

RESEARCH ARTICLE

The effects of multiple obstacles on the locomotor behavior and performance of a terrestrial lizard

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ABSTRACT

Negotiation of variable terrain is important for many small terrestrial vertebrates. Variation in the running surface resulting from obstacles (woody debris, vegetation, rocks) can alter escape paths and running performance. The ability to navigate obstacles likely influences survivorship through predator evasion success and other key ecological tasks (finding mates, acquiring food). Earlier work established that running posture and sprint performance are altered when organisms face an obstacle, and yet studies involving multiple obstacles are limited. Indeed, some habitats are cluttered with obstacles, whereas others are not. For many species, obstacle density may be important in predator escape and/or colonization potential by conspecifics. This study examines how multiple obstacles influence running behavior and locomotor posture in lizards. We predict that an increasing number of obstacles will increase the frequency of pausing and decrease sprint velocity. Furthermore, bipedal running over multiple obstacles is predicted to maintain greater mean sprint velocity compared with quadrupedal running, thereby revealing a potential advantage of bipedalism. Lizards were filmed running through a racetrack with zero, one or two obstacles. Bipedal running posture over one obstacle was significantly faster than quadrupedal posture. Bipedal running trials contained fewer total strides than quadrupedal ones. But on addition of a second obstacle, the number of bipedal strides decreased. Increasing obstacle number led to slower and more intermittent locomotion. Bipedalism provided clear advantages for one obstacle, but was not associated with further benefits for an additional obstacle. Hence, bipedalism helps mitigate obstacle negotiation, but not when numerous obstacles are encountered in succession.

KEY WORDS: Scrub lizard, *Sceloporus woodi*, Bipedal, Quadrupedal, Sprint locomotion, Velocity

INTRODUCTION

The ability to exploit a range of habitats and substrates is important to the survival of most animals. Limbed terrestrial vertebrates routinely traverse uneven terrain in three-dimensionally complex environments. Thus, the ability of animals to efficiently move across terrain containing obstacles is important for key ecological tasks, such as escaping from predators, thermoregulation, dispersal and finding mates (Vanhooydonck et al., 2005; Dickinson et al., 2000). The physical substrate is often composed of vegetation, rocks, woody debris, sand and a variety of other uneven surfaces (Collins et al., 2013). Uneven substrates directly affect the locomotion of

animals by altering the transmission of locomotor forces (Tulli et al., 2012; Higham et al., 2001), influencing maneuverability and the ability to evade predators by sprinting. Furthermore, substrate unevenness requires adjustments in posture and velocity (Collins et al., 2013; Birn-Jeffery and Daley, 2012).

Certain vegetation or substrata (e.g. dense bunchgrass, loose sand) impede small terrestrial vertebrates' (e.g. mammals and lizards) ability to navigate through, in, on and over such habitat structures (Rieder et al., 2010). Some rock-dwelling lizard species, such as *Crotaphytus bicinctores*, frequently encounter uneven surfaces and are less sensitive to changes in the degree of substrate unevenness than smaller sand-dwelling species (Collins et al., 2013). This suggests that complex interactions between kinematic adjustments and specialized morphological structures are an important aspect of locomotion in species that move over uneven substrata. Species that occupy rocky habitats sprint and climb faster than species from leaf litter-dominated habitats, presumably because of selection for longer hind limbs (Goodman et al., 2008). A reduction in limb length and an elongation of the body has evolved as an adaptive response to locomotion through dense vegetation, thus revealing the important role that habitat structure plays in the evolution of morphology and performance of terrestrial organisms (Goodman, 2009; Goodman et al., 2008).

Obstacle negotiation has been studied among a variety of species including guinea fowl (Daley and Biewener, 2011; Clark and Higham, 2011), humans (Sparrow et al., 1996; Perry et al., 2010), cats (McFadyen et al., 1999), cockroaches (Harley et al., 2009) and lizards (Kohlsdorf and Biewener, 2006; Kohlsdorf and Navas, 2007; Olberding et al., 2012; Tucker and McBrayer, 2012; Self, 2012). To negotiate obstacles, anticipatory adjustments are essential for locomotion (McFadyen et al., 1999), especially if postural adjustments are to be timed appropriately. Domestic cats adjust the coordination of their locomotion at the hip and ankle joints to clear obstacles (McFadyen et al., 1999). When humans approach an obstacle (e.g. hurdles), lower limb control is altered by means of knee flexion (McFadyen et al., 1999) in anticipation of the approaching obstacle. However, as obstacle height increases, the lead foot must cross earlier during a stride to allow more time to traverse the higher obstacle, implying that stride length is modified also (Sparrow et al., 1996). Thus, kinematics, behavior and stride length are each adjusted in order to clear an obstacle without contacting it and potentially stumbling (Self, 2012).

Animals often alter their locomotor behavior in response to a change in substrate or its unevenness (Iraeta et al., 2010). Many lizard species switch between quadrupedal and bipedal running posture during locomotion (Snyder, 1952, 1962). The alteration of running posture constitutes a change in locomotor behavior, particularly if in response to a consistent variable such as an obstacle. Bipedal running occurs when the animal lifts its front limbs off the ground above its center of gravity, leaving only the hind limbs in contact with the substrate (Snyder, 1952). Bipedal

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List of abbreviations

AVI	audio video interleave
B	bipedal
COM	center of mass
CWD	coarse woody debris
HLL	hind limb length
Q	quadrupedal
SVL	snout-to-vent length

locomotion may enhance environmental perception in the presence of physical barriers, and may enlarge the animal's visual field by elevating the trunk above the obstacle before crossing (Kohlsdorf and Biewener, 2006; Tucker and McBrayer, 2012). For quadrupeds crossing obstacles, bipedality allows the body's center of mass (COM) to move over the obstacle without extensive change in vertical height (Olberding et al., 2012). Maintaining a balance between body stability and energy expenditure on uneven terrain is important to cursorial avian bipeds, ranging from quail to the larger ostrich (Birn-Jeffery et al., 2014), as well as to smaller, non-avian facultative bipedal species.

Despite the widespread occurrence of bipedalism, the specific biological advantage of the posture to facultative bipeds has remained unclear. A bipedal posture may decrease energy expenditure by having only two limbs in motion (Kohlsdorf and Biewener, 2006; Snyder, 1952, 1962). Alternatively, a bipedal posture may be a mechanical consequence of rapid initial acceleration. Here, the torque generated by the hip would cause a pitching rotation that lifts the head and trunk (Aerts et al., 2003; Van Wassenbergh and Aerts, 2013). Yet for several lizard species, acceleration is not a prerequisite for sustained bipedal running (Van Wassenbergh and Aerts, 2013). Active tail lifting during acceleration results in the upward rotation of the trunk through increased angular momentum of the tail, making sustained bipedal running possible at lower acceleration (Aerts et al., 2003; Clemente, 2014). However, even though bipedal running can be sustained on unobstructed trackways, it may not be maintained during obstacle negotiation by lizards. For example, the six-lined racerunner (*Aspidoscelis sexlineatus*) does not continue running with a bipedal gait after obstacle contact, despite its frequent use of bipedal posture (Olberding et al., 2012).

