

Fall 2012

The Effects of Locomotor Posture on Kinematics, Performance and Behavior during Obstacle Negotiation in Lizards

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THE EFFECTS OF LOCOMOTOR POSTURE ON KINEMATICS, PERFORMANCE
AND BEHAVIOR DURING OBSTACLE NEGOTIATION IN LIZARDS

by

JESSICA D. SELF

(Under the Direction of Lance D. McBrayer)

ABSTRACT

The ability to efficiently move over uneven terrain is critical for most terrestrial animals. Bipedal running is common in lizard species, however the biological advantage of a bipedal running posture remains uncertain. I examined the hypothesis that a bipedal posture is advantageous when crossing obstacles. Particularly, I determined whether kinematic adjustments differ among four focal species with contrasting body forms and ecology. I also examined how sprint speed changed when crossing obstacles with a quadrupedal versus a bipedal posture. I quantified kinematics from high-speed video (300 frames/second) of lizards running down a 3m runway both with and without the presence of an obstacle. Among species, I observed high variation in kinematics, locomotor performance and behavior when crossing obstacles. Within species, mean forward speed (velocity) and kinematics did not change between treatments when employing a bipedal posture. However among species, kinematics differed when using a bipedal posture indicating morphological variation influences how a species utilizes a bipedal posture. Overall, my study suggests an advantage in a bipedal posture when faced with obstacles.

Index Words: Kinematics, Performance, Morphology, Locomotion, Obstacles, Lizards

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B.A., Western Washington University, 2009

A Thesis submitted to the Graduate Faculty of Georgia Southern University in Partial

Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE, BIOLOGY

STATESBORO, GEORGIA

2012

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Electronic Version Approved:
December 2012

ACKNOWLEDGMENTS

This work would not have been completed without the advice and assistance of Lance McBrayer, Roger Anderson, Tim Higham, Jeffery Olberding, Eric McElroy, Peter Zani, Reena Torrence, Andrew Halliburton, Ray Chandler, Michelle Cawthorn, Daniel Williams, the Western Washington University 2011 Lizard Ecology field course and the Vertebrate Zoology group at Georgia Southern University. I would especially like to thank Clint Collins for his hard work and support in the field and emotionally supporting me throughout my career as a graduate student. I would also like to thank my family for always supporting and believing in me. A Georgia Southern University College of Graduate Studies award supported the fieldwork of this study. Research was conducted following the Institutional Animal Care and Use Committee under permit number I09009. I thank the US Fish and Wildlife Service (Oregon permit number: 109-10) and the Bureau of Land Management, Burns District (permit number: 1004-0119), for permission to work in the Alvord Basin on public land.

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INTRODUCTION

Relationships among morphology, biomechanics and locomotor performance have been extensively studied in vertebrates in order to understand the relationship between morphology and how animals move in their environment (Arnold 1983; Garland and Losos 1994; Losos and Miles 1994; Irschick and Jayne 1999; Goodman et al., 2008). These studies tend to focus on movement over flat, uniform surfaces and are concentrated on steady-state running such as endurance and sprint speed (Irschick and Jayne 1999; Irschick et al., 2000; Vanhooydonck et al., 2002; McElroy et al., 2007; Clemente et al., 2008). Such studies reveal how maximal performance is achieved under ideal conditions. However, most small vertebrates use maximal performance speeds in short bursts in order to evade predators or capture food (Husak and Fox 2006). Understanding how animals move through uneven terrain and over obstacles can help us recognize subtle, but crucial, aspects of how animals may navigate their habitats to avoid predators as well as capture prey, and potentially why animals prefer certain substrate types (Arnold, 1983; Collins et al., In Review).

The role of habitat complexity in shaping locomotor behavior and performance is important to consider because animals often encounter natural barriers such as branches, rocks, and woody debris within their environment (Irschick and Garland, 2001). Because small vertebrates such as lizards use short bursts of high-speed locomotion, the ability for animals to negotiate over or around these obstacles is likely under selective pressure. Doing so could ensure successful food acquisition, territory defense, and predator evasion (Garland and Losos, 1994; Irschick and Losos, 1999; Vitt et al., 2003). In lizards, bipedal running is potentially advantageous for crossing obstacles (Kohlsdorf and Biewener,

2006; Olberding et al., 2011). When an animal approaches an obstacle with a bipedal posture, its trunk is elevated above a horizontal position, improving its field of view and elevating its body center of mass (COM) (Avery et al., 1987; Higham et al., 2001; Higham and Jayne, 2004; Olberding et al., 2012). In the lizard *Sceloporus malachiticus*, bipedalism occurred when lizards ran over medium and high obstacles (49%-103% of their limb length) (Kohlsdorf and Biewener, 2006). The lizard *Sceloporus woodi* used bipedal locomotion more than any other strategy, such as quadrupedal running or jumping, when crossing obstacles that lizards could see over (Tucker and McBrayer, 2012). When bipedal, the body COM is already elevated prior to crossing the obstacle, whereas a quadrupedal posture requires lifting of the COM while moving over the obstacle (Kohlsdorf and Biewener, 2006; Olberding, et al. 2012). Enhancing field of view may further aid adjustment of footfall patterns before crossing an obstacle, thereby minimizing slipping or tripping (Kohlsdorf and Biewener, 2006; Olberding et al., 2011; Chen et al., 1991).

It was previously thought that bipedalism arose because it increased speed and was less energetically costly (Snyder, 1952; Snyder, 1962). However, similar-sized bipedal and quadrupedal animals are now known to have the same locomotor costs (Fedak et al., 1982; Roberts et al., 1998). Also, maximal speed of bipedal running is not significantly different from maximal quadrupedal speed (Clemente et al., 2008). Thus, bipedalism does not confer an advantage in efficiency or speed during steady-state running. However, one study examining obstacle crossing in lizards found that velocity does not decrease when an individual runs over an obstacle with a bipedal posture (Olberding et al., 2012). This phenomenon is particularly interesting in animals that use

both bipedal and quadrupedal postures. Therefore, quantifying obstacle-crossing performance among multiple lizard species from different habitats would be useful in testing hypotheses on different locomotor postures, habitat usage, as well as if all species employ similar strategies.

