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Chase T. Kinsey

Georgia Southern University, ck03480@georgiasouthern.edu

Lance D. McBrayer

Georgia Southern University, lancemcbrayer@georgiasouthern.edu

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RESEARCH ARTICLE

Forelimb position affects facultative bipedal locomotion in lizards

Chase T. Kinsey* and Lance D. McBrayer[‡]

ABSTRACT

Recent work indicates that bipedal posture in lizards is advantageous during obstacle negotiation. However, little is known about how bipedalism occurs beyond a lizard's acceleratory threshold. Furthermore, no study to date has examined the effects of forelimb position on the body center of mass (BCoM) in the context of bipedalism. This study quantified the frequency of bipedalism when sprinting with versus without an obstacle at 0.8 m from the start of a sprint. Forelimb positions were quantified during bipedal running at the start of a sprint and when crossing an obstacle. Two species with contrasting body forms (and thus different BCoM) were studied (*Sceloporus woodi* and *Aspidoscelis sexlineata*) to assess potential variation due to body plan and obstacle-crossing behavior. No significant difference in frequency of bipedalism was observed in *S. woodi* with or without an obstacle. However, *A. sexlineata* primarily used a bipedal posture when sprinting. Forelimb positions were variable in *S. woodi* and stereotyped in *A. sexlineata*. Caudal extension of the forelimbs helped shift the BCoM posteriorly and transition to, or maintain, a bipedal posture in *A. sexlineata*, but not in *S. woodi*. The posterior shift in BCoM, aided by more caudally placed forelimbs, helps raise the trunk from the ground, regardless of obstacle presence. The body plan, specifically the length of the trunk and tail, and forelimb position work together with acceleration to shift the BCoM posteriorly to transition to a bipedal posture. Thus, species exhibit morphological and behavioral adjustments to transition to and maintain facultative bipedalism while sprinting.

KEY WORDS: Sprint, Obstacle, Center of mass, *Sceloporus*, *Aspidoscelis*

INTRODUCTION

The ability to capture prey, avoid predation and find mates is contingent on successfully navigating uneven substrates in most terrestrial environments (Garland and Losos, 1994). Physical substrates such as loose rock, thick vegetation and woody debris provide challenges to terrestrial vertebrates (Pounds, 1988). Variation in substrate characteristics directly affects locomotor performance and behavior of terrestrial vertebrates during flight from predators (Cooper and Sherbrooke, 2016; Higham et al., 2001; Collins et al., 2013; Cooper, 1999; Losos, 1990; Irschick and Jayne, 1999). Bipedalism – which is observed in some insects, mammals and reptiles – is one mode of locomotion terrestrial vertebrates use to overcome obstacles (Gatesy and Biewener, 1991; Alexander,

2004; Clark and Higham, 2011; Tucker and McBrayer, 2012; Parker and McBrayer, 2016). During predation events or social interactions, a terrestrial vertebrate's behavior, speed and stability traversing obstacles may impinge upon their survivorship and/or fitness (Stiller and McBrayer, 2013; Schulte et al., 2004; Arnold, 1983; but see Garland and Losos, 1994).

Stereotyped limb movement in quadrupedal locomotion, or gait, has predictable footfalls across various speeds (Snyder, 1952, 1954, 1962; Irschick and Jayne, 1999; Farley and Ko, 1997). Some terrestrial lizards alter their gait and/or posture while sprinting (Schuett et al., 2009; for review, see Russell and Bels, 2001). Facultative bipedalism occurs in some quadrupeds when only the hindlimbs contact the ground, as a result of a posterior shift in the body center of mass (BCoM) (Snyder, 1954). A posterior shift in BCoM during facultative bipedalism occurs in large part through the production of high accelerative forces by the hindlimbs that prevent the forelimbs from remaining in contact with the ground (Aerts et al., 2003). Facultative bipedalism has evolved independently in numerous lizard clades as a consequence of acceleration and changes in BCoM (Aerts et al., 2003; Clemente, 2014). The position of the BCoM varies depending on the length of the trunk and tail relative to the hip (Van Wassenbergh and Aerts, 2013). Lizards with an anteriorly placed BCoM are less likely to exhibit bipedalism compared with lizards with a posteriorly shifted BCoM (Clemente et al., 2008; Clemente, 2014). Thus, body shape is a key determinant in facultative bipedalism. Bipedal lizards can make small changes in the trunk and/or tail angle such that the BCoM is shifted over the hip (Van Wassenbergh and Aerts, 2013; Irschick and Jayne, 1999).

Kinematic data on the role of the hindlimb in bipedal locomotion suggest the hindlimb generates significant power, thereby effecting acceleration and maximal velocity (Van Wassenbergh and Aerts, 2013; Olberding et al., 2012; Snyder, 1954, 1962). Little attention has focused on the role of the forelimb during bipedal locomotion. Forelimb position may aid in obstacle navigation by shifting the BCoM posteriorly (Legreneur et al., 2012). Snyder (1952) suggested there is no difference in limb movement between quadrupedal and bipedal locomotion. Yet, several species of lizards use various forelimb positions while moving bipedally (Irschick and Jayne, 1999). For example, *Aspidoscelis sexlineata* tends to caudally extend the limbs, despite individual variation (Olberding, et al., 2012). Varying forelimb positions may be necessary for maintaining balance, touching or pushing off from an obstacle, or elevating the center of mass for obstacle clearance (Kohlsdorf and Biewener, 2006). Certain forelimb positions during bipedal locomotion, such as caudal extension, could shift the BCoM posteriorly, while continuing to move the forelimbs in a gait cycle may aid in the creation of a pitching motion via nose-up torque and high starting accelerations (Aerts et al., 2003; McElroy and McBrayer, 2010). For example, caudal extension of the forelimbs during obstacle navigation may (1) decrease contact with an obstacle by raising the distance of the limbs away from the obstacle (Self, 2012) and (2) shift the BCoM posteriorly to raise the hip height so that a lizard might clear an obstacle without losing forward speed (Olberding et al., 2012; Irschick and Jayne, 1999).

Department of Biology, Georgia Southern University, PO Box 8042-1, Statesboro, GA 30460, USA.

*Present address: Department of Biological Sciences, 132 Long Hall, Clemson University, Clemson, SC 29634, USA.