Nevertheless, bipedal running may be an advantageous behavioral choice when negotiating obstacles such as vegetation or woody debris. Dense vegetation impacts locomotor performance of lizards by increasing the frequency of intermittent locomotion, or the extent of pausing, and/or to adjust balance between locomotor bouts (Higham et al., 2011a). Because obstacles can be common in some habitats (Collins et al., 2013, 2015), it is likely that the presence and size of obstacles may influence an animal's decision to move intermittently and change body posture (Tucker and McBrayer, 2012). It has been shown that lizards increase vertical limb motion and elevate the head and trunk when approaching an obstacle. This change is often coupled with a decrease in locomotor speed and an increase in the frequency of bipedalism (Kohlsdorf and Biewener, 2006). If lizards cannot sprint at (or near) maximum capacity, then their ability to elude predators would be affected (McMillan et al., 2011; De Barros et al., 2010; Okafor, 2010), particularly on uneven substrates containing obstacles. Whereas some studies have examined bipedal locomotion in lizards from a biomechanical standpoint (Hsieh and Lauder, 2004; Kohlsdorf and Biewener, 2006; Olberding et al., 2012; Van Wassenbergh and Aerts, 2013), the present study will examine a mechanistic link

between bipedalism and ecologically relevant features of the habitat (obstacles).

Surprisingly, studies have yet to develop a firm understanding of how bipedal running in lizards is generated and maintained. Tail elevation is likely important, as a horizontal tail could aid in locomotion over the obstacle (Hsieh, 2003; Self, 2012). In the case of the basilisk lizard, holding the tail horizontally acts as a counterbalance in forward locomotion and generates thrust to propel the animal forward during bipedal running on water (Snyder, 1962; Hsieh, 2003). Or, a horizontal tail may counterbalance the weight of the increased body angle during bipedal running, as it would position the COM of the tail as far as possible from the center of the hip (Irschick and Jayne, 1999b), thus providing a potential benefit for lizards using a bipedal running posture. In contrast, elevating the tail ~12–15 deg above a horizontal plane allows lizards to sustain bipedal running at lower accelerations (Van Wassenbergh and Aerts, 2013; Aerts et al., 2003; Clemente, 2014). However, studies have yet to show that bipedal running can be sustained when lizards negotiate obstacles (Olberding et al., 2012).

Questions and predictions

Despite many habitat types being replete with uneven substrata and various obstacles, studies of animal locomotion over obstacles are limited. The goal of this project is to understand how multiple obstacles affect sprint performance and behavior, and how a bipedal running posture is related to each. To do so, we collected individuals from the field, returned them to a field lab, and chased each down a 1 m sprint racetrack while filming with high speed video. The presence, absence, and/or number of obstacles were randomized by a series of coin flips for each individual. A single sprint trial of each individual in any treatment was retained for analysis.

We will answer the following four questions. First, does mean sprint velocity and locomotor posture differ between running with or without obstacles? We predict that the frequency of bipedal running strides will be greater when lizards encounter obstacles compared with those who do not. We predict that lizards will show a decrease in sprint velocity and an increase in intermittent locomotion when encountering obstacles as opposed to running without them. Second, is bipedal posture a more efficient method of locomotion for lizards when crossing obstacles? Here, efficiency is defined as maintaining a constant velocity with minimal stumbling or stopping. Note our application of the term 'efficiency' is not in reference to energetic efficiency. Instead, we use efficiency in terms of sustained forward locomotion. We quantified this aspect of efficiency in three ways (A,B,C). We predict: (A) lizards running with a bipedal posture while crossing obstacles will retain higher sprint velocity than lizards that only use quadrupedal running to do so; (B) the frequency of intermittent locomotion will decrease when a bipedal posture is used compared with quadrupedal running because bipedalism should allow the animal to step over, not on, the obstacle (Olberding et al., 2012; Self, 2012); and (C) if lizards run with a bipedal posture they will complete the trial in fewer strides than those that run with a quadrupedal gait. Third, will the tail be elevated, or lowered, during bipedal running as the animal crosses an obstacle? We predict the tail will be lowered below the hip height to shift the COM posteriorly when lizards cross obstacles using a bipedal posture. In addition, we predict that a bipedal posture will be associated with a greater body angle and hip height than a quadrupedal posture when crossing obstacles. Fourth, we ask if sprint velocity and intermittent locomotion vary between lizards running across a single versus multiple obstacles. We predict that multiple obstacles will result in a decrease in sprint velocity

compared with a single obstacle, and that the frequency of intermittent locomotion will be greater when there are multiple obstacles compared with only a single obstacle.

Study species

This study focused on locomotor behavior and performance in the Florida scrub lizard *Sceloporus woodi* Stejneger 1918, a species restricted to the sand pine scrub habitat in central Florida (Jackson, 1973). The scrub lizard is a diurnally active, ground-dwelling lizard that uses flat, sandy areas to sprint away from predators (Hokit et al., 1999; Tucker and McBrayer, 2012), and is capable of accelerating to near maximum sprinting speed over a short distance (0.4 m; McElroy and McBrayer, 2010). This species has a demonstrated capacity for sprinting (McElroy et al., 2012; Higham et al., 2011a,b), and commonly employs a bipedal gait while sprinting over obstacles (Fig. 1A) (Tucker and McBrayer, 2012). Disturbance and habitat fragmentation are major impediments to scrub lizard dispersal, survival (Tiebout and Anderson, 2001) and likely locomotion. Furthermore, this species encounters various obstacles and substrates that result from forest management practices (clear-cut logging), which generate considerable amounts of coarse woody debris (CWD) (Tiebout and Anderson, 2001). Scrub lizards prefer shaded open sand substrates, and avoid CWD that may be thermally stressful and impede locomotion (Tiebout and Anderson, 2001). As its scrub habitat is frequently disturbed, lizards must seek new suitable sites without high densities of CWD (i.e. obstacles to maneuver over). Given this, studying running performance and obstacle negotiation is relevant from a mechanistic and an ecological standpoint.