To test the significance of a bipedal posture when crossing obstacles, we compared kinematic, behavior, performance and morphological variables of four species of lizards: *Gambelia wislizenii*, *Crotaphytus bicinctores*, *Sceloporus occidentalis* and *Aspidoscelis tigris*. *Gambelia wislizenii* and *C. bicinctores* are ideal study species because they are closely related within the family *Crotaphytidae* and share a similar body plan. However, *G. wislizenii* occupies sandy habitats, while *C. bicinctores* inhabits rocky habitats (Pianka, 1966; Pianka, 1967). *Sceloporus occidentalis* lives in rocky habitats and is part of the family *Phrynosomatidae* that is rather closely related to the family *Crotaphytidae* (Wiens et al., 2009). *Aspidoscelis tigris* occupies sandy habitats, is similar in body size to the other three species yet has a contrasting body form. Thus, *A. tigris* is a useful outgroup because it is more distantly related (*Teiidae*) to the other study species. Thus when considering obstacle negotiation in these four species, differences in kinematics, speed, morphology, and behavior may represent advantages to the different habitats occupied by these species, or may be related to morphology and evolutionary history.

I address the following questions: (1.) Within species, is there a difference in performance, body posture and kinematic variables when running with and without obstacles? (2) Is there a difference in performance and behavior when crossing obstacles with a bipedal posture versus a quadrupedal posture? In particular, I determine whether

bipedal running allows for crossing obstacles in fewer strides, less of a decrease in speed, and whether it allows for stepping over obstacles rather than stepping on the obstacle. (3) Among species, is there a difference in performance, body posture and kinematic variables when running with and without obstacles? I hypothesize that all species will increase bipedal frequency when faced with an obstacle. I expect that there will be a decrease in speed when crossing obstacles with a quadrupedal posture due to a decrease in field of view and stability. Lastly, I expect all lizard species will similarly alter their body angle, tail elevation, and hip height regardless of a bipedal or quadrupedal posture when crossing an obstacle to offset the required change in substrate evenness.

METHODS

Capture and Husbandry

Lizards were captured by noose (Husak et al., 2007) in the Alvord Basin of southeastern Oregon during June and July of 2011 (Sample sizes were N=15 for *C. bicinctores* [Snout-vent length (SVL \pm S.E.) = 90.0 \pm 1.1mm], N =12 for *G. wislizenii* (SVL = 90.6 \pm 1.6mm), N=13 for *S. occidentalis* (SVL = 80.1 \pm 3.0mm) and N = 14 for *A. tigris* (SVL = 89.6 \pm 0.9mm). The location of each lizard sighting was marked with GPS coordinates and flagging tape. Each individual was released at the point of initial sighting location after all data collection. Immediately upon capture, the lizard's body temperature (T_b) was taken using a cloacal thermometer. The substrate temperature of initial sighting location was measured with an IR thermometer. Both temperatures are used to ensure that body and substrate temperatures were within proper range during the performance trials. Lizards were stored in cloth bags in a cooler until sprinting trials were conducted. Individuals were run 24 to 48 hours after capture; lizards were held for

a maximum of 48 hours before release. Before performance testing, non-toxic, white paint was used to mark the following anatomical landmarks: hip, center of trunk, the base of the tail and 40% of the tail length from the tail base (Figure 1). Locomotor performance of females varies based on reproductive condition (Cooper et al., 1990; Husak, 2005), so only adult males were used.

Performance Testing

Performance trials were conducted inside a wooden runway (3 m L x 0.4 m W x 0.6 m H). One entire three-meter side was made of Plexiglas panels to allow for filming in lateral view. The runway was flat with a substrate of hard-packed natural sand. In one half of the trials a rectangular, wooden obstacle was placed 1.5 meters from the starting line, spanning the runway width (Figure 2). The height of the obstacle was standardized to 30% of the average of each species hind limb length.

Three CASIO high-speed cameras filming at 300 frames/second recorded the length of the runway (Figure 2). Lizards were placed in an incubator that raised their body temperature to 37-40 °C, which is a similar temperature range to their field activity body temperature. Each lizard ran three trials with an obstacle and three without in an order randomized via coin flips. Between each trial, lizards had at least a 30-minute rest before their next run. The individual's run with the highest velocity for all trials with and without an obstacle was retained for analysis.

Video Analysis:

I digitized two-dimensional coordinates for each anatomical landmark using DLTdv3 Software in MATLAB. To calculate sprinting velocity (m/sec), I digitized the position of the shoulder. For behavioral and kinematic analysis, I calculated eight

variables: (1) *Behavior* is defined as an individual stepping on or over the obstacle. (2) *Posture* is measured as or bipedal or quadrupedal posture when crossing the obstacle. (3) *Stride length* is the distance between successive footfalls of the left hindlimb. (4) *Bipedal proportion* is the proportion of a bipedal posture while the individual prepares and crosses the obstacle. I measured the bipedal proportion covered during the first and second one-meter span of the runway. (5) *Froude number* $[(ug^{-1/2})*(L^{-1/2})]$, where u = speed, L = characteristic length (hip height from the ground) and g = gravitational constant] is commonly used to compare among species of different sizes. If the froude number is equal among species, it is suggested they are moving in a dynamically similar way (Irschick and Jayne 1999; Biewener 2003). (6) *Body Angle* is measured with positive values indicating the trunk elevated (above horizontal) and negative values indicating a depression of the trunk (below horizontal). I determined body angle relative to the ground as the angle between the shoulder, pelvis vertex and ground surface. Positive values indicated the trunk was oriented above a horizontal plane through the pelvis (Figure 1). (7) *Hip height* during mid-stance was calculated at 1.5 meters. The hip height was determined as the distance from the hip to the ground surface in centimeters (cm) (8) *Tail elevation* is defined as elevated (above horizontal) when values are positive and depressed (below horizontal) when values are negative (Figure 1). Tail elevation has not been examined in lizards running over obstacles. A horizontal tail could aid in an increase in body angle when crossing obstacles.

Morphology

Fifteen morphological measurements were taken using dial calipers accurate to 0.01mm. The measurements included: tail length, jaw length from the anterior portion of

the ear opening to the tip of the snout, head width, depth of the body at the pectoral girdle, width of the body at the pectoral girdle, the lengths of the humerus, antebrachium, manus, the longest digit (IV) measured from the manus to the tip of the claw; femur, crus, foot, and the longest hind toe (IV). Snout-vent length (SVL) and tail length was measured using a ruler. These measurements are important not only for determining relationships between locomotor morphology and performance among species but also to determine proper obstacle height for each lizard.

