



SYMPOSIUM

The Scaling of Uphill and Downhill Locomotion in Legged Animals

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Synopsis Animals must continually respond dynamically as they move through complex environments, and slopes are a common terrain on which legged animals must move. Despite this, non-level locomotion remains poorly understood. In this study, we first review the literature on locomotor mechanics, metabolic cost, and kinematic strategies on slopes. Using existing literature we then performed scaling analyses of kinematic variables, including speed, duty factor, and stride-length across a range of body sizes from ants to horses. The studies that examined locomotion on inclines vastly outnumbered those focusing on declines. On inclines, animals tend to reduce speed and increase duty factor, but a similar consensus could not be reached for declines. Remarkably, stride-length did not differ between locomotion on inclines and on level terrain, but this may have resulted from data only being available for low slopes ($<30^\circ$). On declines there appears to be a shift in locomotor strategy that is size-dependent. At masses <1 – 10 kg, animals tended to use shorter strides than on level terrain, and the opposite occurred at larger body masses. Therefore, possibly due to stability issues, body mass plays a significant role in the locomotor strategy used when traveling downhill. Although we currently lack sufficient data, differential leg function is likely to be critical for locomotion on slopes, with mechanical demands differing on limbs during movement on level, inclined, and declined surfaces. Our scaling analysis not only highlights areas that require future work, but also suggests that body size is important for determining the mechanics and strategies animals use to negotiate non-level terrain. It is clear that selection has resulted in an incredible range of body size among animals, both extant and extinct, and it is likely that the ability to move up and down slopes has constrained or relaxed these mechanical pressures. Given the lack of integration of ecological data with laboratory experiments, future work should first determine which inclines animals actually use in nature, as this likely plays a key role in behaviors such as predator–prey interactions.

Review of locomotion on slopes and introduction

Terrestrial animals move over complex terrain in a range of different habitats, all of which impart a number of differing kinematic and mechanical demands when compared with moving on level substrates (Biewener and Daley 2007). These differences in locomotor pressures are poorly understood, leaving many questions regarding the locomotor strategies and neuromechanical control of locomotion on slopes unanswered. Lack of understanding of locomotor strategies on non-level terrain is in part, due to the extreme diversity exhibited by legged animals, including differences in the number of legs, posture, speed of movement, and body mass. The latter factor is critical

given its prevailing impact on locomotion and on other aspects of biology (Schmidt-Nielsen 1975).

Quantitative analyses of locomotion using high-speed video began in the 1870s, when Eadweard Muybridge (1887) and Etienne Jules Marey (1879) first observed the details of animal motions by capturing photographic stills in rapid succession. Since then, kinetics, the cause of motion of the body, has been incorporated into locomotor studies through the influential work of Giovanni Cavagna (1975) in the use of force plates. More recently, we have achieved greater understanding of legged locomotion through the development of simple models (Cavagna and Kaneko 1977; Blickhan 1989; McMahon and Cheng 1990), but their utility for

explaining locomotion on non-level surfaces is not clear.

Sloped surfaces place differing mechanical demands on the musculoskeletal system, requiring significant changes in locomotion (Biewener and Daley 2007). When moving on an inclined surface, animals move against gravity (Fig. 1) and require an increase in muscle work to increase the potential energy of the animal's center of mass (CoM). Alongside the increased work, animals must combat a “toppling moment” to prevent pitching backwards and away from the substrate (Fig. 1), which may result in falling down the surface. Declined surfaces, in contrast, force animals to move in the direction of gravity (Fig. 1), resulting in increased passive acceleration. To prevent an uncontrolled head-long rush downhill, which could result in injury or loss of control, animals must generate a greater braking impulse (Krause and Fischer 2013); this will impact the mechanics of muscles, which we discuss further below. Downhill locomotion also results in a “toppling moment”, but, unlike uphill locomotion, where it is a backward pitch, the animal will pitch forward (Fig. 1). These demands differ from those on level terrain, but they can be accomplished through numerous strategies, which will be discussed in more detail below.

How do animals move up inclines?

A variety of animals have been studied moving on inclines, including birds (e.g., Daley and Biewener 2003; Gabaldon et al. 2004), insects (e.g., Herreid et al. 1981; Lipp et al. 2005), mammals (e.g., Prost and Sussman 1969; Shapiro et al. 2011; Franz and Kram 2012), reptiles (e.g., Jayne and Ellis 1998; Higham et al. 2011), and amphibians (Herrel et al. 2013). The majority of legged animals exhibit consistent adjustments in locomotor mechanics in response to inclines. For example, most animals incur a loss of performance, with respect to forward velocity, on an inclined surface (Huey and Hertz 1984; Farley 1997; Irschick and Jayne 1999; Zaaf et al. 2001; Claussen et al. 2002; Pinch and Claussen 2003; Lammers et al. 2006; Russell and Higham 2009; Higham et al. 2011; Holt and Askew 2012; Prenter et al. 2012). This decreased speed is often a result of reduced stride-length (Carlson-Kuhta et al. 1998; Irschick and Jayne 1998; Jayne and Irschick 1999; Zaaf et al. 2001; Claussen et al. 2002; Foster and Higham 2012) and an increase in time the limb is in contact with the ground (Williams et al. 2009a; Foster and Higham 2012; Nudds and Codd 2012). These adjustments in