MATERIALS AND METHODS

Field collection

Field work was conducted within the Ocala National Forest (ONF) located in Marion County, Florida. The ONF covers over 180,000 hectares in central Florida and contains the largest remaining continuous area of scrub habitat (Greenberg et al., 1994). Lizards were collected in the ONF throughout a single field season from May to August 2013. Animals were captured within recently disturbed sand pine scrub stands and in longleaf pine islands. Lizards were captured with a slip noose, and temporarily housed in numbered cloth bags in a cool environment. Field active temperature was measured with a cloaca thermometer (Miller and Weber Inc., Richmond, VA, USA) immediately upon capture to ensure each lizard's body temperature during performance trials was kept similar to those experienced naturally. Only adult males were used as females alternate in gravidity throughout the season, and this affects their locomotor performance (Sinervo et al., 1991; Iraeta et al., 2010). Following sprint trials (see below), each lizard was paint-marked and released at the original point of capture. Research in the Ocala National Forest was conducted under protocol with the Institutional Animal Care and Use Committee (IACUC permit no. I12007) and permission from the US Forest Service (USFS permit no. SEM540).

Sprint trials were conducted in a field laboratory within 24 h of capture. We measured the sprint velocity and behavior of 48 adult males [mean snout-to-vent length (SVL) 47.2 ± 0.18 mm; mean hind limb length (HLL) 39.8 ± 0.14 mm]. For the analysis of intermittent locomotion, we included multiple sprints per individual for a

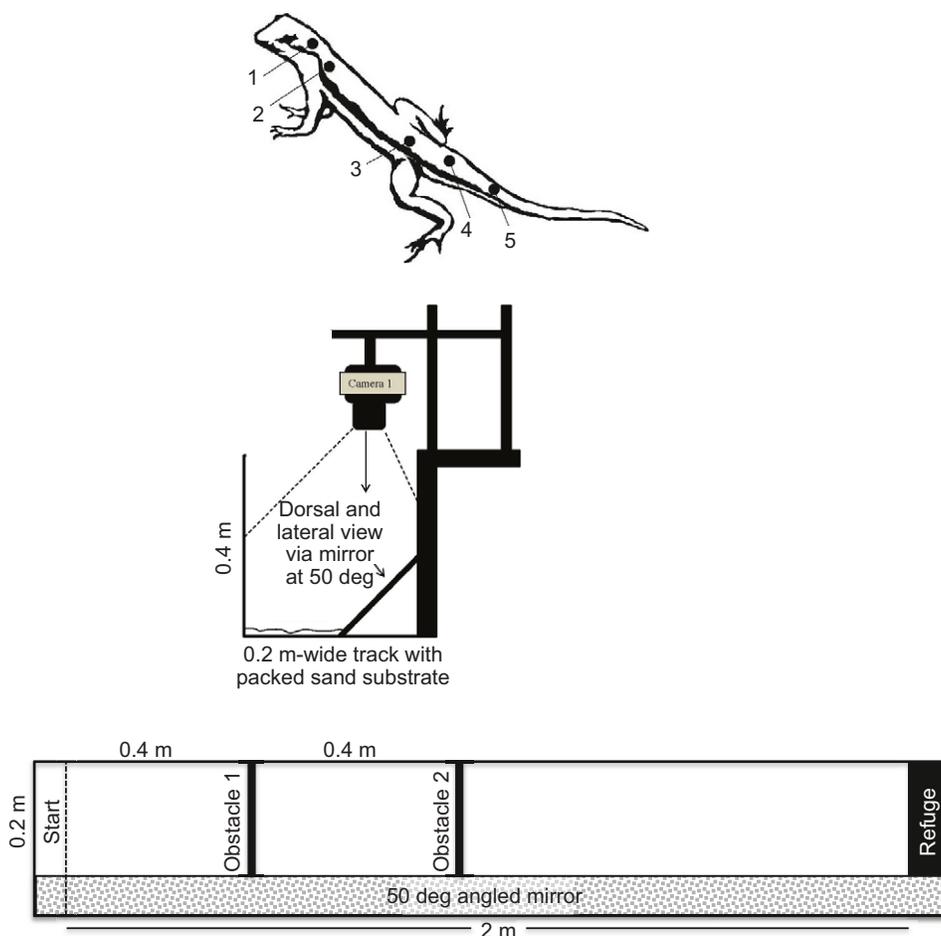


Fig. 1. Schematic diagram of the points digitized and the raceway. (A) Anatomical landmarks digitized: (1) head (posterior to the pineal eye), (2) shoulder girdle, (3) hip (tip of the ilium), (4) base of the tail and (5) 40% of the tail length from its base. (B) View from the starting position down the raceway. (C) View of the racetrack from above showing treatment 2. A series of coin flips were used to randomly assign each trial to an obstacle treatment (0, 1 or 2 obstacles). Obstacle spacing in treatment 1 was 0.4 m from the start position, and in treatment 2 obstacles were placed at 0.4 m and 0.8 m, respectively. Wooden obstacles were cut to heights equaling 35% of the hind limb length of the lizard in the trial. Both dorsal and lateral views were present in each camera.

sample size of 102. Sprint trials were conducted in a rectangular, wooden racetrack (2.4 m long×0.2 m wide with 0.4 m-high sides) that was used to quantify sprint performance, body posture and behavior (Fig. 1B). The substrate was 0.5 in of packed sand for all trials. Each lizard was randomly assigned to one of three obstacle treatment groups immediately prior to a trial. The treatments groups were: 0, no obstacle; 1, a single obstacle; and 2, two obstacles. To avoid pseudo-replication, an individual is only represented one time in the data set; individuals were not re-used in multiple treatments. In each treatment, obstacle height and width was standardized to 35% of the hind limb length for each lizard in each trial. This obstacle size allowed continuous locomotion (Self, 2012). Obstacles were constructed of standard lumber cut to the desired size height and depth; each was 0.2 m wide in order to span the track. Obstacles fit flush with the track sidewalls and across the running path. Lizards could not hide under, or maneuver around, the obstacle. The surface of the obstacle was not treated in any way. In treatment 0, lizards ran without an obstacle. *Sceloporus woodi* can reach near maximum velocity by 0.4 m (McElroy and McBrayer, 2010). Hence in treatment 1, one rectangular obstacle was placed in a perpendicular orientation to the running path of the lizard 0.4 m from the starting point. Treatment 2 consisted of two rectangular obstacles of equal dimensions placed at 0.4 m and 0.8 m from the start. The two obstacles were placed 0.4 m apart so that the lizards would not be able to jump from one obstacle to the other, and might reach maximum velocity once again after crossing the first obstacle.