Statistical Analysis

Variation in body size was standardized for all kinematic, velocity and morphological variables by regressing each variable of interest on SVL and retaining the residuals for analysis. Among species, analysis of variance (ANOVA) and Tukey-Kramer HSD tests were used to test significant differences in mean values of behavior, posture, stride length, stride duration, body angle, hip height, tail elevation, bipedal posture frequency covered during the first two, 1-meter spans and mean velocity of strides at 1, 1.5 and 2 meters when running with and without an obstacle. Differences were evaluated within and among species when running with and without an obstacle. For all analyses, I used JMP v 9.0 and NCSS software, and set $P \leq 0.05$ as the standard for statistical significance. To distinguish kinematic and timing differences among species, I performed a Discriminant Functions Analysis (DFA) on size-corrected stride length, stride duration, velocity, froude number, body angle, hip height and tail elevation variables. To examine morphological differences among species in correlation to kinematic and performance variables, we performed a canonical correlation analysis using size-corrected data.

RESULTS

Behavior

Relatively few differences were observed when examining posture within species. Only one species changed its posture between trials with and without an obstacle, *A. tigris* ran bipedally more frequently through the second meter when an obstacle was present ($F_{1,24} = 28.3$; $P = 0.003$). When an obstacle was not present, $24 \pm 0.07\%$ of the second meter was run with a bipedal posture, whereas a bipedal posture covered $77 \pm 0.09\%$ of the second meter when an obstacle was present (Table 1).

Species crossed obstacles with similar behaviors but different postures ($\chi^2 = 20.47$; $df = 3$; $P < 0.001$). *C. bicinctores* ran bipedally almost exclusively (13 individuals crossed with a bipedal posture, 2 were quadrupedal), while *S. occidentalis* only one individual was observed to cross the obstacle with a bipedal posture (Table 1, Figure 3). The proportion of a bipedal posture during the first two meters varied significantly among species when an obstacle was present (meter 1: $\chi^2 = 13.4$; $df = 3$; $P = 0.004$; meter 2: $\chi^2 = 19.9$; $df = 3$; $P < 0.001$). *Crotaphytus bicinctores* ran an average of $88 \pm 0.07\%$ of the first meter with a bipedal posture, while *S. occidentalis* only covered $10 \pm 0.01\%$ of the first meter bipedally. *Aspidoscelis tigris* and *C. bicinctores* covered $70\%+$ of the second meter with a bipedal posture, while *G. wislizenii* and *S. occidentalis* averaged only 10% of meter two with a bipedal posture (Table 1). This considerable variation exists among species in their use of bipedal locomotion with or without obstacles.

Kinematics

Species changed kinematics when crossing obstacles. *C. bicinctores* took longer strides when crossing an obstacle ($F_{1,25} = 5.29$; $P = 0.029$; $x = 38.4 \pm 2.5$ cm with an

obstacle and $x = 30.8 \pm 2.4$ cm without), whereas the other three species did not change stride length (Table 3). *G. wislizenii*, *A. tigris* and *S. occidentalis* each increased their body angle when crossing an obstacle (*G. wislizenii*, $F_{1,22} = 7.75$; $P = 0.018$, *A. tigris*: $F_{1,24} = 5.51$; $P = 0.008$, *S. occidentalis*: $F_{1,23} = 6.61$; $P = 0.018$) (Table 1, Figure 4). Froude number significantly decreased in *G. wislizenii* when crossing obstacles ($F_{1,22} = 5.07$, $P = 0.0357$). Froude number for the three remaining species did not change with the presence of an obstacle (Table 1).

With the exception of tail elevation, all kinematic variables differed among species (Table 1). *C. bicinctores* took significantly longer strides than the other three species ($F_{1,24} = 16.2$; $P < 0.001$). Froude number in *G. wislizenii* was significantly lower than all other species ($F_{1,22} = 28.3$; $P < 0.001$), indicating *G. wislizenii* exhibits different speeds when faced with an obstacle. Body angle was significantly higher in *C. bicinctores* and *S. occidentalis* compared to *G. wislizenii* and *A. tigris* ($F_{3,45} = 7.5$; $P < 0.004$) (Figure 4). *C. bicinctores* had a significantly higher hip height than the other species ($F_{3,45} = 10.2$; $P < 0.001$). Tail elevation was not significantly different among species when crossing obstacles. However, among species tail elevation was variable when running without an obstacle ($F_{3,45} = 7.73$; $P < 0.001$), indicating all species made similar tail alterations when crossing obstacles.

Performance

Only *G. wislizenii* changed velocity in response to the presence of an obstacle. *Gambelia wislizenii* decreased velocity during the stride crossing an obstacle ($F_{1,22} = 4.02$; $P = 0.05$), as well as the stride after crossing the obstacle ($F_{1,22} = 5.6$; $P = 0.027$)

(Table 2). Therefore, *G. wislizenii* crossed obstacles with a quadrupedal posture at a lower speed and continued to run slow after the obstacle.

There was a significant difference in velocity among species during the strides at meter one ($F_{3,45} = 9.8$; $P < 0.001$) and 1.5 ($F_{3,45} = 15.5$; $P = < 0.001$); *C. bicinctores* and *A. tigris* ran significantly faster than *G. wislizenii* and *S. occidentalis*. *C. bicinctores* maintained a higher velocity in the stride after the obstacle compared to the other three species ($F_{3,45} = 16.1$; $P < 0.001$) (Table 1). Thus, species which cross obstacles with a bipedal posture do so at higher velocities than the species employing a quadrupedal posture during obstacle crossing.

Morphology - Kinematics & Performance Relationships

I used Canonical correlation analysis to identify associations between morphology and kinematics/performance. The first and second canonical axes were significant (canonical 1: Wilks' $\lambda = 0.122$, $F_{35,158} = 2.93$, $P < 0.001$; canonical 2: Wilks' $\lambda = 0.346$, $F_{24,134} = 1.98$, $P = 0.008$). The first canonical axis had a canonical correlation of 0.80. The second canonical axis had a canonical correlation of 0.73. For morphology, the first morphological variate extracted 13.5% of the variance in the morphological variables. The second morphological variate extracted 29% of the variance in morphology. The first kinematic and performance variate extracted 15% of the variance in these variables, while the second kinematic and performance variate extracted 39% of the variance in these variables. Overall, the canonical correlation revealed that 43% of the morphological variance explained 54% of the kinematic and performance variance.