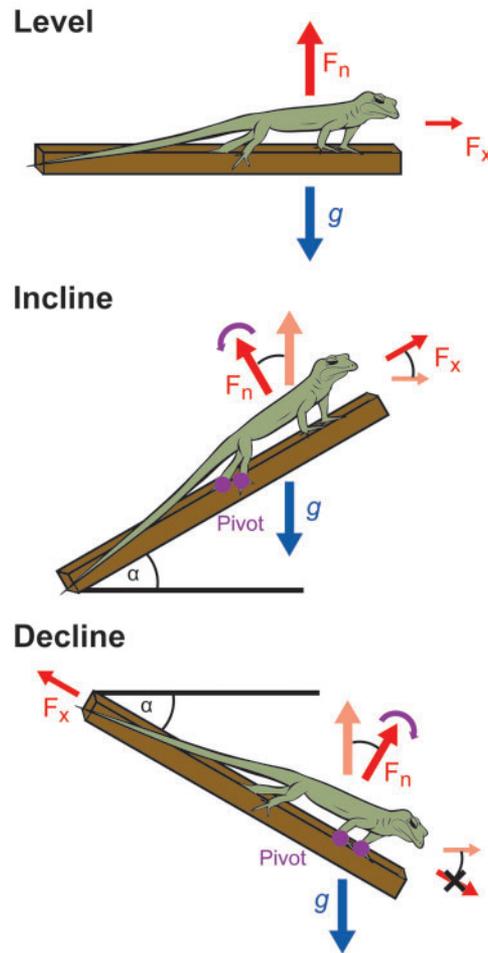


Fig. 1 The mechanical demands of locomotion on slopes. This schematic represents an overview of the change in mechanical demands on animals moving on inclined or declined surfaces. F_n is the normal force or the vertical component of the GRF, F_x is the propulsive force and g is the gravitational pull. Only in the scenario of locomotion on declines is propulsive force not required, but instead a net braking force.

spatio-temporal characteristics are generally observed in lizards and some mammals. Although speed has not been measured on inclines during overground locomotion in humans, stride-length on treadmills increases with incline (Leroux et al. 2002), suggesting that speed may increase if stride frequency remains the same; this still requires a future study to clarify whether speed increases when humans move on inclines. A major issue across studies of locomotion on non-level surfaces is the lack of consistent methodology, exemplified by the wide variety of inclines used. This is challenging, given that different inclines will have varying impacts on locomotion, and so direct comparisons between species may be problematic. Other confounding variables include the type of locomotion (e.g., overground versus treadmill), ambient temperature, hygrometry, and type of substrate

used during the study. Despite the common strategies for dealing with inclines across several studies, there are others that show different alterations in locomotion in response to changes in inclines. For example, some animals maintain the same speed on inclines compared with level substrates (Vanhooydonck and Van Damme 2001; Zaaf et al. 2001; Lauer et al. 2009; Russell and Higham 2009), resulting in the maintenance of spatio-temporal characteristics (Eaton et al. 1995; Farley 1997; Nyakatura et al. 2008). It is clear that a cohesive assessment of the impacts of incline on locomotion is needed.

Animals generally counteract the issue of the “toppling moment” on inclines in one of two ways: (1) assuming a more crouched posture (Carlson-Kuhta et al. 1998; Jayne and Irschick 1999; Leroux et al. 2002; Spezzano and Jayne 2004; Schmidt and Fischer 2011; Stevens et al. 2011; Foster and Higham 2012) and/or (2) adjusting the forelimb in ways that pull the CoM toward the ground (Autumn et al. 2006; Lammers et al. 2006; Lee 2011). This provides a counter torque as the forelimbs pull the CoM toward the surface, while the hind limbs push away from the surface (Autumn et al. 2006). The change in leg function is combined with a net positive output of work (increase in total mechanical energy), which is required to overcome gravity on an incline. Most joints associated with locomotion increase net work when moving uphill (Gabaldon et al. 2004; Lay et al. 2006; DeVita et al. 2007, 2008; Telhan et al. 2010; Franz et al. 2012; Arnold et al. 2013), often through increases in extensor moments. Unfortunately, the majority of studies examining the function of joints on inclines are on humans, providing little evidence for whether this increase in net output results from similar functional changes in other animals.

Muscles actuate the movement of an animal, producing the required force for locomotion in a variety of contexts. Moving up an incline requires an increase in total output of work because of the increase in potential energy of the animal’s body. Because of this, it stands to reason that the muscle work must also increase. Several studies examining the impacts of inclines on locomotion in a variety of animals, including cats, lizards, humans, and birds, have noted an increase in muscular activity, often through increased burst-amplitude (Carlson-Kuhta et al. 1998; Higham and Jayne 2004), intensity (Gillis and Biewener 2002; Crook et al. 2010; Carr et al. 2011), duration of activity (Carlson-Kuhta et al. 1998; Kaya et al. 2003; Lay et al. 2007; Franz and Kram 2012), or increased recruitment of muscle

fibers (Gabaldón et al. 2008). Increases in muscle activity, especially intensity, likely correspond with an increase in motor unit recruitment (Lee et al. 2013). Given that work increases with increased muscular force, and that increased recruitment of motor units will increase muscle force, this should contribute to the increased work that is necessary for moving up inclines.

The increased work output required to move an animal’s CoM up an incline likely results in an increased cost of locomotion. The metabolic cost of locomotion has been measured on a variety of inclines and animals with contrasting results. The majority of studies have noted, as expected, that the metabolic cost of locomotion increases with the steepness of inclines (Raab et al. 1976; Eaton et al. 1995; Farley and Emshwiller 1996; Rubenson et al. 2006; Williams et al. 2009b; Hanna and Schmitt 2011; Holt and Askew 2012; Nudds and Codd 2012; Lees et al. 2013). In contrast, ants, cockroaches, and some small primates did not change their cost of locomotion on inclines compared with level substrates (Herreid et al. 1981; Lipp et al. 2005; Hanna and Schmitt 2011), suggestive that the increased cost of locomotion associated with moving uphill may be more pronounced, and therefore more easily detected, in larger animals. Given that the demands of moving on inclines involve the same basic principles across all mobile, legged animals, a large scaling analysis is required to tease this effect apart.

How do animals move downhill?

