



How to climb a tree: lizards accelerate faster, but pause more, when escaping on vertical surfaces

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Many species of lizards effectively traverse both two and three-dimensional habitats. However, few studies have examined maximum locomotor performance on different inclines. Do maximum acceleration and velocity differ on a level and inclined surface? Do lizards pause more on an inclined surface? To address these questions, *Sceloporus woodi* lizards ($N = 12$) were run in the laboratory on a level trackway and a vertical tree trunk. This species is known to frequently utilize both vertical and horizontal aspects of its habitat. Average maximum acceleration on the vertical surface exceeded that on the level surface, although average maximum velocity exhibited the opposite pattern. The average number of pauses during level locomotion was lower compared to vertical locomotion. In addition, the average location of the first pause on the level surface was 0.51 m, which is farther than the average for vertical locomotion where the first pause was at 0.35 m. The combination of performance and pause data suggests that the relative lack of pausing during level locomotion allows individuals to reach higher maximum velocities on level surfaces because they accelerate over greater distances. The increased pausing when moving vertically could be a result of high energetic demands of vertical locomotion, or greater microhabitat complexity as a result of branching and/or refuges. The faster acceleration exhibited during vertical locomotion by *S. woodi* likely offsets the frequent pauses. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 102, 83–90.

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INTRODUCTION

Locomotion is an essential part of survival and growth for most animals (Szacki & Liro, 1991; Drake *et al.*, 2001; Walker *et al.*, 2005; Higham, 2007). Although terrestrial movement is often simplified to occur on level surfaces, inclined and vertical locomotion are integral parts of movement for many species of animals (Irschick & Jayne, 1988, 1999; Roberts *et al.*, 1997; Jayne & Ellis, 1998; Jayne & Irschick, 2000; Biewener & Corning, 2001; Daley & Biewener, 2003), especially those that live in arboreal habitats. Relative to a level surface, movement on an incline often changes as a result of the force of gravity pulling parallel to movement (to some extent) rather than perpendicular (Cartmill, 1985). Movement in an

arboreal habitat can also be influenced by the presence of tree limbs via the animal choosing whether and how to move onto them (Higham, Davenport & Jayne, 2001; Mattingly & Jayne, 2004, 2005). The fact that trees have variable trunk diameters, as well as the random placement of their branches, also influences arboreal movement (Cartmill, 1985; Losos & Sinervo, 1989; Mattingly & Jayne, 2004, 2005; Astley & Jayne, 2007). Understanding how animals perform on level and inclined surfaces, which characterize arboreal habitats, will highlight morphological and behavioural adaptations that facilitate these movements. Lizards are particularly adept at moving in complex three-dimensional habitats (Higham *et al.*, 2001), making them well-suited for studies of level and vertical performance.

When moving on an incline, organisms must work against gravity acting in opposition to their direction of movement. For example, limb muscles must do

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more work to increase the potential energy of the animal (Roberts *et al.*, 1997; Biewener & Corning, 2001; Daley & Biewener, 2003; Lichtwark & Wilson, 2006). Given the costs of vertical locomotion, it follows that performance differences likely exist between a vertical habitat and a level one. This is important to consider given that maximum locomotor performance is vital for escaping predators and capturing prey (Webb, 1976; Domenici & Blake, 1997; Hale, 1999; Walker *et al.*, 2005; Higham, 2007). Maximum acceleration and velocity are key indicators of maximum locomotor performance, and have been studied widely in a variety of vertebrates (Irschick & Jayne, 1999; Vanhooydonck & Van Damme, 2001; Irschick, 2003; Walker *et al.*, 2005). A key study by Walker *et al.* (2005) found that increased acceleration performance of guppies increased their chances of survival, which can ultimately lead to an increase in individual fitness. Although maximum acceleration is not often affected by incline, velocity can decrease with incline depending on the size of the animal (Huey & Hertz, 1982; Irschick & Jayne, 1998, 1999; Jayne & Ellis, 1998; Jayne & Irschick, 2000; Astley & Jayne, 2007). Thus, identifying differences that may exist between level and vertical locomotor performance is critical for understanding what parameters of performance are most important in different habitats or ecological contexts.