The first canonical axis indicated a significant relationship between body angle and tail elevation with pectoral depth. This axis also defined a significant relationship

between velocity, foot length and hind foot toe length. Therefore, longer feet were correlated with higher speeds and a more robust chest was correlated with higher body angles and tail elevations. The second canonical axis indicated a relationship between hip height, stride length, velocity and femur length, tibia length, foot length, and pectoral depth (Table 3). Therefore, longer hindlimbs and a robust chest were correlated with higher velocity, body angle, hip height and higher tail elevation when crossing obstacles.

Use of Bipedal versus Quadrupedal Posture

Each species crossed the obstacle using both bipedal and quadrupedal postures in at least one trial. However, only one *S. occidentalis* individual crossed the obstacle with a bipedal posture. Given the rare occurrence of bipedalism in *S. occidentalis*, this species was excluded from further analysis. During bipedal locomotion, *C. bicinctores* and *G. wislizenii* were significantly more likely to step over the obstacle (*C. bicinctores*: $\chi^2 = 4.6$; $df = 1$; $P = 0.03$, *G. wislizenii*: $\chi^2 = 2.7$; $df = 1$; $P = 0.033$) (Table 2, Figure 3). *G. wislizenii* and *A. tigris* had a significantly higher velocity when crossing an obstacle with a bipedal posture (*G. wislizenii*: $F_{1,22} = 7.9$; $P = 0.018$, *A. tigris*: $F_{1,24} = 7.9$, $P = 0.014$). Although their velocity was not significantly different when crossing an obstacle quadrupedally, *C. bicinctores* did take significantly fewer strides during the second meter when using a bipedal posture to cross the obstacle ($F_{1,25} = 7.9$; $P = 0.014$) (Table 2). This indicates that a bipedal posture may confer a locomotor advantage when crossing obstacles.

The size-corrected DFA was highly significant (Wilks' $\lambda = 0.50$; $F_{5,43} = 8.6$; $P < 0.001$) for bipedal versus quadrupedal postures when crossing obstacles. The first axis explained 100% of the variation in posture. Velocity, hip height and stride length had

high positive loadings (Table 4). Bipedal posture had high positive loadings for velocity, hip height and stride length compared to a quadrupedal gait when crossing obstacles. The DFA for running with a quadrupedal posture with and without an obstacle was highly significant (Wilks' $\lambda = 0.57$; $F_{5,43} = 7.1$; $P < 0.001$). The first axis explained 100% of the variation in obstacle presence. Velocity had a high positive loading, while body angle had a high negative loading. The absence of an obstacle had a high positive loading, while the presence of an obstacle had a negative loading (Table 4). Thus, when using a quadrupedal posture, velocity was higher without an obstacle. When crossing an obstacle quadrupedally, velocity was lower, and body angle was higher. For bipedal running with and without an obstacle, the DFA was not significant (Wilks' $\lambda = 0.91$; $F_{5,43} = 0.7$; $P = 0.61$). Therefore, individuals do not make kinematic adjustments, or change speed, when crossing obstacles with a bipedal posture. This further supports the hypothesis that a bipedal posture is advantageous when crossing obstacles.

DISCUSSION

The goal of my study was to determine whether species differentially alter their body angle, tail elevation and hip height in order to offset the required change in the height of the COM when crossing obstacles. I specifically wanted to examine the hypothesis that a bipedal posture is advantageous when crossing obstacles. Among species, I observed variation in behavior, performance and kinematics when crossing obstacles. *Crotaphytus bicinctores* and *A. tigris* crossed obstacles with a bipedal posture more frequently than *G. wislizenii* and *S. occidentalis*, which both used a quadrupedal posture when crossing obstacles (Table 1). Crossing obstacles with a quadrupedal posture was associated with lower velocities and stepping on the obstacle, whereas a

bipedal posture correlated with stepping over the obstacle without touching it (Table 2). Velocity did not decrease when crossing obstacles with a bipedal posture compared to running without an obstacle present, regardless of posture. Given these results, I conclude that bipedal running confers an advantage when crossing obstacles. However, different species maintain a bipedal posture with different kinematic adjustments due to morphologic distinctions.

Anticipation of Obstacles

In my study, three species used a bipedal posture when approaching obstacles. *Crotaphytus bicinctores* ran bipedally regardless of the presence or absence of an obstacle. *A. tigris* used a bipedal posture more frequently during the second meter when approaching the obstacle, while *G. wislizenii* tended to run bipedal more frequently in the presence of an obstacle during the first meter of running (Table 1). Thus, *A. tigris* and *G. wislizenii* use a bipedal posture during preparatory strides as they approach obstacles. In birds, pigeons use visual planning during locomotion of uneven terrain and increase hip height when approaching obstacles (Birn-Jeffery and Daley 2012). In lizards, a bipedal posture is likely used in preparation of crossing obstacles, possibly enhancing their field of view (Avery et al., 1987; Higham et al., 2001; Higham and Jayne, 2004; Kohlsdorf and Navas, 2007) and improving their ability to clear obstacles altogether (Table 2).

We quantified two modes of obstacle crossing, stepping on the obstacle and stepping over the obstacle. *Sceloporus occidentalis* commonly stepped on the obstacle (92% of the individuals) and did so with a quadrupedal posture, while *C. bicinctores* almost exclusively (87% of the individuals) ran over the obstacle with a bipedal posture without touching it (Table 2, Figure 3). *C. bicinctores* tended to stumble when

stepping on an obstacle with a quadrupedal posture, indicating a hindrance when using a quadrupedal posture. Olberding et al. (2012) detected little difference in specific kinematic adjustments of the hindlimb when stepping over an obstacle compared to unobstructed running. However, significant alterations were made when stepping on obstacles (Olberding et al., 2012). Bipedal running raises hip height due to an elongation or abduction of the hindlimbs (Irschick and Jayne, 1999), thus the hindlimbs can completely clear obstacles more readily (Kohlsdorf and Biewener, 2006). Humans and other animals increase stability by adjusting posture and foot placements to avoid stumbling over obstacles (Biewener, 2003; Clark and Higham, 2011; Daley and Biewener, 2011). Hence, a bipedal posture and the behavior of clearing obstacles work simultaneously to reduce any adjustments of the hindlimb that might be required to cross an obstacle (Chen et al., 1991; Daley et al., 2006; Collins et al., In Review).