[‡]Author for correspondence (lancemcbrayer@georgiasouthern.edu)

 L.D.M., 0000-0003-2395-7078

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The objective of this study was to determine the role of obstacle placement and forelimb position during facultative bipedal locomotion in lizards. Two species, *Sceloporus woodi* and *Aspidoscelis sexlineata*, were selected based on their different body plans (thus BCoM), and each often exhibits bipedal locomotion. *Sceloporus woodi* run bipedally more frequently when encountering an obstacle versus without an obstacle (Parker and McBrayer, 2016). Furthermore, *Sceloporus woodi* run bipedally when an obstacle is within their acceleration threshold (0.4 m), but not when multiple obstacles are present in succession (Parker and McBrayer, 2016). *Aspidoscelis sexlineata*, however, employ a bipedal posture when crossing obstacles over long distances (Olberding et al., 2012). Although many species of lizards have been documented sprinting bipedally, no published studies have examined bipedalism with an obstacle placed beyond the initial acceleration threshold, i.e. after the initial two to five steps (0.4–0.5 m) of locomotion (McElroy and McBrayer, 2010). Transitioning to a bipedal posture at an obstacle when already near maximal velocity suggests that bipedalism may occur as a behavioral adaptation to maintain forward speed, and is not only dependent on initial acceleration. We predicted that (i) lizards use a bipedal posture more frequently with an obstacle present than without, and (ii) bipedal posture is used more at the obstacle, rather than at the start of the trial. In terms of velocity, we predicted that (iii) a bipedal posture will allow for maintenance of forward speed over the obstacle more than quadrupedal posture. Furthermore, we predicted that (iv) caudal extension of the forelimbs shifts the BCoM posteriorly more than other forelimb positions, and (v) forelimb positions are variable within the acceleration threshold but fixed when navigating an obstacle beyond the acceleration threshold.

MATERIALS AND METHODS

Study species and field site

This study quantified the frequency of bipedal posture, and the position of the forelimb, when crossing obstacles during sprint locomotion. Two facultative bipedal species with differing body plans were chosen as study species: the Florida scrub lizard (*Sceloporus woodi* Stejneger 1918) and the racerunner [*Aspidoscelis sexlineata* (Linnaeus 1766)] (Fig. 1A). *Sceloporus woodi* is found in open sandy habitats in peninsular Florida (McCoy et al., 2004; Jackson, 1973). *Aspidoscelis sexlineata* has an elongated trunk and a forward BCoM compared with *S. woodi* (Clemente, 2014); it is found throughout the southeastern and central USA and in sympatry with *S. woodi* in Ocala National Forest, FL, USA, where habitat fragmentation and roller chopping have produced natural locomotor obstacles (Hokit and Branch, 2003; Tiebout and Anderson, 2001). *Aspidoscelis sexlineata* very commonly use bipedal locomotion which is attributed in part to a posteriorly placed BCoM when sprinting bipedally (Clemente, 2014). The contrasting body plan, yet similar masses and habitat use, makes the two species ideal to compare both forelimb positions during bipedal running and when traversing obstacles outside of their acceleration threshold.

Research in the Ocala National Forest was conducted under protocol (Institutional Animal Care and Use Committee permit no. I15011 and I150112; State of Florida Fish and Wildlife Conservation Commission permit no. LSSC-15-00027; and US Forest Service permit no. SEM540).

Field collections

Field collection occurred May to August 2016 and 2017. Eighty-eight adult male *S. woodi* and 35 *A. sexlineata* were noosed using a thin filament tied in a slipknot at the end of a fishing pole. Males were retained in cloth bags and transported to the animal facility at

Georgia Southern University. Each lizard was kept in a separate 45 l tank with sandy substrate and a hide, and fasted for 24 h to ensure digestion did not affect locomotor performance. Lizards were kept on a 12 h:12 h light:dark cycle and misted with water every morning. Crickets were fed *ad libitum* every 3 days. After sprint trials, most lizards were released at the point of capture. Recaptures on subsequent trips were avoided by toe clipping and painting landmarks on each released individual. Only males greater than 42 mm snout–vent length (SVL) were used in the analyses. Females are likely to be gravid, which affects locomotor performance (Iraeta et al., 2010).

Sprint trials

Landmarks were placed externally on each lizard using non-toxic paint (Fig. S1) in order to visualize limb and tail position in the video. Two Mega Speed X4[®] high-speed video cameras with RICOH lenses (50 mm, F/1.4 VGA) mounted on tripods recorded sprint trials (300 frames s⁻¹; resolution 1080×1024 pixels) from above along a custom-built racetrack. The racetrack substrate was lined with cork to avoid slippage. A mirror was placed at a 45 deg angle along the racetrack wall to provide dorsal and lateral views of each lizard (Fig. S2). Lizards were subjected to a trial with an obstacle at 0.8 m from the start and a trial without an obstacle. Trials were assigned at random to each day. Obstacles were constructed of wooden blocks which spanned the width of the track to prevent lizards from maneuvering around the obstacle. Obstacle height and width were standardized to 35% of hindlimb length for each lizard (Self, 2012). Lizards with broken or regenerated tails were noted and excluded from any analysis. Lizards were warmed to field active body temperature (~36°C) in an incubator before each trial. Each lizard was held completely still at the start of the track, then released. Taps on the tail were used to coerce the individual down the racetrack to a hide. Only ‘successful’ sprint trials were used for analysis, defined as avoidance of side walls, pausing or reversing direction. Bipedal trials were defined as completion of at least one full stride without the forelimbs touching the ground. Bipedalism at the obstacle was assigned as the use of only the hindlimbs for at least one full stride within four stride lengths preceding the obstacle. Bipedalism at the start of the trial was assigned as using only the hindlimbs for at least one full stride during the first four strides of a sprint. Whether a forelimb touched an obstacle when crossing was noted for each species. All videos were calibrated using a 30-point calibration cube, as well as a 10 cm ruler painted on the race track wall (Parker and McBrayer, 2016). Videos were uploaded to the computer, spliced using Microsoft Movie Maker (compressed AVI file) and digitized in MATLAB using DLTdv5 software (Hedrick, 2008). A landmark was painted at the junction of the frontal and parietal scale to calculate sprint velocity from each video. Trunk angle was quantified from videos for individuals using a bipedal posture, from a lateral view, by measuring the tangent angle of a right-angled triangle from three points: the landmark on the hip, the landmark on the scapula and a point directly under the scapula and in line with the hip such that a right-angled triangle was formed. Trunk angle data were examined in light of four forelimb positions during bipedal runs via ANOVA. Gross limb position was easily distinguished on the video, but image resolution prevented us from confidently collecting 3D joint kinematics with little error. Thus, 3D joint kinematics were not quantified.

