et al., 2021). As the cockroach physically interacts with a large obstacle, the potential energy landscape over body rotation degrees of freedom has a few attractive, low-energy basins. The animal body is not in static equilibrium and tends to fall into one of these basins, and falling into each basin results in a distinct locomotor mode. Only some of these modes lead to crossing the obstacle, meaning that successful traversal requires escaping from any undesirable basins. Cockroaches can use a variety of strategies to transition among basins or even modify the

potential energy landscape to facilitate transitions, such as capitalizing on kinetic energy oscillations from walking or actively adjusting body shape or leg movements.

Locomotor transitions have also been observed in vertebrates. Lizards can cross single obstacles smaller than body size by adjusting kinematics (Olberding et al., 2012) (see above). However, when approaching obstacles approximately at body size, lizards are forced to slow down, explore, and shift to a new locomotor mode (such as climbing) (Parker and McBrayer, 2016; Kohlsdorf and Biewener, 2006; Tucker and Mcbrayer, 2012).

'Terrain roughness' regime ($\kappa > \sim 1$)

Once obstacles become very large compared with body size, they may require a change in path planning. While path planning may also occur in response to smaller-scale ground roughness (Clifton et al., 2020a), terrain roughness cannot be negotiated within a few steps, thus requiring longer duration preparation. The navigational mechanisms that animals use to discern and respond to large features in the environment have been studied broadly. We will not provide a thorough review of this literature but briefly highlight key themes relating to terrestrial locomotion.

Most studies that examine animal movement in relation to large-scale substrate features focus on path choice and sensory cues. Animals use celestial patterns, landmark features, polarized light and magnetoreception to navigate very long distances (Johnsen and Lohmann, 2005; Warrant and Dacke, 2011; Muheim, 2011), and they often rely on chemosensation, odometry and visual detection of obstacles or optic flow at somewhat shorter scales (Serres and Ruffier, 2017; Wittlinger et al., 2006; Wallraff, 2004). Some animals, such as jumping spiders, may even visually scan for detours that require moving farther away from prey (Jackson and Wilcox, 1993; Tarsitano, 2006). Several studies at these scales use biologists to quantitatively measure trajectories of large mammals (e.g. zebra, cheetah, leopards) navigating natural areas with large rough terrain features (e.g. trees, hills, and mountains) (Hubel et al., 2016, 2018; Van Der Weyde et al., 2017; Curtin et al., 2018; Suraci et al., 2019; Bartlam-Brooks et al., 2020; Rafiq et al., 2020a,b; Alting et al., 2021). Studies of ants (Wehner, 2020; Cheng et al., 2009; Palavalli-Nettimi and Narendra, 2018) and beetles (Byrne et al., 2003) have elucidated how insects sense then navigate around cluttered obstacles. Presumably, other factors, such as food/water partitioning, shelter locations, and interactions with predators or conspecifics, also shape the paths that walking animals choose. Animals tend to optimize net energetic gain (Wilson et al., 2012; Shepard et al., 2013), and directly traversing large terrain roughness features (rather than moving around them) may incur a higher energetic cost or greater chance of injury.

However, few studies have focused on understanding the role of large-scale terrain roughness on walking biomechanics. This is not surprising as it poses significant technological challenges in: (1) mapping of the large terrain structures, (2) fine-scale tracking of an animal's position (and even kinematics) relative to these structures, and (3) measurement of movement over long distances and duration. However, with the advancement of biologists and portable drone-based cameras, it is becoming increasingly feasible to obtain fine-grained animal movement data (e.g. body and appendage kinematics) in this terrain roughness regime.

Outlook

In the context of walking biomechanics, it is becoming increasingly clear that studying walking on rough substrates is essential for better understanding the mechanical, sensory and

control aspects of locomotion in natural contexts. Measurement methods capable of reconstructing surface profiles are increasingly becoming accessible to researchers for both laboratory and field settings. Research on human biomechanics has already started to incorporate methodologies for quantifying kinematics, muscle activity and energetics for humans walking on rough laboratory substrates (Gates et al., 2012; Voloshina et al., 2013; Blair et al., 2018; Hawkins et al., 2017) and natural terrain (Holowka et al., 2022), demonstrating dramatic shifts in walking strategies for non-flat substrates. Thus, there is an exciting path forward in the study of non-human walking biomechanics on rough ground. We believe that the metrics, protocols and examples of work outlined in the previous sections will help guide future research.

We propose a new geometric ratio for characterizing walking biomechanics on rough substrates: the roughness ratio, κ , defined in Eqn 1. This non-dimensional metric will facilitate comparison of walking performance across absolute size scales to examine if common walking dynamics and control phenomena are utilized by animals that range in size. We do not advocate that κ is calculated to extended significant digits, but rather it should be used to broadly categorize the different regimes of animal-ground interaction. When κ is very small ($\ll 0.1$), the importance of the interaction is at the foot-ground level where adhesion and/or friction dominate. Conversely, when κ is large ($\gg 1$), the obstacles exceed leg length, requiring navigation around or over these obstacles. In the intermediate range of κ , obstacles influence limb stepping patterns and body stability. This ground roughness is especially likely to contain subdivisions in how it affects walking (e.g. $\kappa=0.1$ vs. $\kappa=0.8$), which may be observed through further experimentation. The general regimes that we outline are not fixed and likely vary based on several aspects of an animal's physiology, morphology and behavior.

We encourage future studies of walking biomechanics to report relevant metrics of both animal morphology (e.g. foot-ground contact diameter, claw length, leg length, hip height, body length, visual range) and surface roughness (e.g. R_q , R_z , S_x , S_y). We propose that authors calculate κ to facilitate comparison with other studies. As we continue to build a library of observations of walking over rough ground, we may identify common locomotion principles correlated with κ regimes that are independent of animal absolute size, while recognizing important factors that result in diverging strategies and behaviors. It is thus our hope that this non-dimensional ratio may facilitate the identification of potentially common walking dynamics and control strategies, leading to a deeper understanding of animal evolution and ecological patterns.

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Competing interests

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ECR Spotlight

This article has an associated ECR Spotlight interview with Glenna Clifton.

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Table S1.

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