Kinematic Adjustments

Body angle increased in all species when crossing obstacles, except *C. bicinctores*, which maintained a high body angle in all trials. *Sceloporus occidentalis* ran almost exclusively quadrupedally yet increased their body angle when crossing obstacles (Figure 5). Thus, *S. occidentalis* likely elevates their head via extending their forelimbs or depressing their hindlimbs or both. Previous studies have reasoned that a bipedal posture before and during obstacle crossing could aid in enhancing field of view (Kohlsdorf and Biewener, 2006; Olberding et al., 2012; Tucker and McBrayer, 2012). Interestingly, hip height did not change within species when comparing trials with and without obstacles (Table 1). My study supports Kohlsdorf and Biewener who observed no change in hind limb extension with an increase in obstacles size (Kohlsdorf and

Biewener, 2006). As a result, forelimb extension must be responsible for increases in body angle. My results imply body angle is a key kinematic adjustment when crossing obstacles regardless of posture and that bipedal running may be a consequence of extreme forelimb extension to either prepare for an obstacle, or see over it.

Tail elevation has been observed to increase as body angle increases during steady-state running (Irschick and Jayne, 1999). When negotiating obstacles, holding the tail at a horizontal position could stabilize the body COM (Irschick and Jayne, 1999) and therefore allow the animal to move over the obstacle without stumbling. However, previous studies examining lizards running over obstacles did not analyze tail elevation. I observed that 40% of the base of the tail was elevated near a horizontal position when crossing obstacles for all species; in addition there was a significant difference among species in tail elevation when an obstacle was not present (Table 1). Regardless of body angle, horizontal tail elevation must aid in stability when crossing obstacles; the weight of the tail counter balances the weight of the trunk as it is elevated to clear the obstacle, and hence aids in stabilizing the COM (Irschick and Jayne, 1999).

In horses, different-sized individuals switch gaits from a walk to a run at different speeds, yet do so at the same froude number (Griffin et al., 2004; Griffin et al., 2004). Additionally, changing from a run to a walk is thought to improve stability (Diedrich and Warren, 1995; Diedrich and Warren, 1998a; Diedrich and Warren, 1998b). A similar explanation is also likely when animals cross obstacles. *Gambelia wislizenii* likely changed gait from a run to a walk when crossing obstacles, thus lowering their froude number. *C. bicinctores* and *A. tigris* had similar froude numbers and frequently crossed obstacles with a bipedal posture and higher velocities, however, their body angles

were significantly different. This indicates that *C. bicinctores* and *A. tigris* had dynamically similar gaits, even though their body angles were significantly different when doing so. Therefore, altering body angle either improves stability or enhances perception, or a combination of the two.

Effects of Morphology on Obstacle Crossing Performance and Kinematics

Morphological differences among similar-sized species have major impacts on overall performance and kinematics of animal locomotion (Garland and Losos, 1994; Irschick and Jayne, 1999; Higham and Jayne, 2004; McBrayer, 2004; Olberding, et al., 2012). Within the subfamily *Lygosominae*, species with greater limb lengths have higher performance when sprinting, climbing and clinging compared to shorter limbed species (Goodman et al., 2008). Yet short leg lengths may aid in increased stability when running over uneven terrain, therefore improving performance in those environments (Demes et al., 1995; Irschick and Losos, 1999; Kerdok et al., 2002; Irschick et al., 2005; Channon et al., 2011; Collins et al., In Review). Even with a low body angle when crossing obstacles, *Aspidoscelis sexlineatus* maintains high speeds by tucking their forelimbs back and sustains a near horizontal posture when crossing obstacles (Olberding et al., 2012). This study implies that species with a more robust chest cross obstacles with a higher body angle and species with longer hindlimbs and longer feet cross obstacles faster. Furthermore, longer hindlimbs allows for higher body angles, hip heights, and longer strides when crossing obstacles (Table 3). *Aspidoscelis tigris*, was similar in snout-vent length, yet morphologically very different than *C. bicinctores* in body shape (Table 5). Both species attained similar speeds when crossing obstacles, yet did so with different body angles and hip heights. *Crotaphytus bicinctores* has a broad chest and employed a

high body angle. Due to a robust chest, the COM is probably located higher in the trunk, making the front of the body heavier. Moving the COM more anteriorly towards the hips allows the body to lift into a bipedal posture, likely stabilizing the individual when crossing an obstacle. Overall, our results suggest that morphology does affect performance and kinematic adjustments when crossing obstacles.

Most habitats contain natural barriers such as branches or rocks. *A. tigris* is likely under predation pressure from *G. wislizenii* in the Alvord Basin (Eifler et al., 2008). *Aspidoscelis tigris* are habitat generalists and therefore likely cross barriers when evading their predators (Peterson, 1987; Anderson, 1993; Heaton et al., 2006). *Gambelia wislizenii* remains close to shrub cover while ambush foraging and in case of a predators approach (Steffen and Anderson, 2006). Thus quickly crossing obstacles may not be essential if they are seldom in the open and forced to cross them. This would explain why *G. wislizenii* did not increase bipedality, and decreased velocity when crossing obstacles. Similarly, I observed *S. occidentalis* avoiding predators by moving short distances to another side of a boulder, therefore rarely crossing obstacles. Instead they darted short distances to a different position, out of site of the predator. Thus, obstacle crossing performance may be influenced not only by posture, morphology, and kinematics, but also by the relative frequency with which species cross obstacles in their native habitat. The relevance of maximal performance such as spring speed or obstacle crossing efficiency compared to an animal's behavior in their environment must be considered. Therefore, additional data on flight distance and habitat use for these species would enhance understanding of the necessity and frequency of crossing obstacles within their environment.