Ethogram and BCoM analysis

To understand forelimb function during bipedalism, an ethogram was constructed by reviewing a subset of sprint trials of both *S. woodi* (Parker and McBrayer, 2016) and *A. sexlineata* (collected

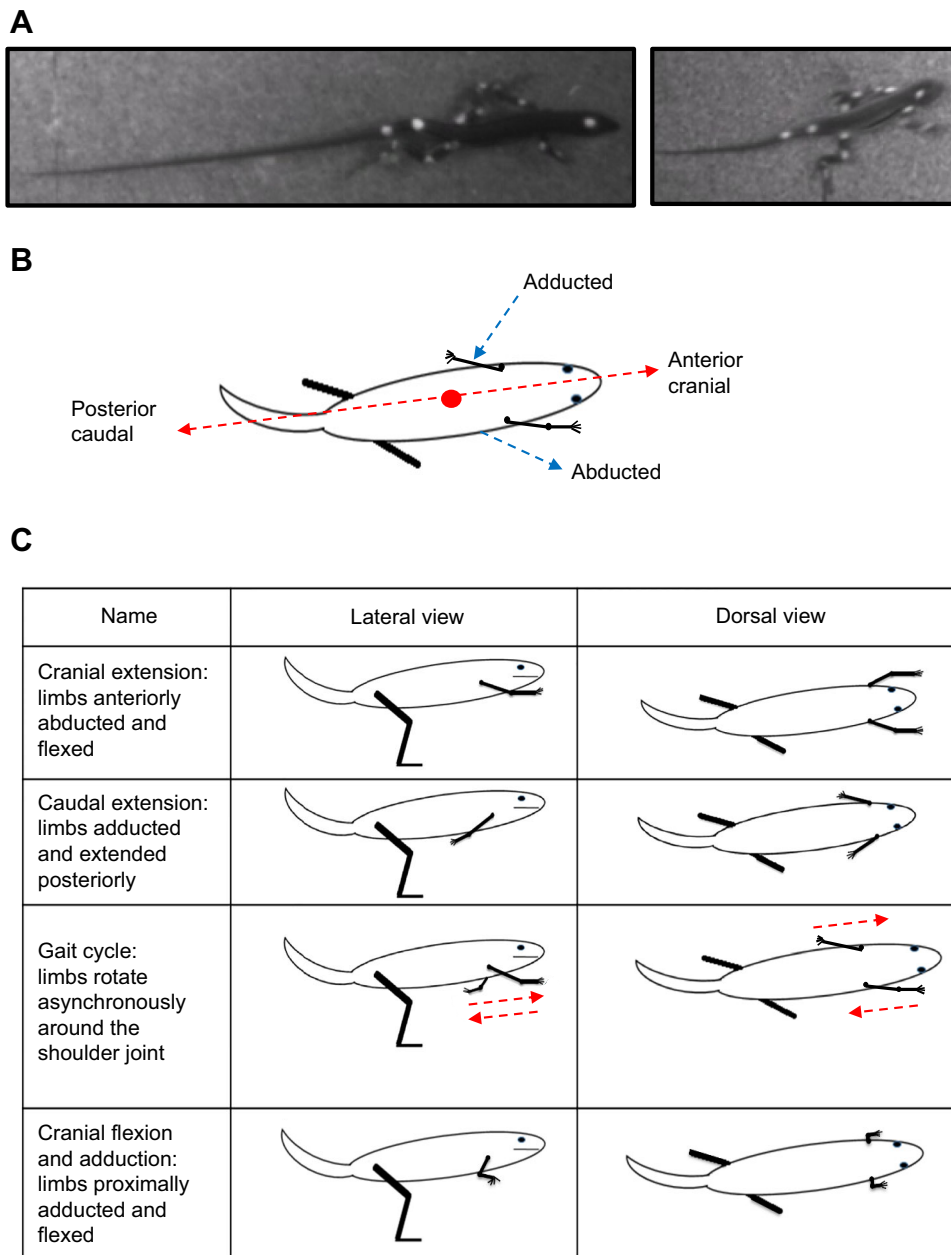


Fig. 1. Ethogram of common forelimb positions observed during bipedalism in lizards. (A) The more streamlined *Aspidoscelis sexlineata* (right) and stockier *Sceloporus woodi* (left) have differing body plans. In both frames, the forelimbs are in a gait cycle. (B) A diagram showing the anterior–posterior and abduction–adduction axis (where adduction is towards the mid-line and abduction is away from the mid-line). (C) Four commonly noted forelimb positions used during bipedal locomotion. Lateral and dorsal views are shown.

summer 2016) (Fig. 1). Images from Irschick and Jayne (1999) were also used to determine variation in forelimb position. Forelimb positions were assigned to one of four categories: cranial extension, caudal extension, gait cycle and cranial flexion and adduction. The frequency of each was quantified during review of high-speed videos for each trial. Forelimb positions were defined based on to the forelimb position relative to the trunk, with angles associated with anterior (cranial) or posterior (caudal) positions. For example, cranial extension was defined as having the forelimbs anteriorly abducted and flexed more than 90 deg around the shoulder joint. Caudal extension was defined as forelimbs adducted and extended posteriorly at angles less than 90 deg around the shoulder joint. Forelimbs exhibiting a gait cycle rotated asynchronously around the shoulder joint. Finally, limbs exhibiting cranial flexion and adduction were proximally adducted and flexed toward the midline. Each definition was determined from the dorsal view.

