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Posture, speed, and habitat structure: three-dimensional hindlimb kinematics of two species of padless geckos

Patrick O. Fuller, Timothy E. Higham*, Andrew J. Clark

Department of Biological Sciences, Clemson University, 132 Long Hall, Clemson, SC 29634, USA

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ABSTRACT

Differences in habitat use are often correlated with differences in morphology and behavior, while animals in similar habitats often exhibit similarities in form and function. However, this has not been tested extensively among lizards, especially geckos. Most studies of gecko locomotion have focused on the ability to adhere to surfaces. However, there are several species of geckos that have either secondarily lost adhesive capabilities or simply lack the capability. We quantified the three-dimensional locomotor kinematics for two desert-dwelling padless geckos, *Teratoscincus scincus* and *Eublepharis macularius*, on a level trackway over a range of speeds. Our results indicate that *T. scincus* landed with a high relative hip height of $48.7 \pm 2.4\%$ of total limb length at footfall, while *E. macularius* exhibited hip heights averaging only $36.0 \pm 1.8\%$ of total limb length for footfall. The three-dimensional knee angle of *T. scincus* averaged $120.6 \pm 3.9^\circ$ at footfall, while *E. macularius* averaged only $101.6 \pm 1.8^\circ$ at footfall. In addition, the femur of *E. macularius* was elevated to a much greater extent (i.e., was closer to being perpendicular to the long axis of the body) than that of *T. scincus* and every other lizard that has been studied, suggesting they move with a “hyper-sprawled” posture. Both of these gecko species live in deserts, but *T. scincus* is psammophilic while *E. macularius* inhabits a rocky, more densely vegetated environment. Benefits of the more upright posture of *T. scincus* on open sandy habitat may include a greater field of view and more efficient locomotion. The more sprawled posture of *E. macularius* may lower its center of gravity and aid in balance while climbing on rocks or shrubs.

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1. Introduction

Animals move in many different habitats and for many reasons including competition for mates, foraging for food, finding more desirable habitats, or escaping predators. The structure of the habitat will impose constraints and impart demands on an animal. For example, living in relative open areas might necessitate high-speed sprinting in order to escape a predator or limit the distance an individual can approach prey before being recognized. Conversely, living in a habitat that is highly structured might allow an animal to move a short distance and hide from a predator or might favor predators that can climb and cling to steep surfaces. Thus, habitat structure likely has a strong influence on the relationships between morphology, behavior, and fitness, and these relationships are critical for understanding the evolutionary history and diversity of extant animal species (Arnold, 1983).

Morphological differences may account for the diversity in locomotor behavior exhibited by many species (Arnold, 1983; Rewcastle, 1983; Lauder and Reilly, 1991; Blob, 2001). For example,

limb length has been correlated with natural locomotor behavior within several lizard taxa such as *Tropidurus* species in South America (Vitt et al., 1997), *Anolis* in the Caribbean (Irschick and Losos, 1998), *Rhoptropus* in Namibia (Higham and Russell, 2010), and *Niveoscincus* in Australia (Melville and Swain, 2000). Relative limb length appears to relate to habitat within each of these taxa. However, morphology and habitat type need not always be correlated (Schulte et al., 2004). For example, studies have shown that some *Liolaemus* iguana populations in open areas were selected for short, fat bodies and cryptic lifestyles whereas many other taxa adopt long limb lengths and thin bodies for running fast in this type of habitat (Jaksic et al., 1980; Schulte et al., 2004). Natural selection by predation likely drives such populations towards either cryptic or escape-oriented antipredator strategies, but both may be equally viable (Schulte et al., 2004), highlighting the complexity involved in interpreting morphological diversity. In addition to limb length, understanding the posture of different species might provide considerable insight into the demands of a particular habitat.

Terrestrial lizard locomotion has been studied extensively, but few studies (Farley and Ko, 1997; Zaaf et al., 1999) have examined locomotion in terrestrial geckos, and these studies typically focus on eublepharids. Geckos are a particularly diverse group of lizards, occupying both arboreal and terrestrial habitats from lush rainfor-

* Corresponding author.

E-mail address: thigham@clemson.edu (T.E. Higham).