Advantages of Bipedal Locomotion

Previous studies have found that bipedality does not confer an advantage in speed or energy efficiency during steady-state locomotion on flat substrates (Aerts et al., 2003; Clemente et al., 2008). I study provides comparative evidence in support of the hypothesis that bipedal locomotion is advantageous in order to efficiently cross obstacles (Kohlsdorf and Biewener, 2006; Olberding et al., 2012). The absence of a reduction in speed when using a bipedal posture indicates an advantage in bipedality when crossing obstacles (Olberding et al., 2012). Individuals that run over an obstacle either faster, or with longer or fewer strides, should take less time to cross the obstacle, and thus have advantages in evading predators (Cooper and Vitt, 1991; Husak et al., 2006). Because small vertebrates such as lizards use short bursts of high-speed locomotion (Husak and Fox, 2006), a bipedal posture may be advantageous for not only enhancing field of view, but also for maintaining high speeds by increasing stride length and hip height to efficiently move over uneven terrain. I study demonstrates that during quadrupedal running over obstacles, an increase in body angle was an essential modification for obstacle negotiation. Therefore, a tradeoff between maintaining a high running speed and forelimb extension to see over or prepare to navigate an obstacle was apparent. Although bipedal running likely confers an advantage when crossing obstacles, this behavior may not be imperative if the animal does not frequently interact with obstacles within their environment.

Table 1. Size corrected mean values of behavior, kinematics and velocity when running with and without an obstacle for four species of lizard. Values are means \pm S.E.M. * Indicate p-values are ≤ 0.05 compared within species, with and without an obstacle. Shared letters indicate species means with an obstacle are not significantly different based on Tukey-Kramer HSD. Behavior is defined as an individual stepping on or over the obstacle. Posture is measured as bipedal or quadrupedal posture when crossing the obstacle. Stride length is the distance between successive footfalls of the left hindlimb. Stride duration is the elapsed time between successive footfalls of the left hindlimb. Bipedal proportion is the proportion of bipedal posture covered during the defined one-meter span. Body Angle is a measure of trunk elevation above horizontal (+), horizontal (0) or below horizontal (-). Tail is defined as elevated above horizontal (+) and below horizontal (-).

Variable	<i>C. bicinctores</i> N=15		<i>S. occidentalis</i> N=13		<i>G. wislizenii</i> N=12		<i>A. tigris</i> N=14	
	<i>With</i> <i>Obstacle</i>	<i>Without</i> <i>Obstacle</i>	<i>With</i> <i>Obstacle</i>	<i>Without</i> <i>Obstacle</i>	<i>With</i> <i>Obstacle</i>	<i>Without</i> <i>Obstacle</i>	<i>With</i> <i>Obstacle</i>	<i>Without</i> <i>Obstacle</i>
Behavior (on, over)	5,10		8,5		9,3		7,7	
Posture (biped, quad)	13,2		1,13		3,9		8,6	
Stride Length (cm)	38.4 \pm 2.5* _B	30.8 \pm 2.4	16.8 \pm 1.5 _A	17.5 \pm 1.6	19.9 \pm 1.9 _A	22.5 \pm 2.1	24.3 \pm 1.8 _A	25.4 \pm 1.67
Stride Duration (sec)	0.11 \pm 0.01 _A	0.11 \pm 0.01	0.15 \pm 0.03* _A	0.10 \pm 0.01	0.13 \pm 0.01 _A	0.11 \pm 0.01	0.11 \pm 0.01 _A	0.09 \pm 0.0
<i>0-1meter</i>								
Bipedal Proportion	0.88 \pm 0.07 _C	0.77 \pm 0.09	0.18 \pm 0.05 _A	0.23 \pm 0.07	0.57 \pm 0.07 _B	0.33 \pm 0.13	0.24 \pm 0.07 _A	0.28 \pm 0.07
<i>1-2 meter</i>								
Bipedal Proportion	0.75 \pm 0.08 _B	0.77 \pm 0.2	0.10 \pm 0.01 _A	0.15 \pm 0.08	0.10 \pm 0.04 _A	0.15 \pm 0.08	0.77 \pm 0.06* _B	0.18 \pm 0.09
Body Angle	12.7 \pm 2.4 _C	6.1 \pm 2.8	9.0 \pm 1.6* _B	3.2 \pm 1.6	5.2 \pm 1.32* _A	-1.9 \pm 2.0	1.4 \pm 1.8* _A	-4.0 \pm 1.4
Hip Height (cm)	4.7 \pm 0.3 _B	4.3 \pm 0.2	2.7 \pm 0.3 _A	2.3 \pm 0.2	3.1 \pm 0.2 _A	3.4 \pm 0.2	3.1 \pm 0.2 _A	3.0 \pm 0.1
Tail Elevation	1.2 \pm 3.1 _A	7.6 \pm 2.6	-1.5 \pm 2.5 _A	-0.96 \pm 1.5	-6.9 \pm 2.4 _A	-3.6 \pm 2.5	-4.2 \pm .5 _A	-5.2 \pm 1.7
Meter 1 Velocity (m/s)	3.3 \pm 0.2 _B	3.3 \pm 0.1	2.2 \pm 0.1 _A	2.2 \pm 0.1	2.1 \pm 0.3 _A	2.4 \pm 0.3	2.8 \pm 0.1 _B	2.7 \pm 0.1
Meter 1.5 Velocity (m/s)	3.5 \pm 0.2 _C	3.5 \pm 0.1	2.0 \pm 0.1 _A	2.2 \pm 0.1	1.9 \pm 0.2* _A	2.5 \pm 0.3	2.8 \pm 0.1 _B	2.9 \pm 0.2
Meter 2 Velocity (m/s)	3.4 \pm 0.2 _C	3.3 \pm 0.1	2.2 \pm 0.1 _A	2.0 \pm 0.2	1.9 \pm 0.2* _A	2.5 \pm 0.2	2.8 \pm 0.2 _B	2.8 \pm 0.2
Froude Number	6.5 \pm 4 _B	6.4 \pm 0.3	4.9 \pm 0.3 _A	5.8 \pm 0.4	4.2 \pm 0.4* _A	5.7 \pm 0.6	5.9 \pm 0.4 _B	6.7 \pm 0.3

Table 2. Mean values of behavior and velocity during bipedal and quadrupedal locomotion when crossing an obstacle. Values are means \pm S.E.M. * indicate significantly different χ^2 and t-test values for intraspecific comparisons with an obstacle.

Stride number is the number of strides taken in the one-meter span containing an obstacle. *S. occidentalis* was excluded from analysis because of rare occurrence of bipedal locomotion.