Trials were filmed with two Casio Exilim EX-F1 high speed digital cameras (Dover, NJ, USA) at 300 frames s^{-1} . Both cameras filmed dorsolaterally from above the track. Each camera had a 0.5 m field of view and captured both a dorsolateral view of the running lizard and its reflection in a mirror on one side of the track. The mirror was angled at 50 deg to ensure that the lateral side of the lizard would be in view. Lizards were warmed to 34–38°C in an incubator for 1 h prior to running. Individuals were placed at the starting position, released, and chased down the track using light tail-taps, loud hand-clapping, etc., to coerce them toward a dark refuge. Each lizard was run 2–4 times to try to get a single successful trial for each. A trial was considered successful and retained for sprint performance analysis if the lizard completed the 1 m distance in a continuous run. If a lizard paused, ran into the mirror or reversed direction, then the trial was not included in the analysis of sprint data, although such observations were recorded to describe locomotor behavior.

Morphological measurements

Prior to performance testing, three morphological measurements were taken on each individual using a ruler or dial caliper (General Hardware Manufacturing Co., New York, NY, USA) accurate to 0.01 m. Hind limb length was measured from the hip joint to the tip of the longest toe with a caliper and averaged between both hind limbs. Snout-to-vent length and tail length (original tail and newly regenerated) were measured using a ruler. These measurements determined proper obstacle height for each lizard. Only adult males with a snout-to-vent length of at least 42 mm were included in the study.

Video analysis and statistics

Each video was digitally clipped and converted to a compressed file (.AVI) using Adobe Premiere Pro Elements software (San Jose, CA, USA). These files were then viewed in DLTdv5, a video digitization program within MATLAB software (Natick, MA, USA; Hedrick,

2008). Videos were calibrated using a custom 30-point calibration cube. A scale bar with 10 cm increments was visible on the racetrack; it was digitized in order to standardize the distance (in pixels) for each video. Prior to performance trials, five anatomical landmarks were painted on each lizard using non-toxic white paint (Fig. 1). Posterior to the pineal eye, a mark was drawn on the top of the head to use as a landmark for manual digitization of the body position and subsequently calculate sprinting velocity ($m s^{-1}$). To smooth digitization errors, velocity data was reviewed line by line in a spreadsheet. Single observations of very large values (values $\geq 3.5 m s^{-1}$ observed for 1/300 s) were deleted and replaced by the average of the five adjacent velocity values. Very few lizard species, and this species in particular, are known to sprint over $3 m s^{-1}$, hence this cutoff is justifiable. Furthermore, a smoothing filter was applied to a subset of trials, yet did not perform as well as this method.

Obstacle crossing posture (bipedal or quadrupedal) was quantified at the last full stride before coming in contact with the first obstacle. Obstacle crossing behavior was determined by whether a hind foot touched (on) the obstacle, or whether the animal cleared (i.e. stepped over) the obstacle with no contact. The frequency of bipedal and quadrupedal running was measured as the number of full strides completed using each posture, whereas total strides were quantified as the total number of combined strides within each trial (bipedal+quadrupedal strides). Strides were defined as the initial footfall of the hind limb and a subsequent footfall of the same hind limb. If a stride was completed with no contact from the front limbs, then it was classified as bipedal. Alternatively, the total number of strides of each posture was quantified by counting the total number of strides completed with a bipedal posture, versus the total number of strides using a quadrupedal posture. Intermittent locomotion (frequency of pausing within a trial) was also quantified.

Hip height, tail elevation, and body angle were measured at mid-stance of the last full stride before reaching the obstacle at 0.4 m. Trials without an obstacle could also be compared, given that the first obstacle was placed at 0.4 m, by measuring these three variables at this same position (0.4 m) during a trial in treatment 0. Hip height was measured as the distance from the hip mark on the ilium to the substrate in centimeters. To determine tail elevation, paint marks were placed at the base of the tail and 40% of the tail length from the tail base (Fig. 1A). The vertical distance in centimeters between the base of the tail and the substrate directly below the tail point was compared with the distance between the 40% tail length mark and the substrate below. Negative values indicate that the distance between the base of the tail and substrate was greater than the distance between the 40% tail length mark and substrate, thus resulting in a tail that was lowered below the hip height. Only lizards with original unbroken tails were used in this analysis. Body angle was quantified by calculating the angle (in deg) between the marks on the shoulder and the hip (ilium) relative to two horizontal points on the substrate. Positive values indicate the shoulder is higher than the hip to give an elevated body angle, whereas negative values indicate the body is angled toward the substrate. Data were analyzed with one-way ANOVAs with Tukey–Kramer *post hoc*, Welch's ANOVA, Kruskal–Wallis and Chi square tests. All statistical tests were performed using JMP Pro v10.0 software (Cary, NC, USA); alpha was the standard $P < 0.05$. Forty-seven percent of all trials (48/102) were analyzed for the study, though data from all trials across all treatments ($N=102$) were used to test predictions regarding intermittent locomotion.

Table 1. Locomotor performance and behavior of *S. woodi* running over obstacles

Variable	<i>N</i>	0 obstacles (<i>n</i> =14)	With obstacle (<i>n</i> =34)	1 obstacle (<i>n</i> =20)	2 obstacles (<i>n</i> =14)
Behavior (on/over)	34	–	9,25	6,14	3,11
Crossing posture (B,Q)	34	–	14,20	10,10	5,9
Posture at 0.4 m (B,Q)	48	5,9	15,19	10,10	5,9
Velocity (m s ⁻¹)	48	2.3±0.06 ^A	2.4±0.05	2.9±0.09 ^A	2.5±0.07 ^A
Bipedal velocity	35	2.3±0.05	–	2.6±0.07 ^B	2.2±0.04 ^C
Quadrupedal velocity	22	2.3±0.16	–	2.2±0.08 ^B	2.1±0.15 ^C
B velocity – over	13	–	2.5±0.07 ^D	–	–
Q velocity – over	12	–	2.3±0.08 ^D	–	–
Pauses	102	0.44±0.1	0.6±0.09	0.54±0.15	0.61±0.1
Total strides	48	7.0±0.27	6.74±0.18	6.7±0.22	6.9±0.29
Bipedal strides	48	1.6±0.4	1.9±0.3	2.1±0.45	1.5±0.27
Total strides with bipedal	35	6.7±0.37 (<i>n</i> =9)	6.6±0.20 (<i>n</i> =26)	6.5±0.27	6.6±0.32
Total strides with quadrupedal	13	7.6±0.24 (<i>n</i> =5) ^E	7.3±0.3 (<i>n</i> =8) ^E	7.0±0.32	7.7±0.7

Data are presented as either frequency or means±s.e.m. for performance and behavior among obstacle treatments. Total sample size is indicated (*N*), as well as the sample size for each treatment (*n*). Behavior was quantified as stepping on or over the obstacle. Posture (B, bipedal or Q, quadrupedal) was quantified in the stride prior to the obstacle. Posture at 0.4 m was quantified as the posture at this position in treatment 0 (no obstacle) and obstacle treatments (1–2). Dashes indicate variables that could not be quantified for the specified condition. Posture velocity was excluded from the ‘with’ column as it was not necessary to analyze all trials together. B and Q velocity is presented for trials where the lizard stepped over (not on) the obstacle. Total strides (excluding/ignoring posture) and bipedal strides were counted across the one meter trial. Total strides (including/with posture) were quantified as the sum number of strides completed when the specified posture was used at any point in the trial. Shared superscript letters A–E indicate a significant difference at $P \leq 0.05$.