Fig. 1. Dorsal photographs of (A) *Eublepharis macularius* and (B) *Teratoscincus scincus*.

est to barren desert (Grismer, 1988). While geckos are often studied for their adhesive capabilities (e.g., Autumn et al., 2002; Russell and Higham, 2009), many species lack this ability (Russell and Bauer, 2002). These padless geckos use similar habitats as many non-gecko taxa, but as Schulte et al. (2004) suggest, life history may play an important role in locomotor behavior. Two species of padless geckos that live in arid terrestrial environments of southwestern to central Asia are the more commonly studied *Eublepharis macularius* (leopard gecko) and the less frequently studied *Teratoscincus scincus* (frog-eyed gecko) (Fig. 1). Analyzing the locomotor behavior and morphology of these species and relating these traits to habitat will allow us to better understand the influences of ecology and provide a structure for understanding the potential evolutionary dynamics of these traits within geckos.

Werner and Broza (1969) classified both *T. scincus* and *E. macularius* as desert-dwelling geckos, although their habitats may differ in substrate and heterogeneity. Szczerbak and Golubev (1996) described the distribution and habitat of these species in the wild. *T. scincus* appears most frequently in arid, open sandy deserts of central Asia east of the Caspian Sea. *E. macularius* persists in a more southerly range in the deserts from Iran to northern India. Its habitat can be described as steep, rocky, and often supporting extensive shrub cover. Thus, these desert-dwelling geckos exhibit substantial differences in habitat structure, and ultimately ecology.

Most lizards exhibit a sprawled posture in that limb movement occurs in the frontal rather than the parasagittal plane, in contrast to most birds and mammals (Rewcastle, 1983). It is important to note that the extent to which an animal is sprawled varies considerably among species within taxonomic groups (e.g., Werner and Broza, 1969; Reilly and Elias, 1998; Blob, 2001; Higham and Jayne, 2004). Werner and Broza (1969) hypothesized that desert-dwelling species of geckos lacking toe pads would benefit from a more upright posture relative to geckos that utilize adhesion. However, desert-dwelling species, as mentioned above, can occupy habitats that are substantially different from one another. In one scenario, a more erect posture could help geckos in open desert environments to see over small obstacles such as ripples in the sand,

Table 1

Values for six morphological traits for *T. scincus* and *E. macularius*. $N=4$ for each species.

Variable	<i>T. scincus</i>	<i>E. macularius</i>	<i>p</i> -Value
SVL (cm)	8.18 ± 0.37	10.65 ± 0.26*	0.0016
Mass (g)	18.57 ± 2.72	51.10 ± 3.47**	0.0003
Hind limb length (cm)	3.55 ± 1.44	4.41 ± 0.76*	0.0018
Femur length (cm)	1.11 ± 0.04	1.54 ± 0.04	0.1358
Tibia length (cm)	1.12 ± 0.05	1.51 ± 0.02	0.1828
Tarsal plus metatarsal length (cm)	0.53 ± 0.03	0.63 ± 0.02*	0.0380
Fourth toe length (cm)	0.79 ± 0.04	0.74 ± 0.01**	0.00001

Note that, with the exception of SVL and mass, the *p*-values are based on size-corrected morphological variables.

* $p < 0.05$.

** $p < 0.001$.

which would help with predator and prey detection (Werner and Broza, 1969). Alternatively, a more sprawled posture may be beneficial for lizards that climb because it lowers their center of gravity, which improves balance and enables an individual to hold a limb off the substrate without falling (Rewcastle, 1983; Jayne and Irschick, 1999). In addition to differences in posture *per se*, different species might obtain a given posture in different ways. For example, individuals may assume more vertical limb segment positions (and thus a more upright posture) by increasing femur depression or by extension or flexion of the knee, whichever brings the lower limb closer to vertical. Understanding how and why species of lizards adopt different postures can provide insight into how ecology and behavior are interrelated.

Our study compares the locomotor kinematics of *T. scincus* and *E. macularius* to test the hypothesis by Werner and Broza (1969) that all desert-dwelling padless geckos exhibit similar locomotor movements and postures. The following questions were assessed: (i) are three-dimensional kinematics similar between desert-dwelling geckos? (ii) Do desert-dwelling geckos exhibit similar body postures and if not, which aspects of posture are dissimilar? An alternative hypothesis is that only those species living in open sandy desert habitats will benefit from a more upright posture.