After sprint trials were completed, a sample of lizards that ran bipedally (12 *A. sexlineata* and 20 *S. woodi*) were killed with

MS-222 to assess the change in positional BCoM due to forelimb position. The BCoM of a subset of these lizards was measured using two scales (0.0001 g accuracy) (as described in Clemente, 2014) set parallel to each other, with a wooden beam placed across each scale; the scales were tared to the mass of the beam. Each lizard was placed horizontally along the beam such that the most anterior point of the head was in line with the edge of the beam. The hindlimbs were retracted and the tail extended straight for each lizard to reduce error in measuring the BCoM. The BCoM was calculated from frozen, then slightly thawed lizards with the forelimbs placed in cranial, caudal and alternating (gait cycle) positions to quantify the effects of the forelimb on BCoM. Cranial and caudal positions were averaged together to obtain the flexed/adducted position.

Statistical analysis

One-hundred trials of *S. woodi* and 36 trials for *A. sexlineata* were retained for analysis. Statistical comparisons across species were not made because of a lack of phylogenetic inference that can be made

Table 1. Summary statistics of locomotor behavior in sprint trials with and without an obstacle

	<i>Sceloporus woodi</i>		<i>Aspidoscelis sexlineata</i>	
	Obstacle (n=51)	No obstacle (n=49)	Obstacle (n=18)	No obstacle (n=17)
No. of bipedal runs	20	17	16	15
No. of quadrupedal runs	31	32	2	2
Bipedal at start of trial	16	17	12	15
Bipedal at 0.8 m	11	6	14	14
Forelimbs touch obstacle	19	–	3	–
Pause on obstacle	6	–	1	–
Pause before obstacle	10	–	0	–
Pause after obstacle	26	–	2	–

Numbers are the frequency of occurrence for each behavior among species and trials (n is sample size). Posture at the start of a trial was quantified by assigning the first four strides of a sprint as either bipedal or quadrupedal. Bipedalism at 0.8 m was quantified as bipedal posture in the four strides preceding the obstacle at 0.8 m from the start. Pauses before and after an obstacle were quantified in the four preceding strides of the obstacle.

from a two-species comparison. Chi-squared tests were used to test the frequency of bipedal posture within each species in trials with or without an obstacle. Mean velocity when crossing an obstacle was calculated by averaging the velocities of the two strides before and after obstacle navigation. Sprint trials in which bipedal posture was used were retained to quantify the position of the forelimbs. Chi-squared tests were used to test the frequency of forelimb positions at the start of the trial with and without an obstacle, and at the obstacle. A one-way ANOVA was used to analyze variation in BCoM between caudal and cranial forelimb positions within each species. Trunk angle data were pooled from trials with or without an obstacle. A one-way ANOVA was used to test for differences in trunk angle across the four forelimb positions to examine the effects of forelimb position on pitch. All analyses were conducted using JMP (v. 12.1.0 SAS Institute) and figures were created in Microsoft Excel (v. 16.0 Microsoft). Alpha was set to $P < 0.05$.

RESULTS

Frequency of bipedal posture with and without an obstacle

We assessed whether the frequency of occurrence of bipedal posture differed in the presence or absence of an obstacle in *S. woodi* and *A. sexlineata* (Table 1, Fig. 2). Whether species ran bipedally more at the start of a sprint as opposed to when encountering the obstacle was also quantified. The presence or absence of an obstacle did not affect the frequency of bipedal posture in *S. woodi* ($P = 0.64$, $\chi^2 = 0.219$,

d.f.=1, $n = 100$). Also, the frequency of bipedal posture was not different at the start of a trial versus at the obstacle in *S. woodi* ($P = 0.088$, $\chi^2 = 2.905$, d.f.=1, $n = 40$). Regardless of obstacle presence, *S. woodi* primarily ran quadrupedally (Table 1, Fig. 2B). The frequency of bipedal posture in *A. sexlineata* was not affected by the presence or absence of an obstacle ($P = 0.95$, $\chi^2 = 0.004$, d.f.=1, $n = 35$). Furthermore, the frequency of bipedal posture was not different at the start of a trial versus at the obstacle for *A. sexlineata* ($P = 0.13$, $\chi^2 = 2.288$, d.f.=1, $n = 30$). *Aspidoscelis sexlineata* primarily used a bipedal posture regardless of obstacle presence (Table 1, Fig. 2A).

Sprint velocity as lizards crossed an obstacle with a bipedal or quadrupedal posture was quantified for a subset of lizards (Table 2). The mean velocity of *S. woodi* was significantly faster when crossing an obstacle with a bipedal posture ($2.57 \pm 0.12 \text{ m s}^{-1}$) versus a quadrupedal posture ($2.01 \pm 0.09 \text{ m s}^{-1}$) ($P = 0.0003$, d.f.=1, $n = 22$). Although bipedal posture was used in 89% of trials, the posture used by *A. sexlineata* did not affect sprint velocity during obstacle navigation ($P = 0.12$, d.f.=1, $n = 7$). A trend was observed towards faster mean velocities using a bipedal posture ($3.03 \pm 0.24 \text{ m s}^{-1}$), but only two of seven trials involved lizards using quadrupedal posture ($1.75 \pm 0.45 \text{ m s}^{-1}$); thus, this conclusion is speculative.

Effects of forelimb position on BCoM

Four forelimb positions were common during bipedal locomotion: limbs adducted and extended posteriorly (caudal extension), limbs