Intermittent locomotion could potentially alleviate the increased demand of vertical locomotion by providing short periods of recovery between locomotor bouts. When the path of movement involves turning, such as on the branches of trees, lizards will frequently pause before changing their route onto the branch or twig (Higham *et al.*, 2001). Although, during level locomotion, organisms often rely on longer distance movements in the absence of hiding places or refuges, organisms in arboreal habitats have options other than moving in straight lines, so that turning is incorporated in their movements (Jayne & Ellis, 1998; Higham *et al.*, 2001). Increased pausing in terrestrial habitats appears to confer an advantage in predator detection both visually and auditorily (Vasquez, Ebensperger & Bozinovic, 2002). In terrestrial habitats with increased complexity of vegetation, squirrels pause more frequently to better adjust to their surroundings for predator detection and avoidance (Schooley, Sharpe & Van Horne, 1996). Because arboreal habitats are inherently more complex with branches and round, three-dimensional surfaces, it is possible that more frequent pausing could compensate for the difficulties of navigating a complex habitat.

From an energetic perspective, the benefits of pausing are dependent upon a variety of factors such as the distance traveled and time before pausing

(Saltin & Essen, 1971), the speed during motion (Kramer & McLaughlin, 2001), and the influence of the particular environment in which locomotion is taking place (Higham *et al.*, 2001). In addition, the duration of the pause can also influence the benefits. For example, shorter pauses appear to yield the greatest metabolic savings (Gleeson & Hancock, 2001). These factors are often overlooked, making it difficult to assess the overall costs and benefits of pausing (Kramer & McLaughlin, 2001). It takes energy to accelerate and decelerate, and therefore one potential cost of pausing is an increased energy demand on the individual. Ghost crabs, however, benefit from pausing by exhibiting decreased lactate accumulation in the muscle tissue, increasing the length of time that crabs are able to move and the distance that they are able to travel before fatiguing (Weinstein & Full, 1992). From the energetic standpoint, the ability to recover, even in small amounts, from fatigue is considered to be the most important benefit of intermittent locomotion.

To examine potential differences in level and vertical locomotor performance, and to assess how pausing is incorporated into locomotion, we addressed the following questions: (1) is there a difference between maximum acceleration and/or maximum velocity during level versus vertical locomotion; (2) is there a positive correlation between maximum acceleration and maximum velocity during both level and vertical locomotion; and (3) do lizards pause more frequently during vertical locomotion versus during level locomotion? To answer these questions, we quantified vertical and horizontal locomotion in a small semi-arboreal lizard (*Sceloporus woodi*). Sceloporine lizards have a demonstrated capacity for sprinting on a treadmill and moving both vertically and horizontally in its environment (Fig. 1), making them ideal subjects for this performance study (Bonine & Garland, 1999; Bonine, Gleeson & Garland, 2001, 2005). Because of the increased muscular demands of moving vertically, we expected both acceleration and velocity to be lower during vertical movement compared to level locomotion. In addition, we expected to find a positive relationship between maximum acceleration and velocity in both level and vertical locomotion. Finally, we expected the incidence of pauses during locomotor bouts would be equal because we used a vertically oriented log without any branches; thus, it was similar in habitat complexity to our horizontal runway.

MATERIAL AND METHODS

STUDY ANIMALS

We collected 20 male *S. woodi* lizards (Fig. 1) from the Ocala National Forest in Florida under collecting



Figure 1. *Sceloporus woodi* clinging to the side of a tree (A), illustrating their ability to move vertically, and standing on sand (B), illustrating their ability to move horizontally. Note that the posture in (A) is considered a typical head-down foraging posture when on a vertical surface. Both photographs were taken in the Ocala National Forest by Roger Anderson.

permits SEM451 and WX07348B to L.D.M. The average snout–vent length for the lizards was 50.9 ± 0.8 mm. The lizards were shipped to Clemson University and housed individually in 10-gallon aquaria with a sandy substrate. In the laboratory, lizards were fed crickets every other day and provided with water ad libitum. Lighting was maintained under a 12 : 12 h light/dark cycle.