Unlike locomotion on inclines, fewer studies have investigated the effects of declines on locomotion. Although there are relatively fewer studies, similarly to inclines, they cover a broad range of animals such as birds (Gabaldon et al. 2008; Nudds and Codd 2012), insects (Holt and Askew 2012), mammals (Gottschall and Kram 2005; Gregor et al. 2006), and reptiles (Higham and Jayne 2004; Krause and Fischer 2013). There is no general strategy for dealing with declines, although this is likely related to the scarcity of studies examining locomotion downhill. As is the case for locomotion uphill, an increase in flexion at the joints during the stance phase (Smith et al. 1998; Jayne and Irschick 1999; Leroux et al. 2002; Stevens et al. 2011; Krause and Fischer 2013) occurs in animals moving downhill, which helps keep an animal’s CoM closer to the substrate. This reduces the “toppling moment” that threatens to cause a downward headlong rush.

Even though the progression of an animal moving downhill is assisted by the increased contribution

from gravity, forward velocity is commonly reduced (Pinch and Claussen 2003; Kivell et al. 2010; Shapiro and Young 2010; Holt and Askew 2012). This loss of performance may be a result of decreased stability, with animals choosing to move slower to reduce the risk of injury from loss of contact with the surface. To prevent the headlong rush downhill animals also tend to alter the function of their legs by using the forelimbs as brakes, with zero or minimal positive work (Lammers et al. 2006; Lee 2011). One aspect of the net braking function of the forelimbs (or hind limbs in bipeds) is that, due to gravitational acceleration, the peak ground reaction force (GRF) increases as a means of decelerating the animal (Gottschall and Kram 2005; Gregor et al. 2006; DeVita et al. 2008; Telhan et al. 2010).

Compared with locomotion on level surfaces, activity of the muscles of the limbs typically decreases when moving downhill (Smith and Carlson-Kuhta 1995; Smith et al. 1998; Gillis and Biewener 2002; Crook et al. 2010), given that the limb exhibits net absorption of energy rather than net positive output of work (Gabaldon et al. 2004). This occurs through eccentric muscle contractions, which might increase the risk of muscular injury (Hoyt et al. 2006). The net energy absorption of the CoM is assisted by changes in joint extensor moments resulting in changes of work by the muscles (Gregor et al. 2006; Lay et al. 2007; Telhan et al. 2010; Franz and Kram 2012; Franz et al. 2012; Arnold et al. 2013). The lack of net positive output of work required for locomotion on a decline suggests that the metabolic cost should be reduced. This is the case for horses (Hoyt et al. 2006), but not for other animals such as geese and dogs (Raab et al. 1976; Nudds and Codd 2012). Metabolic cost, which is measured as oxygen consumption, may also appear reduced due to changes in the type of muscle fiber used, such as using glycolytic fiber types rather than oxidative ones (Ivy et al. 1980; Crow and Kushmerick 1982; Bassett and Howley 2000; Seibel and Drazen 2007). Animals are expected to respond similarly across non-level terrain, as they all deal with the same changes in mechanical demands; it is merely a question of difference in the number limbs that respond to the changes in mechanical demands that differ. Currently though the source of these different responses in non-level terrain cannot be isolated.

Scaling of non-level locomotion

As animals increase in body mass they need to cope with increased GRFs, resulting in increased muscle forces (Biewener 1982). As musculo-skeletal

properties do not differ significantly among species (Biewener 1982; Currey 2002), it is not surprising that many animals ameliorate the increased GRF by adopting a more upright posture of the limbs (Biewener 1989). This allows larger animals to align their joints with the GRF, thereby reducing joint moment, and thus reducing the stresses on muscles required to maintain posture. Some large animals also adjust bone robustness by altering bone size (Biewener 2005; Doube et al. 2009), and other exceedingly large animals, such as elephants, reduce their locomotor performance by avoiding running gaits (Hutchinson et al. 2003), which require high forces. Studying the scaling of locomotion can reveal fundamental aspects of animals' movements and the limits of terrestrial locomotion (Spence 2009).

The scaling of locomotion on level surfaces has been examined in detail (see review by Biewener 2005), but no attempt has been made to determine the scaling of locomotion on slopes. This is unfortunate given that limits of performance are more likely to be reached during locomotion uphill or downhill (Biewener and Daley 2007). Using every study of legged locomotion of animals moving on inclines and/or declines, our goal in this study was to determine the scaling relationships for several important variables related to kinematics. We expected isometric relationships and that y -intercepts would likely shift up or down, depending on the variable of interest during locomotion on slopes. This first attempt to synthesize scaling information for locomotion on non-level surfaces not only provides a framework for future investigations, but also sets up a number of testable hypotheses regarding how animals move in demanding habitats.

Methods

We used published (60 papers) and unpublished results for both invertebrates and vertebrates in our scaling analyses (Fig. 2). This included 57 different species, with 4 species of invertebrates. We excluded any papers that did not state body mass. Our search criteria included any papers that noted speed alongside other kinematic variables such as duration of stride, duty factor, and stride-length. A smaller subset was analyzed (47 studies incorporating 51 species; see Supplementary Table S2), based on kinematic variables that included large enough data set to allow analyses; these variables are described below. Although the incorporation of phylogenetic information would be ideal, the limited number of studies

and extremely broad taxonomic sampling precluded any phylogenetic analyses.

Selection and categorization of data

Given the range of treatments used in the studies reviewed here, it was necessary to categorize the data to prevent trends being concealed by large variances. Locomotor parameters, especially spatio-temporal variables, change significantly with increasing speed (Cavagna et al. 1988; McMahon and Cheng 1990); therefore, we separated data into two categories of speed, as described below.