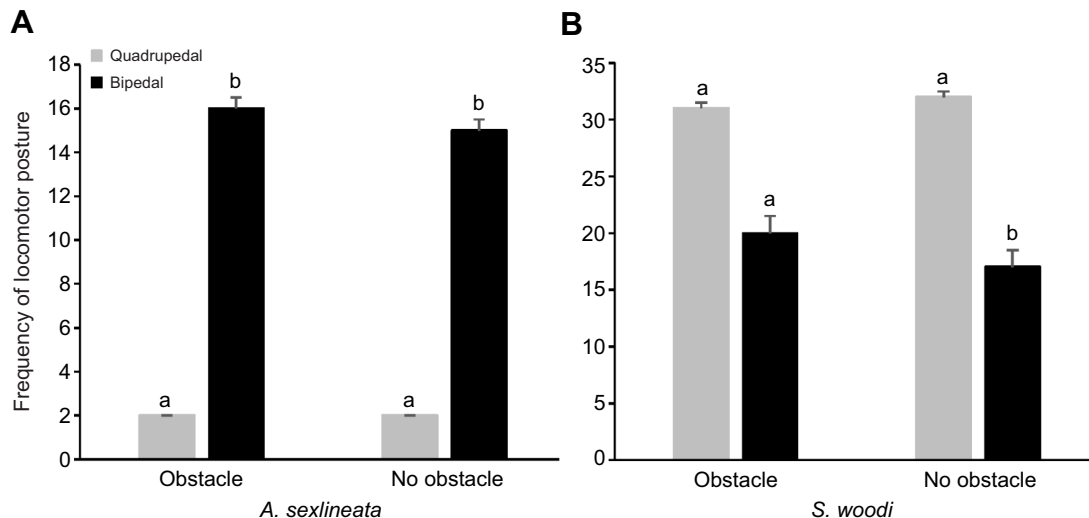


Fig. 2. Frequency of bipedal and quadrupedal posture within each treatment (obstacle, no obstacle). (A) Bipedal posture was used significantly more than quadrupedal posture with and without an obstacle for *A. sexlineata*. (B) Quadrupedal posture was used significantly more than bipedal posture in trials without an obstacle present. Differing letters indicate $P \leq 0.05$ from χ^2 analysis.

Table 2. Velocity during locomotion over an obstacle at 0.8 m

	<i>Sceloporus woodi</i>		<i>Aspidoscelis sexlineata</i>	
	Bipedal	Quadrupedal	Bipedal	Quadrupedal
Mean velocity (m s ⁻¹)	2.57±0.12	2.01±0.09	3.03±0.24	1.75±0.45
Residuals (V/SVL)	0.39±0.11	-0.24±0.08	0.25±0.34	-0.95±0.53
Sample size	7/22 trials	15/22 trials	5/7 trials	2/7 trials

Mean (\pm s.e.m.) velocity was calculated from the first two strides before and after obstacle navigation. Mean velocity (V) was regressed on snout-vent length (SVL) to account for variation due to size and analyzed using a one-way ANOVA. Mean velocity was significantly different between bipedal and quadrupedal locomotion in *S. woodi* (significant differences are shown in bold).

abducted and extended anteriorly (cranial extension), limbs adducted and flexed proximally (cranial flexion and adduction), and a gait cycle where limbs rotate around the shoulder axis (Fig. 1). Cranial extension in *S. woodi* shifted the BCoM 13.51±0.56 mm anterior of the hip while caudal extension moved the BCoM 12.25±0.56 mm posterior of the hip (Fig. 3) ($P=0.04$, $t=2.02$, $n=46$). *Sceloporus woodi* using a bipedal posture, with limbs flexed and adducted, had significantly greater trunk angles, and thus pitch, than when using a gait cycle, but not than with limbs cranially extended ($P=0.0003$, $F=12.76$, $n=20$). In *A. sexlineata*, cranial extension moved the BCoM 9.80±2.25 mm anterior of the hip while caudal extension moved the BCoM 8.47±2.50 mm posterior of the hip (Fig. 3) ($P=0.01$, $t=2.03$, $n=36$). Trunk angle in *A. sexlineata* was significantly greater when limbs were caudally extended as opposed to a gait cycle during a bipedal run, leading to greater pitch ($P=0.0013$, $F=19.686$, $n=12$).

Forelimb position in *S. woodi*

In trials without an obstacle present, there was no difference between the use of the four categories of forelimb position either at the start or at 0.8 m from the start ($P=0.4513$, $\chi^2=1.591$, d.f.=1, $n=23$) (Fig. 4A,

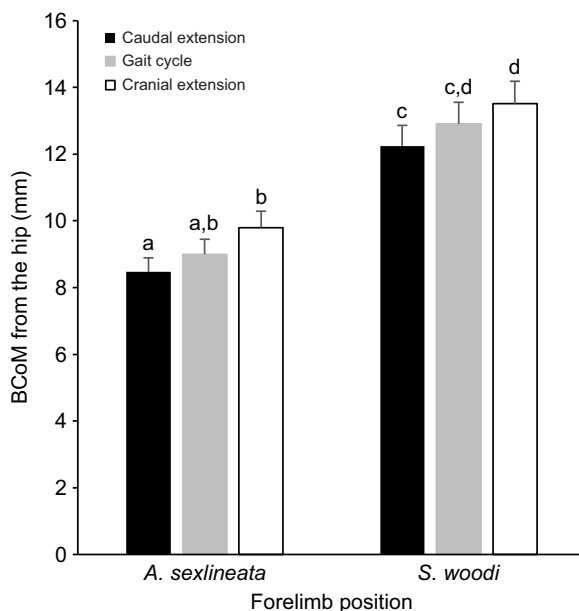


Fig. 3. The body center of mass (BCoM) of the three forelimb positions for both species. The BCoM with forelimbs in caudal extension (8.47±2.50 mm) was significantly different from that with forelimbs in cranial extension (9.80±2.25 mm) but not gait cycle in *A. sexlineata*. In *S. woodi*, cranial extension shifted the BCoM anteriorly (13.51±0.56 mm) while caudal extension moved the BCoM posteriorly (12.25±0.56 mm). Data were analyzed using a one-way ANOVA; s.e.m. is represented by bars. Differing letters indicate $P<0.05$.

B). When running bipedally at the start of a sprint trial, *S. woodi* used a gait cycle motion of the forelimbs in 47.1% of the trials and limbs were flexed and adducted in 41.2% of trials. Limbs were cranially extended in 11.7% of trials, while caudal extension was never observed. Thus, limbs were in a gait cycle or flexed and extended more often than they were cranially or caudally extended ($P=0.0028$, d.f.=3, $n=17$). During bipedal locomotion 0.8 m from the start (yet without an obstacle present), lizards used a gait cycle motion in 66.7% of trials, while limbs were flexed and adducted in 33.3% of trials. Cranially and caudally extended limbs were not observed; thus, gait cycle and flexion adduction were used significantly more than cranial or caudal extension ($P=0.03$, d.f.=3, $n=6$).