LABORATORY PERFORMANCE TRIALS

Before the laboratory trials, the individuals were warmed to an optimal running temperature of

31–35 °C using an incubator. From a starting stationary position, each individual was encouraged to run on vertical and horizontal surfaces by gently tapping the base of the tail or simply moving a hand towards the lizard. The horizontal surface was a 1-m level wooden trackway with 600 grit sandpaper as a substrate. Flood lights were used to illuminate the field of view, although they were only used for the burst of activity so as not to heat up the room or the lizard. The trackway had plexiglass sides and was approximately 10 cm wide. Lizard movement was recorded using a Photron APX RS camera (Photron USA) operating at 250 fps, an appropriate frame-rate for quantifying maximum velocity and acceleration (Walker, 1998). Second was a vertical ‘trackway’ made of a branchless tree limb mounted vertically on a wall. This tree limb was 11 cm in diameter and had a relatively uniform surface (similar to the horizontal trackway). The diameter was sufficiently large to limit the lizards wrapping their limbs around the tree. We only tested the lizards running up the vertical tree. Each individual ran four to six trials on each surface and the single trial exhibiting maximum acceleration and velocity was retained.

MEASUREMENTS

For each lizard, we digitized the tip of the snout in every video frame using DLTdv3 custom Matlab software (The Mathworks) (Hedrick, 2008). Videos were scaled and x -coordinate data were output from Matlab. Instantaneous velocity was calculated as the first derivative of the displacement data, which was smoothed using a quintic smoothing spline in IGOR PRO software (WaveMetrics). Acceleration was calculated by obtaining the second derivative of the displacement. A pause was defined as a cessation in forward movement (over multiple frames).

STATISTICAL ANALYSIS

We performed linear regressions between maximum acceleration and velocity for level and vertical trials. After verifying the assumptions of parametric tests, we performed paired t -tests on the average number of pauses and the average location of the first pause for level and vertical trials. All analyses were conducted using SYSTAT, version 13 (Systat Software Inc.). $P < 0.05$ was considered statistically significant. All data are reported as the mean \pm SEM

RESULTS

Maximum acceleration across all horizontal trials was in the range 50.8–97.3 ms^{-2} (Figs 2, 3), which corresponds to the range of speeds found by McElroy &