RESULTS

Performance, posture and behavior between trials with and without an obstacle

Mean velocity (m s⁻¹) over the 1 m track was not significantly different between all treatments with obstacles (treatment 1+2) and without (treatment 0) ($\chi^2_{1,48}=0.27$; $P=0.60$). For trials without an obstacle, sprint velocity was not significantly different between those containing bipedal running and those containing only quadrupedal running ($F_{1,12}=0.202$; $P=0.661$) (Fig. 2). There was also no difference in velocity of bipedal running with an obstacle compared with bipedal running without obstacle ($F_{1,33}=0.7337$; $P=0.398$). The frequency of the use of bipedal posture prior to the obstacle was not significantly greater with obstacles present than without ($\chi^2_{2,46}=0.291$; $P=0.590$). Lizards averaged 6.74±0.18 total strides along the 1 m track when facing an obstacle, compared with 7.0±0.27 total strides without an obstacle ($\chi^2_{2,46}=0.875$; $P=0.350$) (Table 1). Lizards averaged 1.9±0.3 bipedal strides over the 1 m run when an obstacle was present, and 1.6±0.4 bipedal strides without an obstacle ($\chi^2_{2,46}=0.352$; $P=0.553$) (Table 1). Hence, neither the total number of strides, nor the number of bipedal strides, used with an obstacle was different. An alternative stride analysis was also used to tease apart trials containing bipedal running. Here, the total stride number was quantified between lizards using a bipedal posture at any point during the 1 m run and those using only quadrupedal running throughout the 1 m run. All treatments (0–2) were combined in this analysis; low sample sizes made it impossible

to compare among each obstacle treatment. Lizards using a bipedal posture completed the 1 m run in significantly fewer total strides (6.6±0.17) than those using only a quadrupedal posture (7.4±0.21) ($\chi^2_{2,46}=5.807$; $P=0.016$) (Fig. 3, Table 1). Finally, there was no significant difference in the frequency of pausing with obstacles versus without ($\chi^2_{1,100}=0.195$; $P=0.659$).

Bipedal versus quadrupedal locomotion over obstacles

The frequency of each posture used was analyzed independently within each obstacle trial to see if increasing obstacle number would elicit the same behavioral change. Posture was quantified during the last full stride prior to crossing each obstacle. In treatment 1, the observed frequencies of bipedal (B) and quadrupedal (Q) posture before the first obstacle were not different (50% Q; 50% B; $\chi^2_{1,19}=0.0$; $P=1.0$). In treatment 2, the frequency of a given posture was not different before the first obstacle (64.3% Q; 35.7% B; $\chi^2_{1,13}=1.143$; $P=0.285$); however, a quadrupedal posture was used significantly more before the second obstacle (93% Q; 7% B; $\chi^2_{1,13}=10.286$; $P=0.0013$).

Mean velocity and the frequency of each posture were analyzed between obstacle-crossing behaviors (stepping on versus stepping over the obstacle) for obstacle treatments (1–2). This analysis examined whether stepping over an obstacle using a bipedal posture was faster than stepping over with a quadrupedal posture. No significant difference in velocity between postures was found among obstacle-crossing behaviors (stepping on versus over)

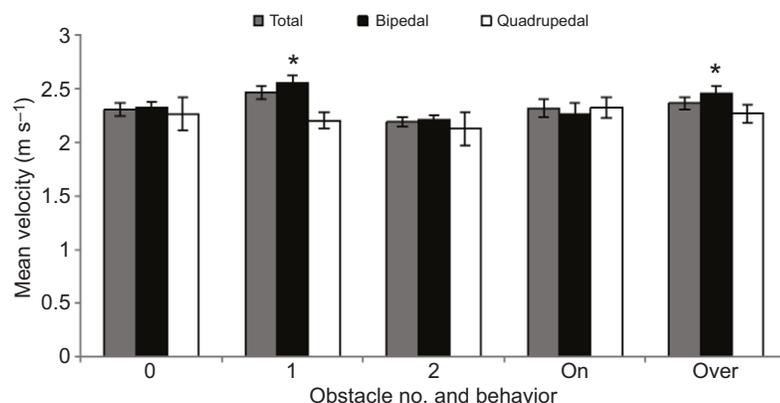


Fig. 2. Mean velocity (±s.e.m.) by obstacle treatment and obstacle crossing behavior for total velocity (postures combined), bipedal and quadrupedal posture. Mean velocity was greatest with one obstacle. Bipedal running was faster than quadrupedal with one obstacle. Crossing over the obstacle with a bipedal posture was faster than crossing over the obstacle with a quadrupedal posture. * $P \leq 0.05$.

Table 2. Raw kinematic data for bipedal and quadrupedal running in *S. woodi*

Variable	N	0 obstacles (n=14)	With obstacle (n=34)	1 obstacle (n=20)	2 obstacles (n=14)
Body angle at 0.4 m (deg)	48	10.47±2.0	12.3±1.4	12.5±1.7	12.1±2.3
Bipedal body angle (deg)	20	17.0±3.0 ^A	18.0±2.0 ^B	16.2±2.7 ^C	21.3±2.5 ^D
Quadrupedal body angle (deg)	28	7.0±1.8 ^A	8.0±1.1 ^B	8.7±1.4 ^C	7.0±1.8 ^D
Hip height (cm)	48	2.3±0.14	2.3±0.1	2.3±0.13	2.3±0.2
Bipedal hip height (cm)	20	2.6±0.1 ^E	2.7±0.1	2.7±0.14 ^F	2.6±0.12
Quadrupedal hip height (cm)	28	2.1±0.2 ^E	2.1±0.1	1.9±0.11 ^F	2.2±0.2
Tail angle at 0.4 m (deg)	47	-0.31	-0.28	-0.34	-0.17
Tail elevated (B,Q)	20	2,2	1,5	1,1	0,4
Tail lowered (B,Q)	37	3,7	14,13	9,9	5,4
Bipedal tail (R,L)	20	2,3 ^G	1,14 ^G	1,9	0,5

Data are presented as either frequency or means±s.e.m. for posture kinematics among obstacle trials. Total sample size is indicated (N), as well as the sample size for each trial type (n). All variables are measured before reaching the obstacle at 0.4 m. Body angle (total and by posture) is quantified as positive or negative values in degrees relative to the angle between reference points and the substrate, and tail angle (total and by posture) is quantified as positive or negative values relative to linear measurements between reference points and the substrate. Tail elevation (by posture) was quantified as the frequency of the tail being raised above (positive numbers) the hip height, or below hip height (negative). Bipedal tail is the frequency of raised (R) or lowered (L) tails when using a bipedal posture. One individual was excluded from tail elevation because of a missing tail. Shared superscript letters A–G indicate a significant difference at $P \leq 0.05$.