With an obstacle present, there was a significant difference between the use of the four forelimb positions at the start of a trial and at 0.8 m from the start ($P=0.0074$, $\chi^2=9.811$, d.f.=1, $n=28$). When using a bipedal posture at the start of the trial, *S. woodi* used a gait cycle motion in 56.2% of trials and limbs were flexed and adducted in 43.8% of the trials. Caudally and cranially extended limb positions were not observed. Thus, gait cycle and flexion adduction were used significantly more than caudal or cranial extension ($P<0.0001$, d.f.=3, $n=16$). When running bipedally at 0.8 m over the obstacle, limbs were flexed and adducted in 75% of the trials and cranially extended in 16.7% of the trials, and a gait cycle motion was used in 8.3% of the trials. Caudally extended limbs were not observed; therefore, limbs were flexed and adducted, or cranially extended more frequently than a gait cycle or caudal extension ($P=0.001$, d.f.=3, $n=12$). *Sceloporus woodi* touched the obstacle with their forelimbs 19 out of 51 trials, and all instances were with a quadrupedal posture (Table 1, Fig. 5) ($P=0.07$, $\chi^2=3.35$, d.f.=1, $n=51$).

Forelimb position in *A. sexlineata*

The frequency of forelimb position during bipedal locomotion at the start of a trial and at 0.8 m from the start without an obstacle was quantified for *A. sexlineata* (Fig. 4C,D). In trials without an obstacle present, there was no difference between the use of the four categories of forelimb position at the start or at 0.8 m ($P=0.2450$, $\chi^2=1.352$, d.f.=1, $n=29$). During bipedal locomotion at the start of the trial, limbs were caudally extended in 93.3% of the trials while gait cycle was used in 6.7% of the trials. These behaviors were used significantly more than cranial extension or flexion adduction, which were not observed ($P<0.0001$, d.f.=3, $n=15$). While running bipedally at 0.8 m from the start, caudal extension was used 100% of the time ($P<0.0001$, d.f.=3, $n=12$).

In trials with an obstacle, there was no difference between the use of the four categories of forelimb position at the start or at 0.8 m for *A. sexlineata* ($P=0.2721$, $\chi^2=12.206$, d.f.=1, $n=27$). When running bipedally at the start of a sprint trial, caudal extension was used 100% of the time ($P<0.0001$, d.f.=3, $n=14$). Only 1 out of 17 *A. sexlineata* touched the obstacle while sprinting bipedally, and this individual immediately transitioned to a quadrupedal posture after contact.

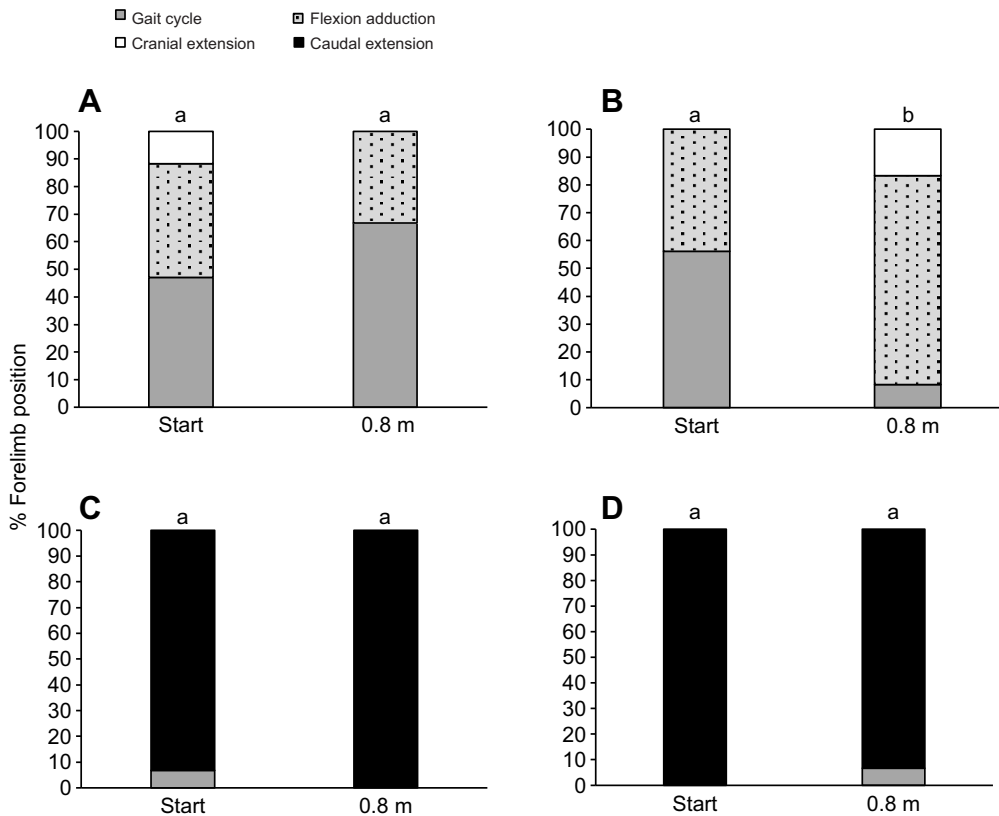


Fig. 4. The frequency of forelimb positions during bipedal locomotion at the start of a sprint trial and at 0.8 m with and without an obstacle for *S. woodi* and *A. sexlineata*. (A) In trials without an obstacle, *S. woodi* used flexion adduction and gait cycle significantly more than other forelimb positions both at the start of the sprint and at 0.8 m. (B) In trials with an obstacle, *S. woodi* used both flexion adduction and gait cycle at the start of the sprint trial, but used flexion adduction when crossing an obstacle. (C,D) In trials without an obstacle (C) and trials with an obstacle (D), *A. sexlineata* used caudal extension when running bipedally. A χ^2 analysis was used to compare the percentage of different forelimb positions used within two separate trials. Comparisons were not made across species or trials. Different letters indicate $P \leq 0.05$.