Variable	<i>C. bicinctores</i> N=15		<i>G. wislizenii</i> N=12		<i>A. tigris</i> N=14	
	<i>Bipedal</i>	<i>Quadrupedal</i>	<i>Bipedal</i>	<i>Quadrupedal</i>	<i>Bipedal</i>	<i>Quadrupedal</i>
Behavior (on, over)	3,10*	2,0	1,2*	8,1	3,5	4,2
Velocity (m/s)	3.6 \pm 0.2	3.0 \pm 0.8	2.8 \pm 0.2*	1.7 \pm 0.2	3.1 \pm 0.2	2.5 \pm 0.1
0-1 m stride number	4.1 \pm 0.3	4 \pm 0	5 \pm 0	4.9 \pm 0.3	5.7 \pm 0.2	5.6 \pm 0.2
1-2 m stride number	3.1 \pm 0.8*	5 \pm 1.4	4.5 \pm 1.5	5.4 \pm 0.5	4 \pm 0.6	4.7 \pm 0.7

Table 3. Variable-variate correlations from a canonical correlations analysis of 7 morphological variables and 5 speed and kinematic variables for four lizard species. CC1 and CC2 denote to canonical correlation 1 and 2.

Variable	CC1	CC2
<i>Morphology</i>		
Femur length	0.20	-0.72
Tibia Length	0.17	-0.56
Hindfoot	-0.47	-0.66
Hindfoot toe	-0.74	-0.44
Pelvic width	0.14	0.48
Pectoral depth	0.28	-0.59
Trunk length	-0.10	0.07
<i>Performance and Kinematics</i>		
Velocity (m/s)	-0.28	-0.69
Stride Length (cm)	0.10	-0.74
Hip Height (cm)	0.08	-0.85
Body Angle	0.63	-0.41
Tail Elevation (cm)	0.49	-0.20

Table 4. Loadings from two discriminant function analyses of 5 timing and kinematic variables for four lizard species. DF1 denote to discriminate functions 1 for both analyses. For the Obstacle Present DFA, the eigenvalue was 1.0. For the Quadrupedal DFA, the eigenvalue was 0.76. 100% of the variance was explained in the first discriminant function for both analyses.

Variable	Obstacle Present: Bipedal vs. Quadrupedal	Quadrupedal: Obstacle vs. No Obstacle
Stride length(cm)	0.538	-0.023
Velocity (m/s)	0.923	0.486
Body Angle	0.061	-0.652
Hip Height (cm)	0.391	-0.168
Tail Elevation (cm)	0.168	0.087

Table 5. Values for 14 morphological traits for four species of lizard. Values are means (mm) \pm S.E.M. SVL: Snout-vent length.

Variable	<i>C. bicinctores</i> N=15	<i>G. wislizenii</i> N=12	<i>S. occidentalis</i> N=13	<i>A. tigris</i> N=14
SVL	89.6 \pm 1.5	90.9 \pm 0.9	80.4 \pm 1.6	89.4 \pm 1.4
Tail length	175.8 \pm 4.3	183.3 \pm 2.8	94.6 \pm 4.5	196.6 \pm 4.1
Femur length	23.3 \pm 0.4	17.7 \pm 0.3	16.2 \pm 0.5	16.0 \pm 0.4
Crus Length	26.6 \pm 0.5	23.7 \pm 0.3	16.3 \pm 0.6	17.0 \pm 0.5
Hindfoot length	14.3 \pm 0.4	13.3 \pm 0.2	9.8 \pm 0.4	11.5 \pm 0.4
Fourth toe length	11.2 \pm 0.2	10.3 \pm 0.1	10.6 \pm 0.3	8.7 \pm 0.2
Humerus length	15.3 \pm 0.4	11.8 \pm 0.3	14.1 \pm 0.4	10.7 \pm 0.4
Antebrachium length	13.7 \pm 0.3	13.0 \pm 0.2	10.8 \pm 0.3	11.2 \pm 0.3
Forefoot length	5.9 \pm 0.1	5.5 \pm 0.1	4.7 \pm 0.1	4.6 \pm 0.1
Fourth Phalange	11.2 \pm 0.2	10.3 \pm 0.1	10.6 \pm 0.3	8.7 \pm .2
Pelvic width	8.1 \pm 0.2	8.2 \pm 0.1	8.6 \pm 0.2	8.3 \pm 0.2
Pectoral width	16.0 \pm 0.3	13.9 \pm 0.2	13.4 \pm 0.3	11.2 \pm 0.3
Pectoral depth	16.4 \pm .4	13.7 \pm .2	11.7 \pm 0.4	11.0 \pm 0.3
Trunk length	47.2 \pm 1.0	44.2 \pm 0.6	45.0 \pm 1.1	45.9 \pm 1.0

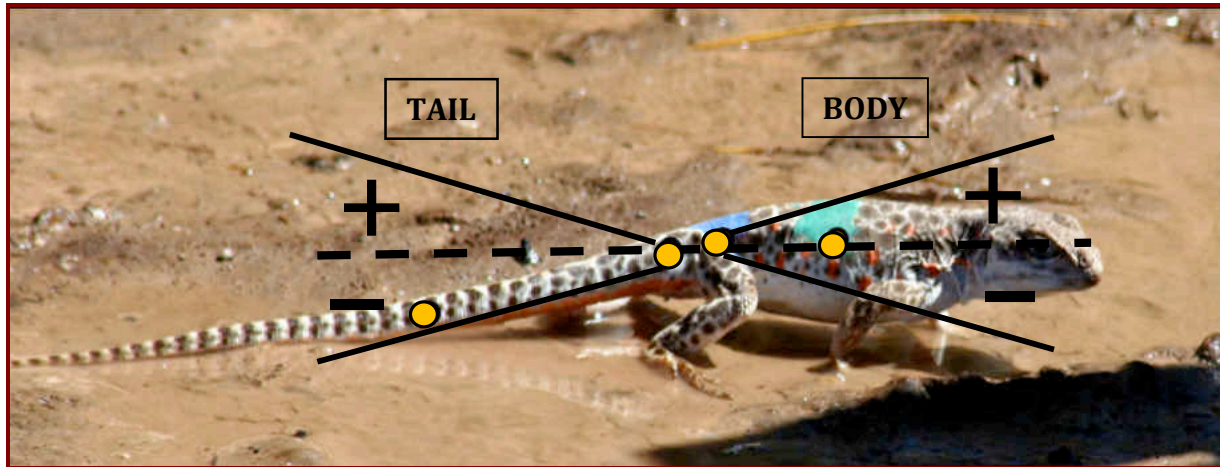


Figure 1. A kinematic diagram depicting the positive and negative values for tail elevation and body angle; negative values indicate a depression of the tail or body and are therefore below horizontal from the ground surface, whereas positive values indicate an elevation of the tail and body. Circles indicate the anatomical landmark locations of paint marks including mid-trunk, hip, the base of the tail and 40% of the tail length from the tail base.