2. Materials and methods

2.1. Animal morphology and housing

Four individuals of *T. scincus* and *E. macularius* were obtained from the pet trade and transported to Clemson University under an approved IACUC protocol. The average snout–vent length (SVL) was 8.18 ± 0.37 cm for *T. scincus* and 10.65 ± 0.26 cm for *E. macularius* (Table 1). The average mass was 18.57 ± 2.72 g for *T. scincus* and 51.10 ± 3.47 g for *E. macularius* (Table 1). On the right hindlimb, the femur, tibia, and metatarsals and phalanges of the fourth toe were measured from photographs of external morphology using ImageJ (Table 1). Total limb length was calculated as the sum of these segment lengths. Linear morphological measurements were scaled to SVL using residuals from least-squares regressions.

The lizards were housed individually in 10 gallon glass aquaria with sand substrate. Each was fed crickets *ad libitum* and watered and misted daily. Tanks were heated with 60 W lamps on a 12 h timer and provided with shelters to allow a temperature range from 25 °C to 35 °C for each lizard. Individuals were returned to their aquarium tanks after the experiment and were not euthanized.

2.2. Running trials

Running trials were performed at 34–35 °C, within the range of temperatures commonly experienced by both species in the

wild. Individuals were stimulated to run across a 1 m level wooden trackway with a sandpaper substrate for traction and Plexiglass sides to prevent escape. The 10 cm wide surface bounded by 10 cm tall Plexiglass sides limited turning motions of the geckos while allowing sufficient breadth for lateral undulations. A 45° mirror affixed above the track allowed dorsal views to be filmed from laterally placed cameras (two Photron APX RS cameras operating at 250 fs⁻¹ or 500 fs⁻¹; Photron USA Inc., San Diego, CA, USA). While both cameras were placed lateral to the track, using two lenses enabled three-dimensional calibration of the trial space. Trials for *E. macularius* were recorded at 250 fs⁻¹, while a faster frame rate of 500 fs⁻¹ was necessary to record the movements of *T. scincus*.

Lizards were prompted to run from left to right by gently waving hands or tapping on the tail. Trials with steady stride sequences in the camera view were recorded for analysis. As many as 4 trials were taken for each individual with at least 5 min in between each trial, until at least 5 steady strides were obtained for each species. The strides used in analyses were those preceded and followed by strides of similar speed. Thus, accelerations during locomotion were avoided.

2.3. Data analysis

Video recordings were digitized using dltDV3 written for MatLab by Ty Hedrick (Hedrick, 2008). In order to obtain three-dimensional joint coordinates, the two camera views were calibrated using a structure made of LEGO building bricks (LEGO, Billund, Denmark) with predetermined dimensions. Following calibration, three-dimensional coordinates were obtained by digitizing the hip, knee joint, ankle joint, and metatarsal–phalangeal joint of the fourth toe on the right hindlimb. In addition, the tip of the snout was digitized in order to quantify forward displacement of each lizard. Points were digitized on every frame for at least five steady strides per individual. Displacement taken at the digitized snout point was measured during the stride sequence to calculate speed, stride length (distance the snout moved between consecutive footfalls), and stride frequency (inverse of the time between consecutive footfalls), whereas points from the right hindlimb were used to find the three-dimensional knee and ankle angles of those limbs as well as the hip height. Speed was calculated for each trial by dividing stride length by stride duration. Hip height was ultimately scaled to the length of the hindlimb, which approximates the maximum achievable hip height, to standardize this measurement between species.

The digitized hip point was the intersection of the upper leg and the trunk, and the hip height was the *y*-value of this point. Hip, knee, ankle, and metatarsal coordinates were used to determine the three-dimensional angles of the knee and ankle throughout each stride. The three-dimensional Pythagorean distance between each point was calculated and then the law of cosines was used to determine the angle. The three-dimensional angles were used to describe the degree of joint extension or flexion, with the largest angles indicating maximum extension and the smallest angles indicating maximum flexion of the joint. In addition, we determined the degree of femur depression such that positive values indicate the knee was below the hip. A value of zero indicates the knee is perpendicular to the long axis of the body.

2.4. Statistics

Scaled morphological variables were compared between the two species using two-sample *t*-tests. Differences in speed, stride length, stride frequency, angular variables, and hip height between the two species were determined using paired *t*-tests (*df* = 6) based