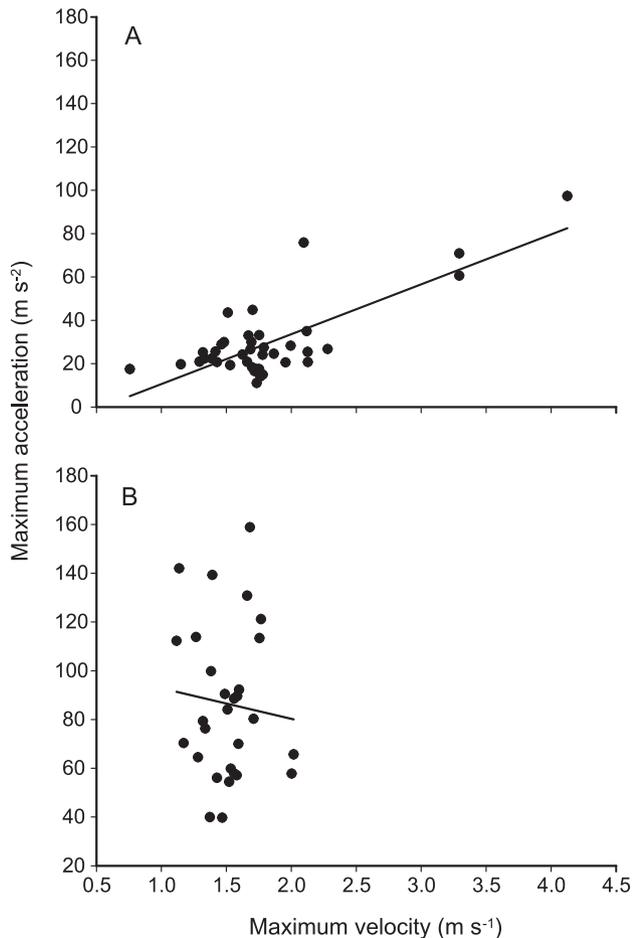


Figure 2. The relationships between maximum acceleration and maximum velocity on the level surface (A; $r^2 = 0.58$; $P < 0.01$) and vertical surface (B; $r^2 = 0.01$; $P = 0.65$) for *Sceloporus woodi*.

McBrayer (2010). Note that Figures 2 and 3 only show the maximum values per individual. Maximum acceleration occurred in almost every case in the first two steps of the run. Maximum velocity across all trials was in the range 2.8–4.1 ms⁻¹ (Figs 2, 3) and, on the horizontal surface, occurred 30.3 ± 2.8 cm from the start.

On the vertical trackway, maximum acceleration across all trials was in the range 103.1–158.9 ms⁻² (Figs 2, 3). Maximum velocity of all trials was in the range 1.8–2.0 ms⁻¹ (Figs 2, 3). Maximum acceleration for vertical acceleration also occurred during the first two steps starting from a stop.

The average number of pauses was significantly less on the horizontal (0.16 ± 0.06) than on the vertical surface (1.56 ± 0.17) ($P < 0.01$; Fig. 4). The average pause location during a run was significantly farther from the starting position on level surface (0.51 ± 0.03 m) than in the vertical trials (0.35 m ± 0.03 m)

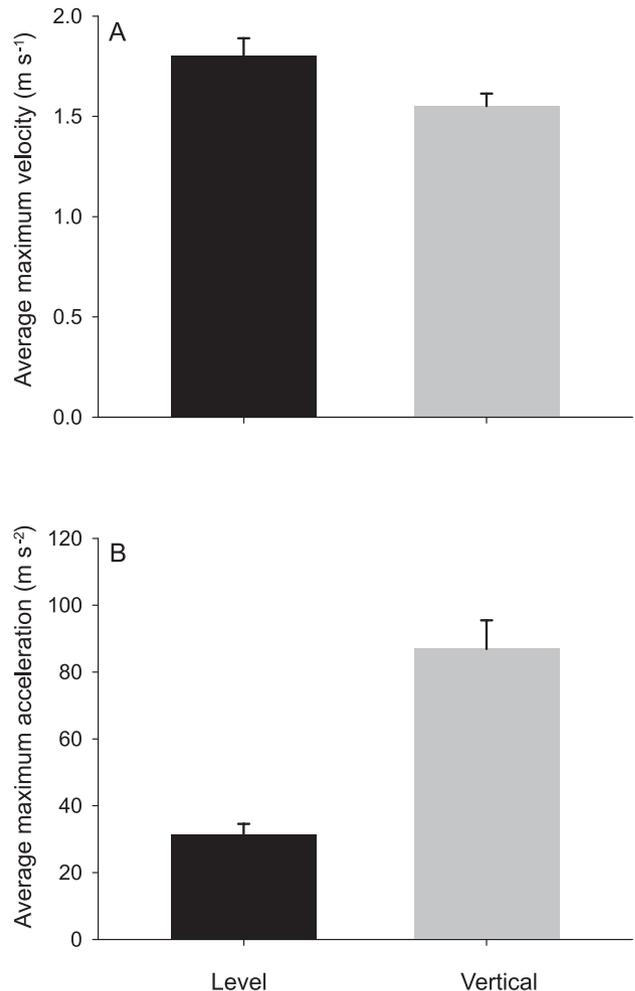


Figure 3. Average level and vertical velocity (A) and acceleration (B) in *Sceloporus woodi*. Note that average velocity was significantly higher on the level compared to the vertical (t -test, $P = 0.03$) and that average maximum acceleration was significantly higher on the vertical compared to the level (t -test, $P < 0.01$).