We normalized speed using a simple morphological measure of leg length—the sum of the lengths of each leg segment. As we were combining multiple studies that did not necessarily calculate the same variables, we were unable to use dynamic measures of leg length such as mid-stance leg length. We avoided using an estimate of standardized leg length, as there are significant complications due to the postural changes associated with body mass (Biewener 1989; Gatesy and Biewener 1991). We also avoided using body length due to the vast variation in shapes of the body among animals, which would also affect the normalization. If these data were not published they were obtained, when possible, from the authors. Otherwise, we ran a scaling analysis on body mass and the sum of the lengths of each leg segment using existing data to fill in missing values. Values were only estimated that fell within the range of data we already possessed. To do this, we used a linear mixed-effect model (LMM). For further details of the model, see the section below on statistical analyses. The model produced a significant fit, indicating that the slope was significantly different from zero ($T_{62} = 27.40$; $P < 0.005$; $r^2 = 0.99$). The exponent and intercept gained from this model ($m = 0.38 \pm 0.03$ CI; $b = 0.20 \pm 0.05$) were then used to calculate the expected sum of lengths of

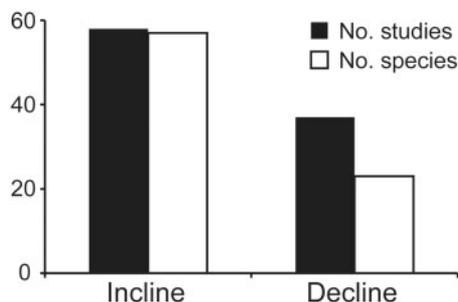


Fig. 2 The number of studies and species used in the current analysis. Many more studies have been performed on animals on inclines when compared with declines. There are also far fewer species studied on declines.

each leg segment for all species missing this information. Using the sum of the lengths of each leg segment, we determined the Froude number (v^2/gl). The Froude number allows analyses in dynamically similar speeds across species, thus removing effects due to size (Alexander and Jayes 1983). Therefore, any differences from isometry highlight differences in locomotor strategy. Froude numbers less than 0.5 indicate vaulting gaits whereas those above 0.5 indicate bouncing gaits. We used this 0.5 limit to separate the data into two distinctive categories of speed, separated by the differing mechanics associated with vaulting versus bouncing gaits. Analyses of speed across slopes used only data obtained from trackway studies. We did not include data from treadmills as this is a pre-determined speed rather than self-selected.

In addition to the variety of speeds used in previous research, there is a vast disparity in the slopes used. Consequently, this led to lack of sufficient data for any specific incline. We therefore used broad bins (0–30°; 30–60°; and 60–90° for both inclines and declines) to include enough data for the analyses of scaling. Although these are relatively broad, these bins provided us with an overview of the general scaling trends across animals.

Statistical analyses

Following the methods of Warner et al. (2013), we used a LMM. Body mass was the fixed effect and species as the random factor because we could not control the sampling of species already in the literature. We also weighted species, which allowed the y -intercept to vary, and so a single species did not skew the results simply because it was an outlier or because there were numerous data points for a particular species. The model used for determining missing values for the summed lengths of each leg segment was

$$\log \sum L_{seg} \sim 1 + \log M_b + (1|S), \quad (1)$$

where L_{seg} is the lengths of segments, M_b is the body mass, and S is the species.

As with Equation (1), we used the LMM to analyze the scaling effect on locomotor variables: speed, duty factor, stride-length, and duration of stance by the following equation:

$$\log \text{var} \sim 1 + \log M_b + (1|S), \quad (2)$$

where “var” is the current variable of interest. All analyses were performed using custom written script in MATLAB (release R2013b; The Mathworks Inc., Natick, MA, USA). Analyses presented in this

article were performed only on hind limb parameters due to a lack of data for forelimbs.

Results

There was almost double the number of studies for inclines as for declines, and the same was true for species, with three times more studied on inclines than on declines (Fig. 2). Surprisingly, even though there was such a large discrepancy between studies and species, this did not alter the range in sizes or slopes between investigations of inclines and declines. Studies examining the impacts of inclines and declines have used species ranging from leaf cutter ants up to horses (a 47-million-fold size range). The range of slopes is also large (-90° declines to 90° inclines). Although at the extreme 90° slope in declines there is a much reduced sample size, consisting of only ants. On inclines at 90° the species consisted of ants, lizards, and primates.

Speed on slopes

Following the assumptions of dynamic similarity, i.e., that animals at the same relative speed move in the same way (Alexander and Jayes 1983), speed is expected to scale isometrically to $M_b^{0.16}$ (Warner et al. 2013), derived from using the geometric scaling for length ($M_b^{0.33}$) and time ($M_b^{0.17}$ (Bullimore and Burn 2004)). As expected, speed decreased with increasing incline when using vaulting gaits (Fig. 3). Speed on inclines consistently scaled with isometry, whereas the data from level surfaces scaled with positive allometry (Supplementary Table S1). Although no significant fits were obtained for bouncing gaits, speed generally decreased with increasing incline (Fig. 3). One reason for the lack of significance for data on bouncing gaits may be that the majority of species examined were lizards that weighed around 2–10 g. This resulted in a large amount of variance over a very small size range, reducing the predictive power of the LMM. A lack of data precluded an analysis of locomotion on downhill slopes.