DISCUSSION

The goal of this study was to understand the mechanisms and tradeoffs associated with facultative bipedal locomotion. It is clearly established that bipedalism involves a shift in the BCoM (Van Wassenbergh and Aerts, 2013; Aerts et al., 2003; Clemente, 2014; Clemente and Wu, 2018), and that the presence of an obstacle often elicits the facultative use of bipedal posture in lizards (Parker and McBrayer, 2016; Tucker and McBrayer, 2012). Here, we placed the obstacles beyond a lizard's acceleration threshold, but this had little effect of the frequency of bipedal posture overall. Furthermore, the forelimbs had predictable patterns of use that aided the posterior movement of the BCoM during bipedalism. *Sceloporus woodi* rarely maintained a bipedal posture during a sprint, despite using it often for short periods (Parker and McBrayer, 2016). Regardless of obstacle presence, the stockier *S. woodi* infrequently used bipedal posture compared with the

streamlined *A. sexlineata*. When running bipedally, the forelimbs of *S. woodi* were generally flexed and adducted. This position did not significantly shift the BCoM posteriorly. Thus, using flexion and adduction only provides clearance over an obstacle, but does not aid in shifting to, or maintaining, a bipedal posture. *Aspidoscelis sexlineata*, which ran bipedally in 89% of all trials, primarily used caudal extension both when crossing the obstacle and at the start of a trial. Extending the forelimbs caudally caused a significant posterior shift in the BCoM (Fig. 3). The posterior shift in BCoM from caudal extension, plus having a very long tail relative to the trunk, is likely beneficial as *A. sexlineata* frequently maintains a bipedal posture over long distances (Olberding et al., 2012; Clemente and Wu, 2018). Given that the degree of facultative bipedalism is variable among taxa, highly contrasting body forms are expected to employ a range of strategies (e.g. forelimb positions) when using bipedal posture. In the species

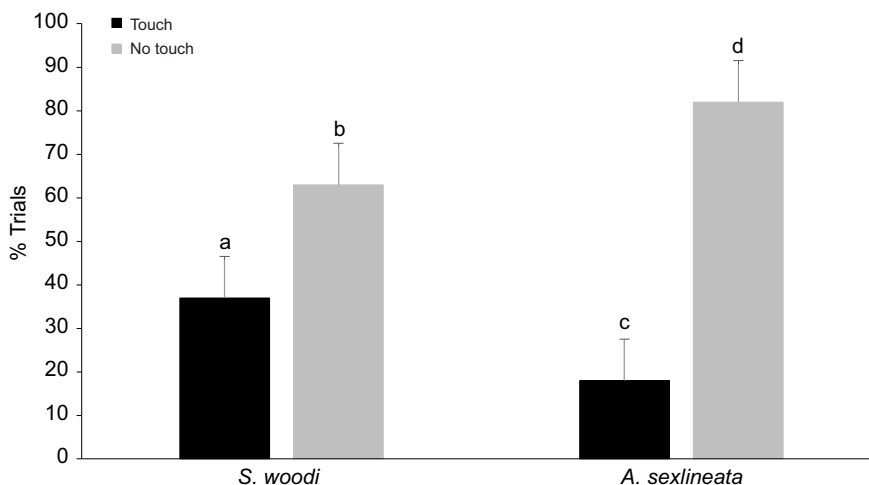


Fig. 5. Frequency of forelimbs touching versus not touching an obstacle during bipedalism. When crossing an obstacle, *S. woodi* touched the obstacle in 37% of the trials. When crossing an obstacle, *A. sexlineata* touched the obstacle in 18% of trials. Overall, *S. woodi* were more likely to touch the obstacle than *A. sexlineata*. Different letters indicate $P \leq 0.05$ via χ^2 analysis.

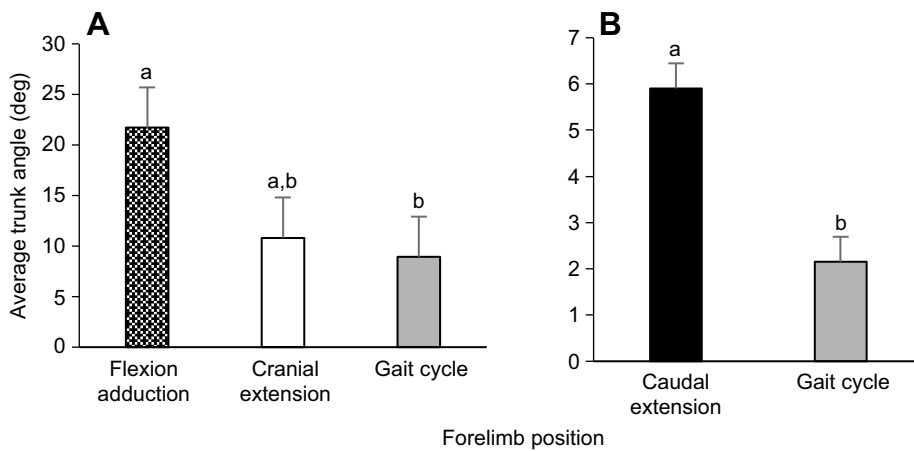


Fig. 6. Average trunk angle for each forelimb position used by each species. (A) Trunk angles were significantly greater in *S. woodi* with forelimbs flexed and adducted than when in a gait cycle, but not with limbs cranially extended ($n=23$, d.f.=2, F -ratio=12.77, $P=0.0003$). (B) In *A. sexlineata*, trunk angles were significantly greater when forelimbs were caudally extended versus in a gait cycle ($n=12$, d.f.=1, F -ratio=19.68, $P=0.0013$).

examined here, the frequency of bipedalism differed regardless of obstacle presence. Forelimb position during bipedal locomotion was variable in *S. woodi*, and the use of a bipedal posture was infrequent. In contrast, forelimb position was stereotyped in *A. sexlineata*, bipedalism was used often, thereby suggesting that forelimb position plays a role in shifting the BCoM posteriorly during bipedal locomotion.