($P < 0.01$; Fig. 5). Pause duration was variable and depended on the individual.

Maximum acceleration on the level surface was positively correlated with maximum velocity ($r^2 = 0.58$; $P < 0.01$; Fig. 2). However, this was not the case for vertical locomotion (Fig. 2). Maximum velocity was greater on the level compared to the vertical surface (t -test; $P = 0.03$; Fig. 3A). In addition, maximum acceleration was greater for vertical locomotion compared to level locomotion (t -test; $P < 0.01$; Fig. 3B).

DISCUSSION

We compared maximum velocity and acceleration of *Sceloporus woodi* running on level and vertical sur-

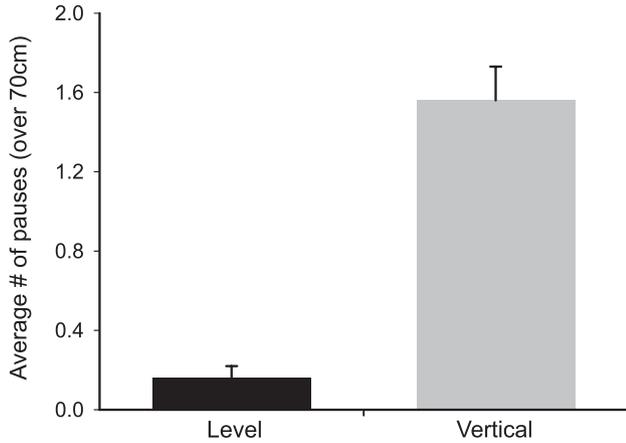


Figure 4. The average number of pauses over the initial 70 cm during level and vertical locomotion. Note that there were significantly more pauses on the vertical compared to the level (t -test; $P < 0.01$).

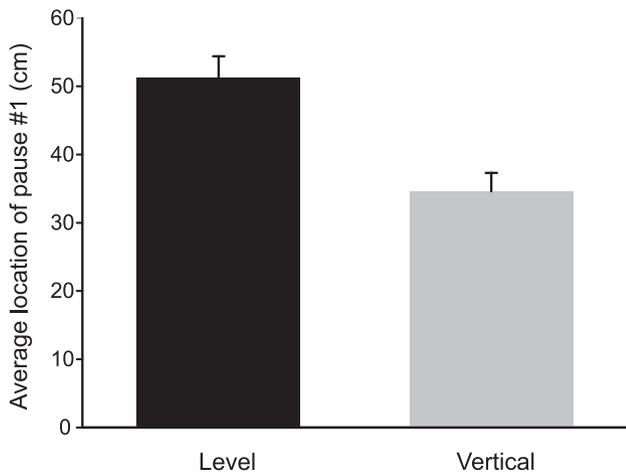


Figure 5. The average location of the first pause during level and vertical locomotion. Note that the average location of the first pause was significantly farther from the start on the level surface compared to the vertical surface (t -test; $P < 0.01$).

faces and found that individuals accelerated faster when moving vertically but reached a lower maximum velocity. This latter point likely reflects the increased frequency of pausing observed for vertical locomotion compared with the level. The consequences and mechanisms of this are discussed below.