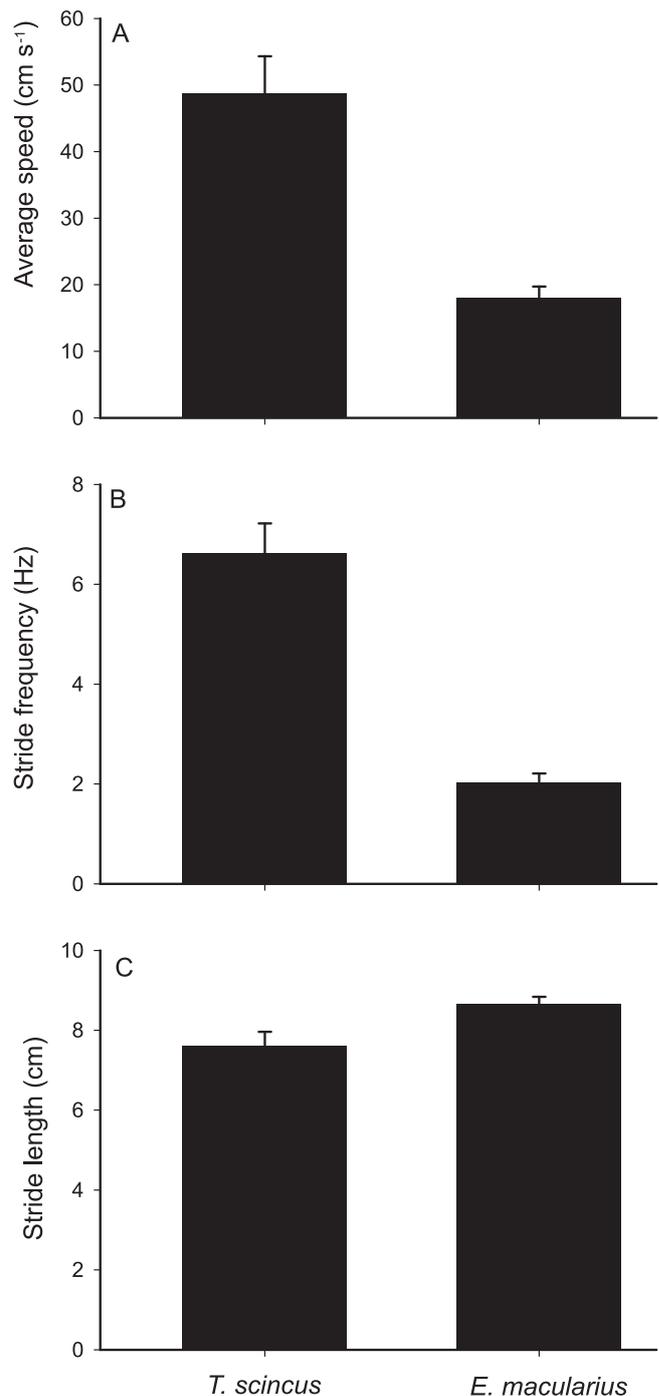


Fig. 2. Mean values of (A) average speed, (B) stride frequency, and (C) stride length for *T. scincus* (left) and *E. macularius* (right). Average speed and stride frequency were significantly greater for *T. scincus*, but stride length did not differ.

on mean values for each individual. A *p*-value < 0.05 was the criterion for statistical significance in all *t*-tests. Given that variation exists in both the *x* and *y* variables, reduced major axis regressions were used to determine the correlations between speed and kinematic variables. Degrees of freedom in the linear regressions with speed (*df* = 19 for *T. scincus*, *df* = 16 for *E. macularius*) account for all trials to show, even within individuals, how parameters correlated with running speed. All strides were included in the regressions with speed rather than averaging across each individual to avoid diluting the effects of speed. To account for the elevated sample