Locomotor frequency with and without an obstacle

Sceloporus woodi exhibits facultative bipedalism (Tucker and McBrayer, 2012). The use of a bipedal posture increases when an obstacle is placed within the acceleration threshold of 0.4–0.5 m (Parker and McBrayer, 2016). However, an obstacle placed beyond this (e.g. 0.8 m) had little effect on the frequency of bipedal posture (Fig. 2). *Sceloporus woodi* has a short tail relative to its trunk which makes sustained bipedalism over long distances difficult. Furthermore, the lack of bipedalism in *S. woodi* during the strides crossing an obstacle suggests that bipedalism is primarily an effect of initial acceleration (Van Wassenbergh and Aerts, 2013). However, those *S. woodi* that ran bipedally over an obstacle had higher velocities than those which ran quadrupedally (Table 2). Hip height is greater during bipedal locomotion than during quadrupedal locomotion (Parker and McBrayer, 2016). Increasing the distance between the lizard and the obstacle decreases potential pausing related to obstacle negotiation (Kohlsdorf and Biewener, 2006). While bipedal posture may occur more frequently at the start of a sprint in *S. woodi*, we provide strong evidence that bipedal posture facilitates obstacle negotiation via sustained velocity when an obstacle is beyond the acceleration threshold (roughly 0.4–0.5 m for small lizards; McElroy and McBrayer, 2010).

Aspidoscelis sexlineata has a long tail relative to its trunk and can maintain a bipedal posture over long distances (Olberding et al., 2012). Regardless of obstacle placement, *A. sexlineata* primarily ran bipedally (Fig. 2). Furthermore, velocities were higher during obstacle navigation when using a bipedal posture. Continual bipedal locomotion with and without an obstacle suggests that bipedalism is a common form of locomotion in this species. Additionally, high velocities during bipedal locomotion may provide a benefit by decreasing pausing and stumbling relating to crossing an obstacle (Kohlsdorf and Biewener, 2006).

Contingency of forelimb position based on body plan

Aspidoscelis sexlineata has a long trunk and can reach a maximum forward speed of around 4 m s^{-1} when navigating obstacles (Olberding et al., 2012). The BCoM of *A. sexlineata* is shifted posteriorly by its long tail and vertically elevated trunk during

bipedalism (Aerts et al., 2003; Clemente, 2014). In conjunction with tail and trunk elevation, *A. sexlineata* uses caudal extension during bipedal locomotion (Fig. 4C,D). This forelimb position aids in further shifting the BCoM posteriorly when maintaining a bipedal posture over long distances. *Aspidoscelis sexlineata* does not modify its hindlimb kinematics when approaching an obstacle (Olberding et al., 2012), but instead makes small adjustments during obstacle negotiation. Likewise, caudal extension of the forelimbs was used both at the start of the trial and when crossing an obstacle (Fig. 4C,D). This suggests that forelimb position may be not only a behavioral adjustment for navigating obstacles but also a mechanism to adjust BCoM, affecting pitch. Indeed, trunk angle increased significantly in *A. sexlineata* when the forelimbs were caudally extended (Fig. 6B). Shifting the BCoM posteriorly aids in maintaining bipedal posture over long distances (Aerts et al., 2003; Clemente and Wu, 2018). Alternatively, forelimbs support the body mass during quadrupedal locomotion (Snyder, 1952). However, *A. sexlineata* touched the obstacle with their forelimbs only three out of 18 trials when sprinting bipedally and immediately reverted to a quadrupedal posture when they did (Fig. 5). Extending the forelimb toward the obstacle leads to a forward shift in the BCoM and decreased trunk angle, likely facilitating quadrupedal locomotion. Maintaining a bipedal posture likely aids obstacle negotiation while maintaining forward velocity (this study; Self, 2012; Olberding et al., 2012).

When sprinting bipedally at the start of a trial, *S. woodi* showed behavioral adjustments of the forelimbs which did not posteriorly shift the BCoM (Fig. 4A,D). The continuing gait cycle of the forelimbs at the start of a trial, little change in trunk angle and lack of sustained bipedalism suggest that bipedalism is a result of high acceleration in this species (Van Wassenbergh and Aerts, 2013). Yet, the forelimbs were primarily flexed and adducted when bipedally crossing an obstacle (Fig. 4A,D), which likely facilitates an increase in trunk angle (Fig. 6A). To avoid collision with an obstacle, lizards must raise both hip height and the forelimbs to avoid touching the obstacle (Irschick and Jayne, 1999). The hips and forelimbs are raised as a product of bipedalism, which enhances obstacle avoidance (Van Wassenbergh and Aerts, 2013). As bipedalism is less frequent in *S. woodi*, keeping the forelimbs flexed and adducted allows obstacle clearance without shifting the BCoM. *Sceloporus woodi* has a short tail relative to its trunk and reached velocities around 2.4 m s^{-1} when crossing an obstacle (Parker and McBrayer, 2016). *Sceloporus woodi* did not touch the obstacle with their forelimbs in 100% of the bipedal trials (Fig. 5). If bipedalism is not a posture for sustained locomotion in *S. woodi*,

then they need only hold the forelimbs up against the trunk to avoid contacting the obstacle so that forward speed is not disrupted (Self, 2012; Kohlsdorf and Biewener, 2006).

Conclusion

Aspidoscelis sexlineata, which has a long tail relative to the trunk, and *S. woodi*, which has a short tail relative to the trunk, were used to understand how bipedal posture and forelimb position vary when lizards are faced with a distantly placed obstacle. An obstacle placed beyond the acceleration threshold had no significant effect on the frequency of bipedal locomotion. Forelimb position was stereotyped in *A. sexlineata*, which primarily uses a bipedal posture, and variable in *S. woodi*, which primarily uses a quadrupedal posture. While bipedalism aids in obstacle negotiation, its occurrence is often an effect of a high starting acceleration in *S. woodi*. However, *A. sexlineata* frequently uses a bipedal posture, and this species positions its forelimbs such that the BCoM is shifted posteriorly, and thereby aids the pitching motion necessary to maintain bipedal posture. Thus, species with body plans that are suited for more sustained bipedal locomotion are likely to employ behavioral adjustments that aid in the maintenance of bipedalism, regardless of obstacle presence. Future studies should model the changes in forelimb position in tandem with ground force reactions and joint kinematics to understand the range of effects that shifts in forelimb position may have on bipedalism. Furthermore, future work should include additional bipedal species with a range of body forms so that phylogenetic inferences can be made regarding how this trait evolves.

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Competing interests

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Author contributions

Conceptualization: L.M.; Methodology: C.T.K.; Formal analysis: C.T.K.; Investigation: L.M.; Writing - original draft: C.T.K.; Writing - review & editing: C.T.K., L.M.; Supervision: L.M.; Project administration: L.M.

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Supplementary information

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