PERFORMANCE

Incline can significantly alter locomotor performance in some situations (Astley & Jayne, 2007) but not in others (Huey & Hertz, 1982). The degree to which incline influences performance also varies between

species (Irschick & Jayne, 1998), and likely depends on several factors related to morphology, physiology, and ecology. Because microhabitats that differ in incline can also exhibit differences in structural complexity (e.g. branches, holes, escape routes, and degree of shelter), it is difficult to generalize about the effects of incline on velocity and acceleration in a diverse array of species. However, intraspecific studies yield critical information regarding the effects of habitat on locomotion. For *S. woodi*, maximum velocity on the level surface was positively correlated with maximum acceleration (Fig. 2A). However, maximum velocity decreased from level to vertical locomotion but maximum acceleration increased (Fig. 2B). Relative to acceleration, longer distances are often required for an animal to reach maximum velocity (Huey & Hertz, 1982). Given this, perhaps the increased pausing on the vertical surface limited maximum velocity by limiting the duration (or distance) in which maximum velocity could be attained. However, the average distance in which maximum velocity was reached on the level surface was 30.3 cm, which precedes the average location of the first pause on the vertical surface (34.6 cm). Thus, it is conceivable that the individuals on the vertical surface could have achieved an equivalent maximum velocity as the horizontal trials, assuming that the acceleration profiles were comparable.

Why then do the trials in the vertical treatment exhibit a lower maximum velocity? We suggest three possible explanations. First, lizards must accelerate and decelerate during locomotion. Perhaps the distance required to accelerate and decelerate exceeds the distance from the start to the first pause on the vertical surface (34.6 cm). Thus, the total distance might be gauged by the lizard and an appropriate maximum velocity selected. Second, the increased acceleration on the vertical surface might require a sufficient increase in energy (as a result of increased muscle power output) that maximum velocity is lower relative to the horizontal surface. Third, very high continuous accelerations can cause small animals to pitch upward at the start of a level run (Aerts *et al.*, 2003). Thus, large accelerations on a vertical surface may cause the body to be pushed away from the tree and thereby increasing the risk of falling. By decelerating and/or pausing after a few high accelerative steps, animals maintain their purchase on the tree, yet rapidly move up the surface. The net result of this is: (1) energy conservation because of not employing high power output over a great distance and (2) a lower maximal velocity because the animal must decelerate to maintain its balance or grip. Indeed, during the vertical running trials, several animals accelerated over distances greater than 34 cm, and ultimately launched themselves off the tree into the

air. They did not appear to be jumping but rather are running so fast that they lost their purchase on the tree trunk.

Unlike maximum velocity, maximum acceleration is commonly achieved within the first one or two steps (McElroy & McBrayer, 2010). Thus, we would not necessarily expect to see a decrease in acceleration on the vertical surface compared to the horizontal. However, the increased acceleration relative to level running is somewhat puzzling. Given their ability to accelerate when moving up a vertical tree, we likely did not elicit the maximum acceleration capacity of the individuals on the level surface. Given that the lizards were stimulated in exactly the same way and our data are comparable to the level running data reported by McElroy & McBrayer (2010), it appears that *S. woodi* adjusts its behaviour when on the level surface so as not to exert itself as it does on the vertical. Field observations of acceleration on the two surfaces are required to corroborate our observations in the laboratory.

Why was acceleration performance lower on the level surface? One possibility is that, on a level surface, the distance to the next refuge is sufficiently long enough to preclude accelerating maximally as a result of high energy consumption. In other words, it would be too costly to accelerate maximally and then maintain a high velocity for a longer period of time. If the distance to the closest refuge is shorter in an arboreal habitat, maximum acceleration would be possible given that the total running distance is lower. This is an important consideration because pausing would allow for removal of lactate (Saltin & Essen, 1971) that would quickly build up if acceleration was maximal.

Alternatively, the characteristics of an arboreal habitat might necessitate a greater acceleration as a result of the pausing that results from the complex structure that often characterizes arboreal habitats. If an animal is being pursued by a predator, or is pursuing a prey item, faster accelerations might offset (to some degree) the relatively low maximum velocity that the animal can achieve. In other words, the total duration of movement over a comparable distance could be similar between a level and vertical habitat, although this duration might be reached via different mechanisms. This was the case for some of the individuals in our study. For example, those individuals that exhibited relatively short pause durations ended up with comparable durations of activity. However, some individuals pause for longer periods of the time, resulting in longer activity durations compared to level trials. Alternatively, other ecological factors might necessitate higher accelerations in an arboreal habitat, such as arboreal-specific predators.