Duty factor

Duty factor is the fraction of time that a limb spends in contact with the ground. Animals running at similar relative speeds are expected to exhibit dynamic similarity and consequently use the same gaits. Therefore, duty factor is expected to scale to M_b^0 . On inclines, particularly for bouncing gaits duty factor was greater compared with locomotion on level substrates (Fig. 4). However, no significant relationship between body size and duty factor was found (Supplementary Table S1 and Fig. 4). The

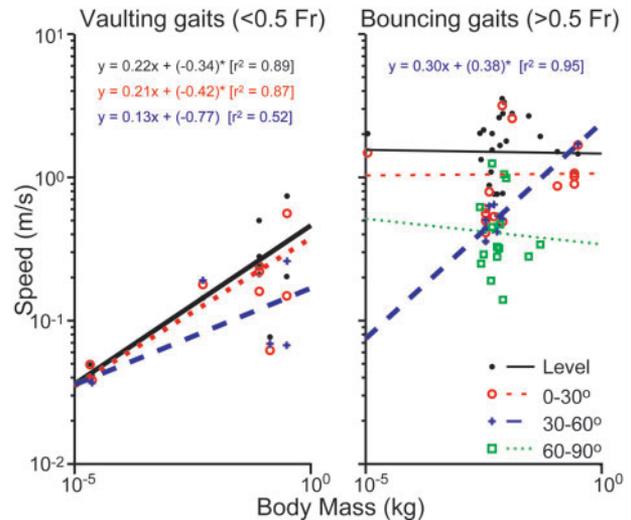


Fig. 3 Scaling LMM results for speed on inclines. Although speed increases with body size, speed tends to be lower on inclines (compared with level surfaces) across the whole range of body sizes. Significant fits are represented by thick lines. Isometry predicts a scaling relationship of $M_b^{0.16}$, where the equation $y = mc + x$ describes the line and “ m ” is the exponent that we use to investigate scaling relationships. * denotes trends significantly different from isometry.

gray short-tailed opossum, particularly on level ground, exhibited a relatively low duty factor, potentially resulting in a lack of significance. For both vaulting and bouncing gaits on declines, duty factor was lower compared with values on level terrain (Fig. 4). The gray short-tailed opossum again had duty factors that were relatively lower than other species on declines. Additionally, the opossum increased duty factor on declines, whereas other animals such as humans and horses decreased duty factor on declines.

Stride-length

Geometric similarity implies that shape is retained as animals increase in size; to accomplish this, linear dimensions need to scale with respect to one another where area is proportional to length² and to volume^{2/3} or mass^{2/3}. Therefore, stride-length should scale to $M_b^{0.33}$. Surprisingly, the slopes of the relationship between body mass and stride-length did not differ between inclined and level surfaces (Fig. 5). For bouncing gaits across level ground, inclines and declines, stride-length scaled with negative allometry (Supplementary Table S1). However, it was only on declines that scaling trends were significantly different from those on level surfaces. On declines there appears to be a crossover point on the lines of best fit (Fig. 5); lower massed species

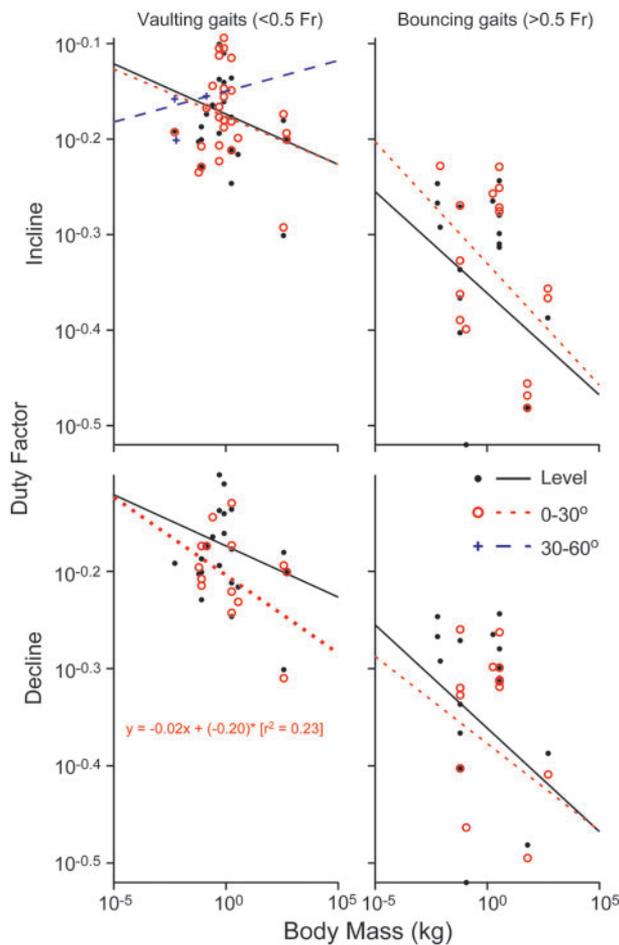


Fig. 4 Scaling LMM results for duty factor for hind limbs only. Duty factor tends to increase with inclines indicating a greater relative portion of the stride spent in contact with the ground. On declines the opposite trend occurs; duty factor is lower on declines. Significant fits are represented by thick lines. Isometry predicts a scaling relationship of $M_b^{0.00}$, where the equation $y = mc + x$ describes the line and “ m ” is the exponent that we use to investigate scaling relationships. * denotes trends significantly different from isometry. The 0–30° decline condition scaled with negative allometry.

tend to use shorter strides in contrast to locomotion on level substrates, whereas larger species use longer strides on inclines than on level ground. This cross-over occurs between 1 and 10 kg both for vaulting and bouncing gaits.

Discussion

Animals face many challenges in their natural habitat, and running on non-level terrain is likely ubiquitous. In addition, it is arguably one of the more challenging tasks, in terms of energetic and mechanics, particularly on steep slopes. Although numerous studies have examined the dynamics of locomotion on inclines and declines, there is a lack

of consensus and cohesive understanding of locomotion on slopes across species. Given the vast range of body sizes across legged animals, there are likely important selective pressures and constraints that have significant consequences for the evolution of body form (Fig. 6). Animals of different sizes will experience different selective pressures and constraints, but it appears here that both the vertebrates and invertebrates studied all have similar scaling patterns associated with slopes. Further analyses on a greater range of legged invertebrate species would highlight whether locomotor strategies are constant across all legged animals. Studies tend to impose steeper slopes on smaller animals, particularly due to experimental setup and safety constraints imposed by using larger animals for a study. However, it is also likely indicative of the ability of smaller animals to more effectively traverse steeper inclines, but this remains unclear without additional work on large animals on steeper slopes. For example, it is unclear whether there is a threshold for body mass on a given incline, above which any animal will be unable to traverse that incline. It is possible that power output may limit these larger species from moving on slopes, as several studies suggest that maximum power output is a limiting factor of maximum performance (Irschick et al. 2003; Williams et al. 2009b; Self et al. 2012).