($F_{3,30}=1.031$; $P=0.393$). Among obstacle treatments (1–2), lizards stepped on the obstacle significantly more when using a quadrupedal posture ($\chi^2_{1,8}=5.44$; $P=0.0196$) (Fig. 4, Table 1). No difference in the frequency of bipedal or quadrupedal posture was found when stepping over (no limb contact) the first obstacle ($\chi^2_{1,24}=0.04$; $P=0.8415$). However, lizards that stepped over an obstacle using a bipedal posture were significantly faster than lizards that stepped over using a quadrupedal posture ($\chi^2_{1,24}=4.050$; $P=0.044$) (Fig. 2, Table 1). Pausing was significantly less frequent when a bipedal posture was used compared with sole use of a quadrupedal posture ($\chi^2_{1,100}=31.717$; $P=0.0001$) (Fig. 5).

Bipedal kinematics of tail elevation, body angle and hip height

Tail elevation was significantly lower among lizards running with a bipedal posture; 85% held the tail below hip height in the stride prior to the obstacle ($\chi^2_{1,19}=9.8$; $P=0.0017$). The tail was held below the hip height significantly more with an obstacle present than without, regardless of posture ($\chi^2_{1,36}=7.811$; $P=0.0052$). Body angle in the stride prior to reaching the obstacle was not significantly greater with an obstacle than without ($\chi^2_{2,46}=0.494$; $P=0.489$) and was not different among obstacle trials ($F_{1,33}=0.280$; $P=0.757$). However, across all treatments (0–2), body angle was significantly greater

(13.88 ± 2.7 deg) when a bipedal posture was used, compared with the body angle during the use of a quadrupedal posture (7.52 ± 1.6 deg) ($\chi^2_{1,46}=20.027$; $P=0.0001$) (Table 2). Body angle was significantly different between postures in treatment 0 ($F_{1,12}=9.936$; $P=0.008$), treatment 1 ($\chi^2_{1,19}=5.491$; $P=0.019$) and treatment 2 ($\chi^2_{1,12}=7.47$; $P=0.006$). Hip height did not differ between running with and without an obstacle ($F_{1,46}=0.068$; $P=0.795$) or among obstacle treatments ($F_{2,45}=0.037$; $P=0.964$). Bipedal hip height was significantly greater than quadrupedal hip height in treatment 0 ($F_{1,12}=4.379$; $P=0.058$), and treatment 1 ($F_{1,18}=4.653$; $P=0.045$); there was not a difference in treatment 2 ($\chi^2_{2,46}=1.960$; $P=0.1615$) (Table 2).

Performance and intermittent locomotion between single and multiple obstacles

Mean velocity was significantly greater over one obstacle (treatment 1; 2.9 ± 0.09 m s⁻¹) than zero (treatment 0; 2.3 ± 0.06 m s⁻¹) and two obstacles (treatment 2; 2.5 ± 0.07 m s⁻¹) ($F_{2,45}=5.719$; $P=0.006$). Lizards had the fastest velocity when running over one obstacle, and slower velocity over both zero and two obstacles (Fig. 2, Table 1). Bipedal running lizards in the one and two obstacle treatment showed significantly higher velocity than lizards that only ran in a quadrupedal posture ($F_{1,32}=4.955$; $P=0.03$) (Fig. 2, Table 1).

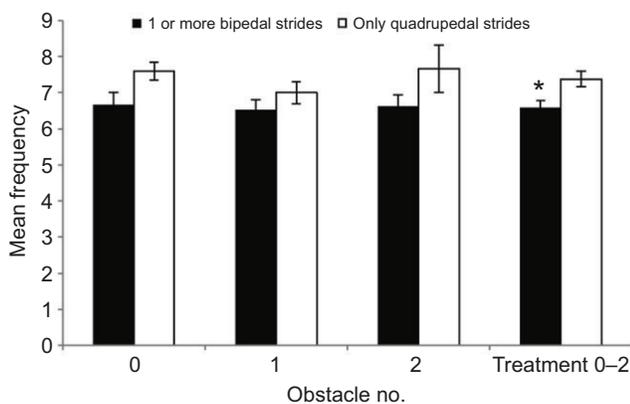


Fig. 3. The mean frequency (±1.0 s.e.m.) of total strides completed when bipedalism was used, and total strides completed when only a quadrupedal posture was used over a 1 m racetrack. Significantly fewer total strides were taken when using a bipedal posture (all obstacle treatments combined). * $P \leq 0.05$.

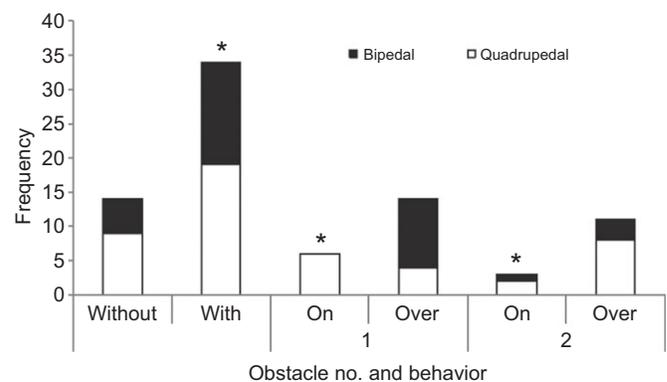


Fig. 4. The frequency of obstacle crossing behavior and posture without an obstacle, with obstacles (treatments 1–2), and within each obstacle treatment type (1–2). 'On' indicates stepping on the obstacle; 'Over' indicates stepping over the obstacle without touching it. Bipedal posture was used significantly more with obstacles than without. The frequency of touching the obstacle with a quadrupedal posture was greater than the frequency of touching the obstacle with a bipedal posture. * $P \leq 0.05$.