WHY PAUSE?

Intermittent locomotion can result from many factors, which can be related to energetics (Weinstein & Full, 1999; Kramer & McLaughlin, 2001), predator avoidance (Schooley *et al.*, 1996; Vasquez *et al.*, 2002), predator detection (Avery *et al.*, 1987), vigilance (Vasquez *et al.*, 2002), processing sensory information (Avery *et al.*, 1987), and dealing with habitat structure (Higham *et al.*, 2001). We found that incline can also alter the degree of intermittent locomotion in *S. woodi*, which might have resulted from multiple factors.

Given that habitat structure can significantly alter locomotion in lizards, it is possible that the lizards in our study associated the vertical surface with a complex arboreal habitat, resulting in more pauses. For example, the complex structure in an arboreal habitat creates the need for more pausing, whether to determine which path to choose (Higham *et al.*, 2001; Mattingly & Jayne, 2004) or simply to reestablish proper bearings with the presence of branches, holes, and a three-dimensional surface (Kohlsdorf & Biewener, 2006; Cooper & Wilson, 2007). The idea that complex habitat structure can increase intermittent locomotion is supported by a study of three ecomorphs of *Anolis* lizards (Higham *et al.*, 2001), in which pausing was quantified as the lizards ran on a straight perch, a perch with a 30° turn angle, and a perch with a 90° turn angle. All species exhibited an increase in the frequency of pausing as turning angle increased, suggesting that the complexity of the habitat forced the animals to pause. As noted above, our set-up did not include increased complexity on the vertical trials, although there may be an association between vertical running and a complex habitat.

Increased pausing can minimize energy expenditure during locomotion. Whether the movement is long or short distance, continuous locomotion generally results in earlier fatigue than shorter movements interrupted by pauses (Kramer & McLaughlin, 2001). For example, frog-eyed geckos, *Teratoscincus przewalskii*, benefit from intermittent locomotion in that they are able to travel longer distances before fatigue (Weinstein & Full, 1999). In the desert iguana, *Dipsosaurus dorsalis*, pauses allow for higher recovery and increased endurance (Hancock & Gleeson, 2005). Although intermittent locomotion is generally considered advantageous, it can also increase the cost of locomotion as a result of repeated bouts of acceleration and deceleration (Alexander, 1989, 2000). Thus, pausing is only beneficial under certain circumstances. Given that we found increased pausing on the vertical surface, the energetic benefit is likely greater in this context than when running on level surfaces. This is not surprising given that moving vertically is energetically more costly because the

animal must increase its potential energy with each stride (Roberts *et al.*, 1997; Daley & Biewener, 2003; Higham & Jayne, 2004; Higham & Biewener, 2008). Future ecological observations and laboratory work incorporating measures of oxygen consumption will determine why intermittent locomotion might differ between vertical and level locomotion (Cooper & Wilson, 2007).

CONCLUSIONS AND FUTURE WORK

The present study revealed that maximum locomotor performance is context-specific, and that maximum velocity and acceleration change in different ways. It is clear that pausing is common during vertical, but not level, locomotion in *S. woodi*. It is ultimately unclear from the present study whether the increased pausing during the vertical trials is the result of the vertical aspect of the locomotion or because of arboreal environments, where there would often be increased structural complexity. Providing lizards with a bare trunk and one with branches could make it possible to assess whether lizards pause because of structure complexity or because of the demands of vertical movement. Most studies focus on performance in a single microhabitat, as we did with either level locomotion or vertical locomotion. Future work could give lizards a choice of different escape routes that vary in substrate inclination and structural complexity (e.g. branches) of the perches. Such experiments will allow us to better understand what prompts individuals to select certain microhabitats.

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