We found that, particularly for vaulting gaits, speed generally decreases on inclines (Fig. 3). This is not surprising, as animals need to perform more work against gravity to move the CoM uphill (Fig. 6). Although there were no significant changes in speed for bouncing gaits on inclines, there still remained a trend of reduced speed with increasing steepness. Lack of a significant fit might be a consequence of the small range in body mass and the large range of Froude numbers used across species. Without multiple speeds for each species, it is difficult to remove the effects of speed from this data set. Reptiles often reduce speed with increasing steepness of slope (Claussen et al. 2002; Pinch and Claussen 2003; Russell and Higham 2009; Krause and Fischer 2013). Future work across a large size range of animals moving on inclines at relatively similar speeds will provide greater clarification, but we expect a consistent reduction in speed on inclines.

Duty factor generally increased with increasing incline; this facilitates a longer period of contact in which to produce the extra work against the ground required to move uphill. Interestingly, duty factor on declines was lower than on level ground, indicating a relatively shorter period of contact with the ground. Although we did not examine metabolic

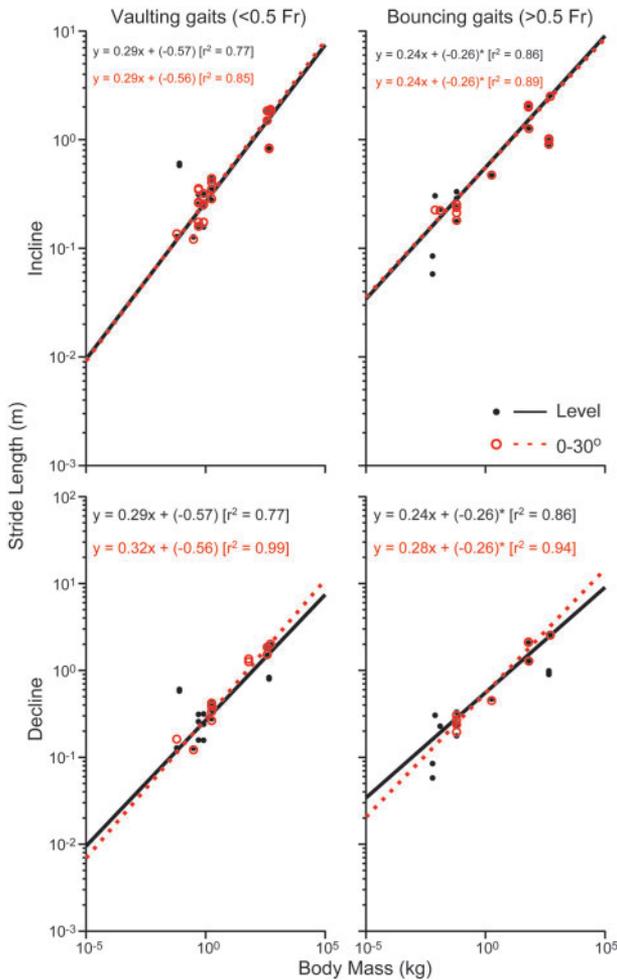


Fig. 5 Scaling LMM results for stride-length for hind limbs only. Stride-length on inclines does not differ from that on level terrain, which is surprising. Data represented here are only for the lowest slope bin. On declined slopes, species with smaller masses tend to use shorter stride-lengths than on level surfaces, but species with larger masses use longer stride-lengths. Significant fits are represented by thick lines. Isometry predicts a scaling relationship of $M_b^{0.33}$, where the equation $y = mc + x$ describes the line and “ m ” is the exponent that we use to investigate scaling relationships. * denotes trends significantly different from isometry. All lines of best fit (both inclines and declines) for bouncing gaits scale with negative allometry.

cost some inferences can be made from changes in duty factor. The metabolic cost of locomotion is mainly due to muscle work associated with the production of GRFs (Kram and Taylor 1990; Minetti and Alexander 1997). Muscle work that generates a GRF can only be produced during the stance phase, so changes in duty factor will affect the time available for generating this force. Models have successfully used this theory to predict locomotor patterns and metabolic costs (Pontzer 2005; Srinivasan and Ruina 2006). Based on previous findings, we suggest that animals will exhibit a consistent elevation of

metabolic cost of locomotion with increasing incline (Fig. 6). The impacts of declines on metabolic cost, however, are more difficult to predict (Fig. 6). Although duty factor decreases, braking forces likely increase, as animals must contend with the increased impacts of gravity. Due to differences in mass, it may be that smaller species will exhibit a reduction in the cost of locomotion on declines, as their mass is such a small component in determining force when compared with gravitational acceleration. Alternatively, larger species will require much larger braking forces (M_b^1), which may result in increased metabolic cost. Thus, although it is not understood, we expect a greater increase in metabolic cost for larger animals on slopes.