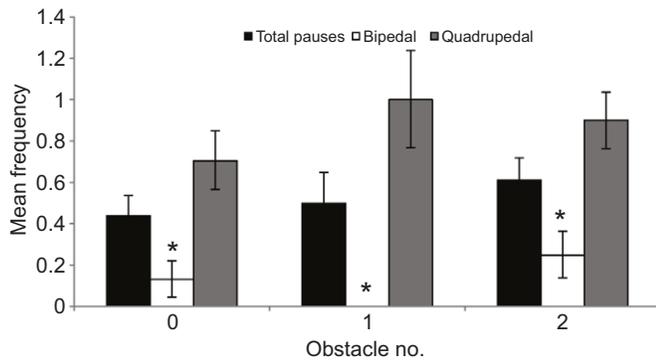


Fig. 5. Mean frequency (± 1.0 s.e.m.) of total pauses, pausing with bipedal running, and pausing with quadrupedal running by obstacle group.

Lizards paused significantly less when a bipedal posture was used compared with a quadrupedal posture. * $P \leq 0.05$.

However, when testing for differences in velocity by posture within each of the obstacle treatments (1–2), mean velocity was only significantly greater with a bipedal posture in the one-obstacle group (treatment 1; $F_{1,33}=8.059$; $P=0.011$) (Table 1). There was also no significant difference in the total number of bipedal strides taken among obstacle treatments ($\chi^2_{2,45}=0.508$; $P=0.776$). The total number of strides within the 1 m run did not differ significantly among obstacle treatments ($F_{2,45}=0.4887$; $P=0.6167$), although the trend was evident (Fig. 3, Table 1). Finally, lizards did not use intermittent locomotion more or less frequently in any particular obstacle treatment ($\chi^2_{2,100}=2.167$; $P=0.338$).

DISCUSSION

The goal of this study was to compare how multiple obstacles affect sprint performance, posture and locomotor behavior. We predicted that multiple obstacles would decrease velocity, increase bipedal running and increase the number of pauses. Mean velocity decreased with multiple obstacles as predicted, but pausing did not vary. However, lizards were less likely to pause or touch on obstacle when using a bipedal posture. Body angle and hip height were greater during bipedal running in anticipation of obstacle crossing. Furthermore, the tail was more likely to be lowered below horizontal just before crossing the obstacle, presumably to maintain an upright bipedal posture. This finding contrasts past reports showing an elevated tail during unobstructed bipedal running (Van Wassenberg and Aerts, 2013; Aerts et al., 2003). Our data demonstrate that bipedal posture results in fewer strides taken, and is advantageous for negotiating a single obstacle by increasing relative velocity. However, bipedal posture is not necessarily advantageous for multiple obstacles in close proximity (e.g. 0.4 m apart). Multiple obstacles have a significant negative impact on small vertebrate sprint locomotion, yet these negative effects may be offset by use of bipedal running when encountering just a single obstacle, or possibly multiple obstacles spaced further apart.

Performance and behavior with and without obstacles

Running over an obstacle significantly decreases sprint speed of quadrupedally running lizards (Kohlsdorf and Biewener, 2006; Self, 2012), as obstacles are physically and visually obtrusive using this posture (Tucker and McBrayer, 2012). Yet, contrary to our prediction, there was no change in sprint speed from running without obstacles to running with an obstacle. Unexpectedly, lizards showed a 6.6% increase in mean velocity from 0 to 1 obstacle,

perhaps resulting from a use of bipedal running (Fig. 2, Table 1). This is supported by the fact that lizards used a bipedal posture with one obstacle more frequently than without any obstacle present (Table 1). A similar pattern has been observed among four other lizard species (*Gambelia wislizenii*, *Crotaphytus bicinctores*, *Sceloporus occidentalis*, *Aspidoscelis tigris*; Self, 2012). With an obstacle present, bipedalism is not used more often when approaching the obstacle compared with no obstacle, and the number of bipedal strides did not increase over the 1 m track (Table 1). Additionally, most lizards were observed switching to a quadrupedal posture when preparing to cross the second obstacle. This finding indicates that lizards rely less on bipedal running after crossing a single obstacle, which likely explains why mean forward speed does not change. For lizards that encounter additional obstacles, use of bipedal running does not appear to have the same benefit because velocity slowed in the two-obstacle trial.

Is bipedal locomotion more efficient than quadrupedal locomotion?

Cluttered habitats prove difficult for maintenance of a straight path of travel and forward speed during movement, requiring a behavioral repertoire to negotiate obstacles (Rieder et al., 2010; Garber and Pruetz, 1995; Tucker and McBrayer, 2012). Quickly maneuvering on or over obstacles can play a vital role in predator evasion in complex habitats (Kohlsdorf and Navas, 2007; Tucker and McBrayer, 2012). When facing a single obstacle, lizards demonstrated a 13.8% faster velocity running with a bipedal posture compared with quadrupedal running (Fig. 2, Table 1). However, six-lined racerunners were unable to continue bipedal running after obstacle contact (Olberding et al., 2012), suggesting a tradeoff where some species may forego a bipedal posture to maintain stability after crossing a barrier. The results of Olberding et al. (2012) differ from ours in that six-lined racerunners did not experience any change in velocity with a single obstacle present, and this species ran much faster than *S. woodi* (*A. sexlineatus*: 4.7 ± 0.5 m s⁻¹, Olberding et al., 2012; *S. woodi*: 2.5 ± 0.07 m s⁻¹, this study). Given this, bipedalism may provide benefits when crossing obstacles at lower velocities, but not higher ones. Yet, this remains to be tested.

Use of a quadrupedal posture is associated with shorter stride length (Irschick and Jayne, 1999a) and a slower velocity over one obstacle (Fig. 2, Table 1). Higher speeds can be achieved by more frequent strides, exhibited in bipedal birds and humans, or by taking longer strides as seen in many quadrupeds (Clemente et al., 2013; Roberts et al., 1998; Gatesy and Biewener, 1991). For example, ground-dwelling species change stride length to increase speed, whereas climbing species modify stride frequency (Zaaf et al., 2001; Clemente et al., 2013). During escape locomotion of *Callisaurus draconoides*, the average bipedal stride is 1.18 times the length of quadrupedal strides (Irschick and Jayne, 1999a). Here, longer bipedal strides likely allow for stepping over an obstacle, rather than stumbling or stepping on it. Stepping over an obstacle should retain greater sprint speed. Bipedal running results in fewer total strides than quadrupedal running, allowing us to infer that *S. woodi* modulates stride length during bipedal running, and/or that bipedal running may also increase speed (Fig. 3, Table 1). Increasing stride frequency would result in shorter, more numerous, strides over the same distance. If shorter strides increase stability, then *S. woodi* should switch to a quadrupedal posture if contact is made with the obstacle. This was precisely the pattern we observed. Unfortunately, we could not quantify stride length in the present study because of blind spots in the mirrored

view along the racetrack. Future studies should examine tradeoffs between stride length and stride frequency for each posture.