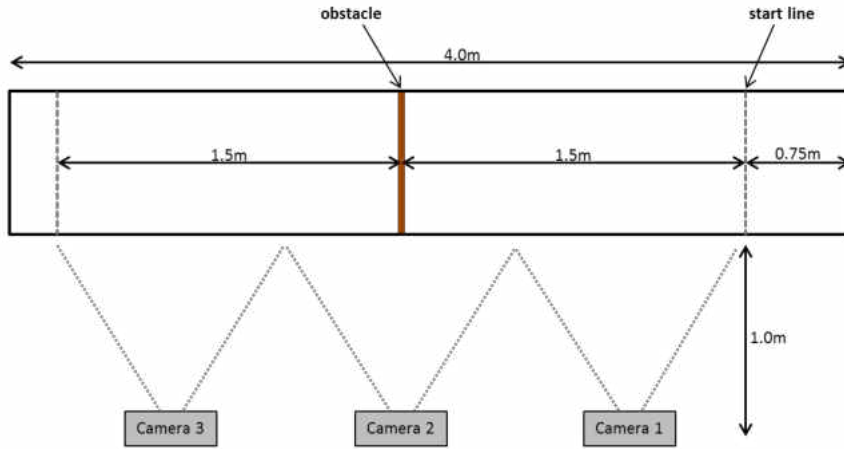


Figure 2. Top view of the three-meter runway and position of each camera. The initial start line was located 0.75 meters from the end of the runway. The obstacle was placed 1.5 meters from the start line. Each camera's field of view contained one meter of the runway. The front four-meter sidewall of the runway was made of Plexiglas to allow lateral filming of performance trials.

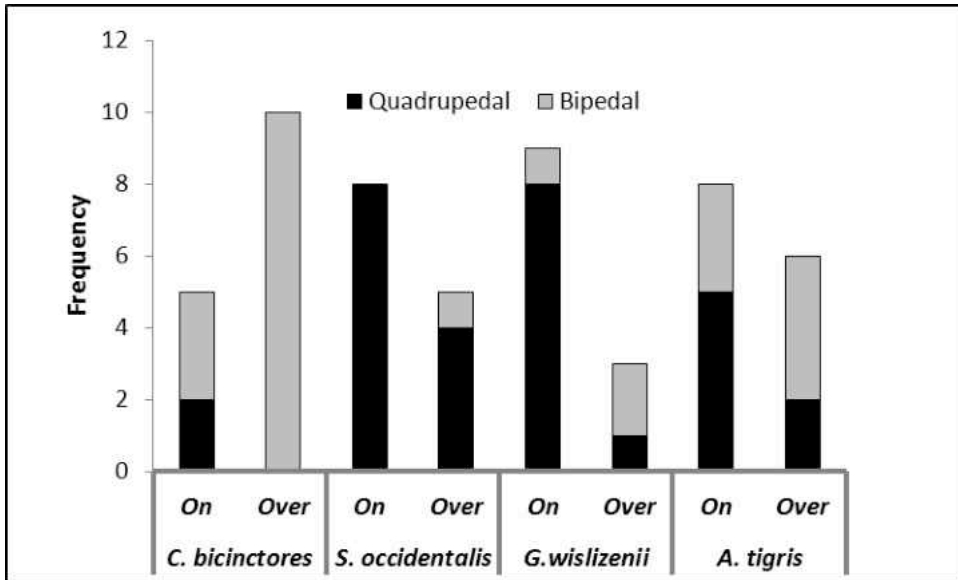


Figure 3. An among species comparison of the frequency of bipedal and quadrupedal postures when crossing obstacles and the behavior frequency of individuals stepping on or over the obstacle.

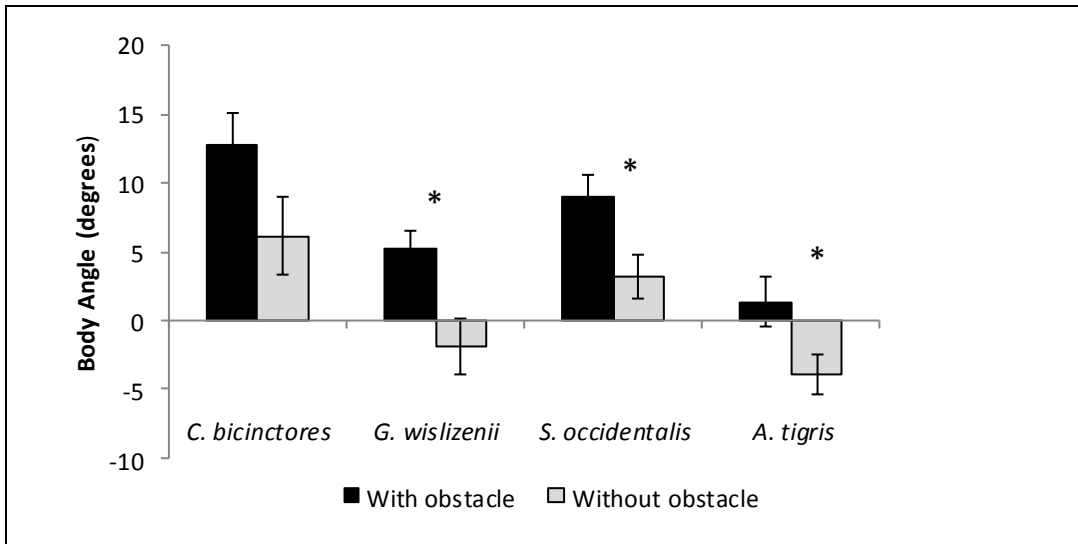


Figure 4. A comparison of body angle among species with and without an obstacle. Positive values indicate the trunk is elevated (above horizontal), negative values indicate a depression of the trunk (below horizontal). * Indicate p-values are ≤ 0.05 compared within species, with and without an obstacle.

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