Similar to the differing metabolic costs of locomotion on downhill slopes; slopes may also result in contrasting strategies due to differing mass-dependent constraints and pressures. Although, we have very few data on stride-length, our results on downhill slopes indicated a cross-over point compared with the level substrate (Fig. 5 and Supplementary Fig. S1); the smaller species used shorter strides compared with the level and larger species longer strides on downhill slopes. This cross-over consistently occurred between 1 and 10 kg. This pattern represents a size-related constraint in which the kinematic strategies used on slopes must change, but more data are needed to rule out an effect of poor, and possibly biased, sampling from the literature. Stride-length in all terrains scaled with negative allometry (Supplementary Table S1), but it was closest to isometry on declines. In-line with the cross-over effect, this shift toward isometric scaling may result from body-size constraints and a requirement for shifts in strategy. Although gravitational acceleration is constant, the force required to maintain posture depends on the mass of the animal. This means that larger species need greater forces for braking on downhill slopes or to propel themselves upwards on uphill slopes. Although our analyses appear to indicate consistent uphill strategies across species, there is lack of a clear strategy for locomotion downhill. Larger animals moving downhill may have greater instability issues (Fig. 6). These stability issues are a direct result of (1) a greater requirement for net absorption of work that leads to an increased risk of injury from eccentric muscle contractions (Newham 1988; Eston et al. 1995; Close et al. 2004) and (2) due to increased CoM height, which is naturally farther from the ground, thereby resulting in greater toppling moments. Crouching to reduce the toppling moment can be greatly detrimental to larger species as it requires increased muscle force (Biewener 1989).

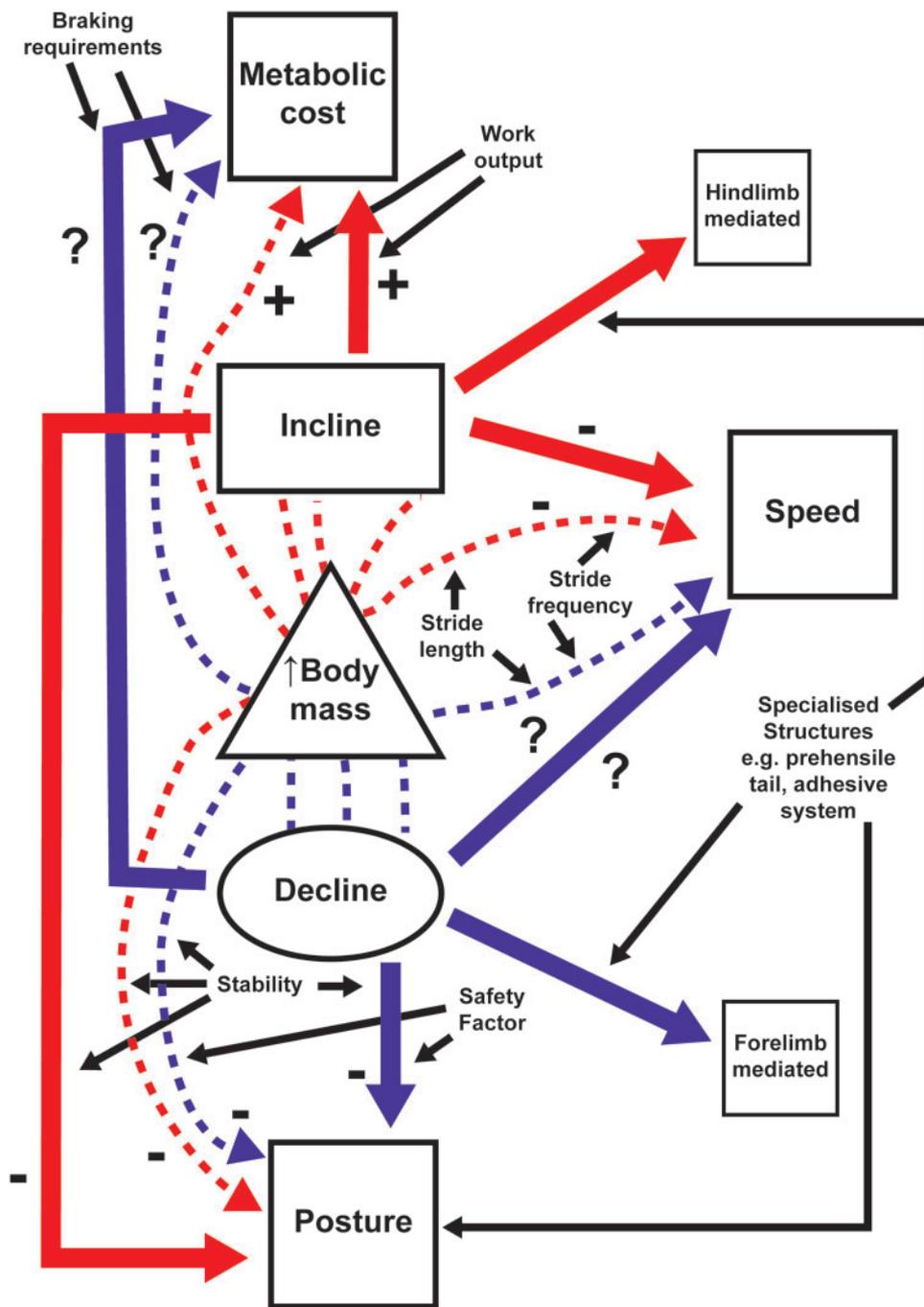


Fig. 6 A schematic highlighting the integrative impacts of slope and body mass on locomotor posture, metabolic cost, locomotor speed, and the increased reliance on hind limbs or forelimbs. Solid colored lines represent direct impacts of slopes (not accounting for body mass) on the variables, whereas dashed lines represent the combined impacts of slope “and” body mass. Specialized structures may offset shifts in posture and in limb function, thereby ameliorating any negative consequences. Lines with question marks indicate current hypotheses that are not fully supported due to lack of data. Although not shown, increasing body size alone, without normalizing data, leads to increases in speed (Heglund and Taylor 1988) and metabolic cost (Heglund and Taylor 1988). With increasing body size, posture becomes more upright (Biewener 1989).