On uneven terrain, pheasants use visual route planning in anticipation of negotiating an obstacle, thereby minimizing the likelihood of a misplaced footfall resulting in stumbling (Birn-Jeffery and Daley, 2012). In similar context, a lizard may choose to run bipedally to avoid obstacle contact, and thus escape a predator with greater efficiency. However, tradeoffs are likely. Humans modify stride length to maximize obstacle clearance, but a high-stepping gait is energetically demanding (Sparrow et al., 1996). Similarly, bipedal lizards must anticipate optimal hind-foot placement to avoid obstacle interference. Olberding et al. (2012) suggested that choosing to step on or over an obstacle was by chance. In contrast, our results suggest that lizards may choose to use a bipedal posture to avoid contacting the first obstacle (Fig. 2). Stepping over the obstacle allowed *S. woodi* to pass the obstacle with less deceleration or perturbation, and maintain a faster velocity compared with stepping on it with quadrupedal running (Fig. 2, Table 1). Further analyses of footfall patterns, stride length and stride frequency leading up to an obstacle would provide useful insights into the tradeoffs among obstacle anticipation, negotiation, and posture selection in lizards.

Bipedal running kinematics

Elevation of the trunk and head serves to improve visual perception and increase the animal's COM potential energy, thus contributing to the work necessary for clearing an obstacle (Kohlsdorf and Biewener, 2006). Two studies show that a bipedal posture is associated with holding the tail horizontally, and suggest that this may increase the stability of the body COM (Irschick and Jayne, 1999b; Self, 2012). However, other studies suggest elevating the tail above the COM is needed during sustained bipedal running and that both tail elevation and bipedal running are related to rapid initial acceleration (Van Wassenbergh and Aerts, 2013; Aerts et al., 2003; Clemente, 2014). When approaching an obstacle, lizards had an average bipedal body angle of 17.7 ± 1.6 deg (Table 2), similar to the body angle of 15 deg observed in Van Wassenbergh and Aerts (2013) and of 25 deg observed in bipedal running cockroaches (Alexander, 2004). Basilisk lizards maintain an upright posture (45 deg) at high velocity by dragging the tail behind through the water (Hsieh, 2003). In contrast, *S. woodi* has a much lower body angle, and a much shorter tail, than bipedal running basilisks. *Sceloporus woodi* can reach maximum speed and accelerate very rapidly (\bar{x} =86% of max) within 0.4 m, and yet, has not been observed to pitch upward at a high angle at the start of a run (McElroy and McBrayer, 2010). Therefore, it seems unlikely that bipedalism and tail elevation are solely the consequences of rapid initial acceleration as has been suggested.

In anticipation of crossing an obstacle, *S. woodi* must hold the tail horizontal or slightly below horizontal to maintain an upright bipedal posture, as elevating the tail would decrease its effectiveness as a counterbalance by anteriorly shifting the tail's COM (Irschick and Jayne, 1999b). In all but one trial (Table 2), bipedal lizards also raised their hip height, a mechanism utilized by birds in anticipation of uneven terrain (Birn-Jeffery and Daley, 2012). Together with an increase in body angle and raising the hips, *S. woodi* depresses the tail to maintain a bipedal posture, and pitch the body COM forward and over the obstacle as it crosses it.

Performance and behavior with multiple obstacles

An increase in the size of obstacles has been shown to decrease sprint speed in *Sceloporus malachiticus* (Kohlsdorf and Biewener, 2006)

and *Sceloporus woodi* (Tucker and McBrayer, 2012) compared with level running. *Sceloporus woodi* had the highest velocity crossing a single obstacle followed by an 11% loss in velocity between the one-obstacle and two-obstacle trials (Fig. 2, Table 1). Many lizard and rodent species have lower escape speeds in dense vegetation compared with open areas (Vasquez et al., 2002; Schooley et al., 1996; Goodman, 2009; Vanhooydonck and Van Damme, 2003). Species utilizing bipedal running may be able to exploit habitat types with uneven substrata because of the increases in visual perception and/or by reaching their maximum speed more quickly (Rieder et al., 2010; Djawdan and Garland, 1988; Rocha-Barbosa et al., 2008; Kohlsdorf and Biewener, 2006). Because two obstacles create the same negative performance effect on stride characteristics and velocity, bipedalism is likely only beneficial when negotiating a single obstacle (Fig. 2, Table 1), or distantly spaced obstacles (which remains untested). Data from the multiple-obstacle treatment clearly shows that bipedalism is more efficient on a single obstacle; the majority of lizards switched to a quadrupedal posture to cross the second obstacle. Beyond a single obstacle, quadrupedal running and intermittent locomotion appear to be more beneficial.

The negative impact of running over obstacles results in the use of bipedal running or intermittent locomotion to counteract the decrease in forward velocity caused by the obstacle. In this study, lizards paused significantly less with bipedal running than individuals that only ran with a quadrupedal posture (Fig. 5). If pausing and bipedalism provide advantages for negotiating obstacles (Kohlsdorf and Biewener, 2006), then it would not be necessary for a lizard to employ each behavior in the same escape run. A disadvantage of pausing during high speed locomotion is the rapid initial acceleration needed after a pause (Higham et al., 2001). Because bipedalism is likely not solely a consequence of rapid acceleration in *S. woodi*, then it is unlikely that this posture would subsequently follow a pause. Pausing in a habitat cluttered with obstacles may be strategically and energetically favorable (Vasquez et al., 2002; Higham et al., 2001), plus allow the animal to assess the terrain and potentially choose an alternative route. Bipedal running in more open habitats may allow for enhanced visual range while still in motion (Olberding et al., 2012), and therefore may be a more efficient strategy than pausing when encountering obstacles.

Conclusion

Animals are faced with behavioral tradeoffs that facilitate their performance efficiency. This study examined changes in locomotor posture associated with obstacles in the flight path. We show that lizard sprint velocity declines as obstacle number increases, and surprisingly, that intermittent locomotion is unchanged (Fig. 2, Table 1). Multiple obstacles elicit behavioral and kinematic shifts in locomotor posture (to quadrupedalism) and stride frequency. For a single obstacle, bipedalism enables maintenance of high forward velocity whereby fewer, longer strides are taken and intermittent locomotion decreases (Figs 2–5, Table 1). Use of a bipedal posture increases the likelihood that an animal may step over an obstacle to minimize disruption of the body COM and likelihood of stumbling (Fig. 4, Table 1). Future research should examine the effects of altering stride length and/or frequency as well as basic kinematics (body angle, hip height, tail height) in both quadrupedal and bipedal postures. Finally, the effect of obstacle spacing, size and orientation on locomotor performance has yet to be adequately understood for either posture.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

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