Therefore, any crouching to improve stability may result in a greater risk of injury for larger animals, particularly over repetitive load cycles (Verheyen et al. 2006). These issues therefore may lead to a different strategy for locomotion downhill for larger

animals. Larger animals may instead increase their stride-length, but reduce stride frequency which results in a reduced speed, but also reduces the number of repetitions of loading cycles. Larger species may also just avoid large downhill grades to

prevent these issues, but this requires further investigation.

Where are we going with locomotion on slopes?

Our synthesis of locomotion on slopes and across species and body size is a start, but the remaining gaps must be filled in order to fully understand the dynamics of moving on sloped surfaces. There is a restricted body of work on declines, alongside restricted sampling of species across both inclines and declines that will be important for understanding the diversity of extant, legged species. Associated with this is the variability in methodologies, so drawing conclusions across size and clades are difficult. We suggest future work should focus on studies across a broad range of body sizes and use the same methods, such as trackways to collect a range of speeds to account for the effects of velocity. Furthermore, using a consistent slope of 30°, for example, would be beneficial for multi-species studies. This relatively shallow angle would be traversable by a range of both terrestrial and arboreal animals, permitting a direct comparison across a range of taxa. Although this may be considered steep for large species, it still provides a sufficiently steep slope requiring significant adjustments in locomotor patterns in small animals.

Ecological relevance

Although many manipulations can be made in a laboratory setting, they are only relevant if they reflect natural variation in an animal's habitat. This requires information regarding patterns of movement in nature. Alternatively, theoretical predictions can be made regarding the optimal strategies for natural movements. For example, Llobera and Sluckin (2007) used a theoretical model to predict the optimal way of moving up or down hills. They suggest that a "zigzag" motion is metabolically beneficial compared with moving directly up or directly down steep slopes. Although this established testable hypotheses, it is currently unclear whether animals actually employ these "zigzag" paths when moving in their natural habitat. In general, few studies have quantified use of habitat prior to laboratory studies, with the exception of some lizards (Jayne and Ellis 1998; Irschick and Jayne 1999; Jayne and Irschick 2000) and primates (Nyakatura and Heymann 2010; Shapiro et al. 2011; Stevens et al. 2011). Future work should integrate ecology and laboratory studies in order to determine the consequences of relevant slopes on locomotor dynamics.

Although large animals generally avoid steep slopes, this tendency is rarely quantified. However, studies on the largest extant terrestrial animal, the elephant, indicate that although large variability in terrain is available, elephants actively avoid steep gradients (Wall et al. 2006; Roever et al. 2012). Elephants do move on 30° slopes, but far less frequently than on shallower slopes (Wall et al. 2006). This avoidance of steep slopes probably arises from several issues including the need to increase caloric intake to replenish the energy used for moving up steep slopes (Wall et al. 2006) and greater toppling moments leading to greater instability when moving on steep slopes in larger animals. It is clear that size plays a major role in determining how animals use their habitat, but more information is needed. One possibility is that strategy simply changes when other constraints arise. For example, primates, including humans sometimes use a rear-first mode of arboreal locomotion when descending a tree trunk (Fontaine 1990; Johnson and Shapiro 1998; Venkataraman et al. 2013). This strategy on a vertical surface likely offers increased stability, but it is unclear how common this behavior may be, or if there are other group-specific strategies for descending.

Habitat type (arboreal versus terrestrial) may reflect a major axis of variation in the strategies employed for traversing slopes. For arboreal animals, specialized structures that facilitate grasping, such as a prehensile tail or zygodactylus limbs (Higham and Anderson 2013; Sustaita et al. 2013) will potentially alleviate some of the force on a certain set of limbs during locomotion (Fig. 6). For example, a prehensile tail will grasp a branch during locomotion downhill, limiting the braking forces required from the forelimbs. This will also increase stability, allowing arboreal animals to traverse steeper slopes than terrestrial animals. Regardless, arboreal animals likely encounter a larger range of inclines than do terrestrial animals, indicating that selection simply may have favored these specialized structures in animals occupying arboreal habitats. Future work should examine how the scaling of locomotion on slopes differs between arboreal and terrestrial species.

Predators and prey often are of different sizes, especially when the predator is gape-limited. In this case, the predator will likely be larger than the prey, although we recognize that predators can be smaller than their prey. Regardless, the impact of size on locomotion up or down slopes may directly impact the outcome of predator-prey interactions. A small prey may benefit from the enhanced ability to move on sloped surfaces during an escape by selecting steep inclines to force the predator into a

sub-optimal situation. Conversely, if the predator is smaller than the prey, it could potentially overcome the prey on inclines. The role of inclines in trajectories of escape is poorly understood, but is something that may be important for determining who prevails in predator–prey interactions. Future work determining whether prey (or predators) use steeper inclines during escapes than during regular activity would provide important information regarding the impact and use of inclines for survival.

Differential function of limbs

Another key aspect is our understanding of the function of forelimbs and hind limbs across slopes. Our analysis here focused purely on the hind limb as there is currently insufficient information in the literature on the mechanics of forelimbs on sloped surfaces. Forelimbs and hind limbs perform functionally different tasks on inclines versus declines (Autumn et al. 2006; Lammers et al. 2006; Lee 2011), so therefore understanding the adjustments in the mechanics of forelimbs are just as important (Fig. 6). Associated with this are ontogenetic effects and whether this changes locomotor patterns, differential functioning of limbs or use of habitat; currently only one study has incorporated ontogeny with locomotion on slopes (Shapiro et al. 2014).

Although we are beginning to understand locomotion on non-level surfaces, particularly with regard to slopes, we still have a surprisingly poor unified concept of how a broad range of animals use non-level surfaces and whether there are fundamental control patterns of locomotion across species and sizes. Current studies show a promising beginning toward filling these gaps, which will lead to a greater understanding of evolution, control priorities, and constraints imposed by body mass.

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Supplementary data

Supplementary Data available at *ICB* online.

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