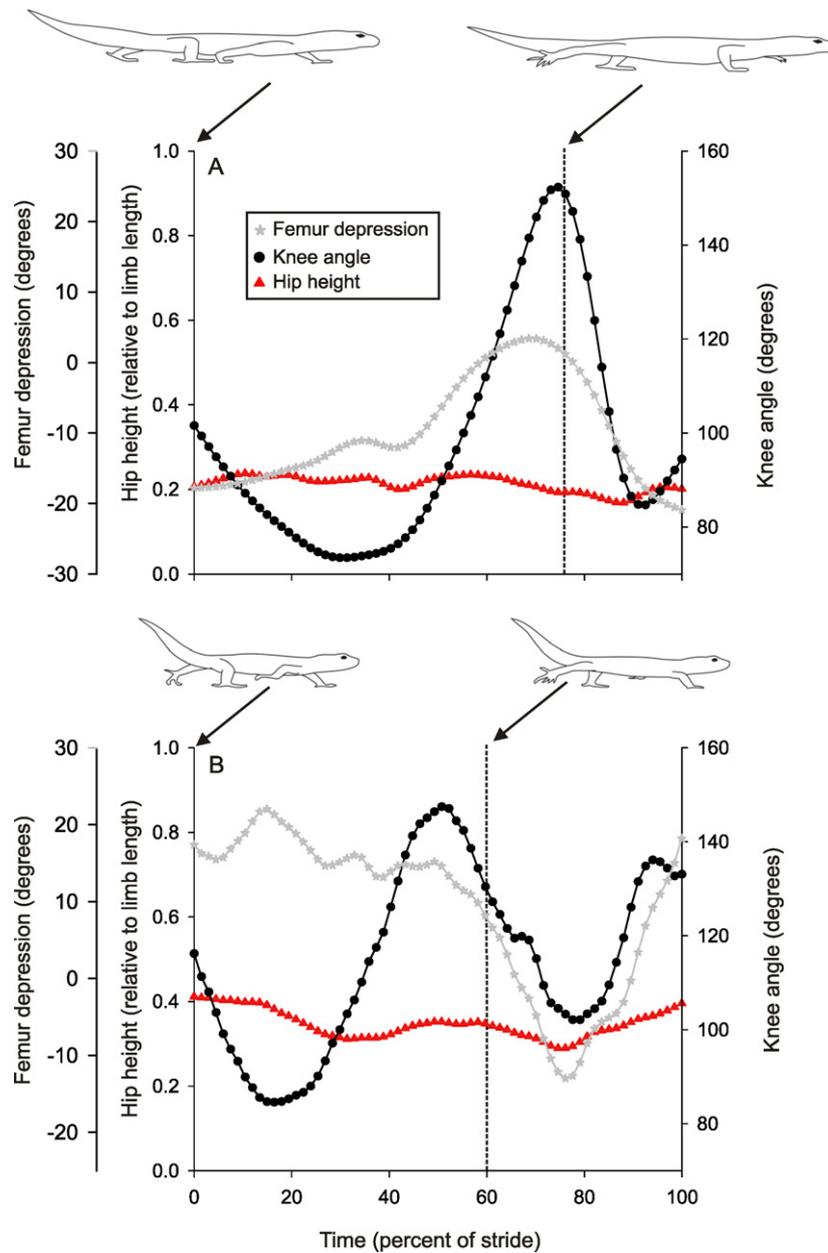


Fig. 3. Representative plots of femur depression (stars), hip height (triangles), and knee angle (circles) for one complete stride of (A) *E. macularius* and (B) *T. scincus*. The vertical dashed line represents the end of stance. Footfall occurs at time 0 and at 100% of the stride. Note that the femur was more depressed, hip height (scaled to total limb length) was higher, and knee was more extended for *T. scincus*.

size, a p -value < 0.01 was the criterion for statistical significance for all tests of linear correlation.

Values in the manuscript are mean \pm S.E.M.

3. Results

3.1. Morphology

The geckos tested exhibited little variation within species, but some notable morphological differences appeared between *T. scincus* and *E. macularius* (Table 1). *T. scincus* was smaller than *E. macularius* with respect to both SVL and mass ($p = 0.002$). When scaled to SVL, *T. scincus* averaged a significantly longer relative hind limb length than *E. macularius* ($37.0 \pm 0.3\%$ SVL versus $35.6 \pm 0.3\%$ SVL; $p = 0.002$). However, *T. scincus* maintained

similar femur and tibia proportions to *E. macularius* ($p = 0.136$; $p = 0.183$; Table 1). The ankle to metatarsal length and the length of the fourth toe were significantly longer in *T. scincus* than in *E. macularius*.

3.2. Performance

T. scincus moved significantly faster ($0.48 \pm 0.06 \text{ m s}^{-1}$) than *E. macularius* ($0.18 \pm 0.02 \text{ m s}^{-1}$; $p = 0.034$; Fig. 2A), although both species exhibited overlap in the range of speeds (0.10 – 0.98 m s^{-1} for *T. scincus* and 0.09 – 0.32 m s^{-1} for *E. macularius*). Stride frequency was $6.12 \pm 0.59 \text{ Hz}$ for *T. scincus*, while only $2.03 \pm 0.18 \text{ Hz}$ for *E. macularius* ($p = 0.008$; Fig. 2B), although stride length was similar at $8.16 \pm 0.77 \text{ cm}$ for *T. scincus* and $8.74 \pm 0.27 \text{ cm}$ for *E. macularius* ($p = 0.504$; Fig. 2C).

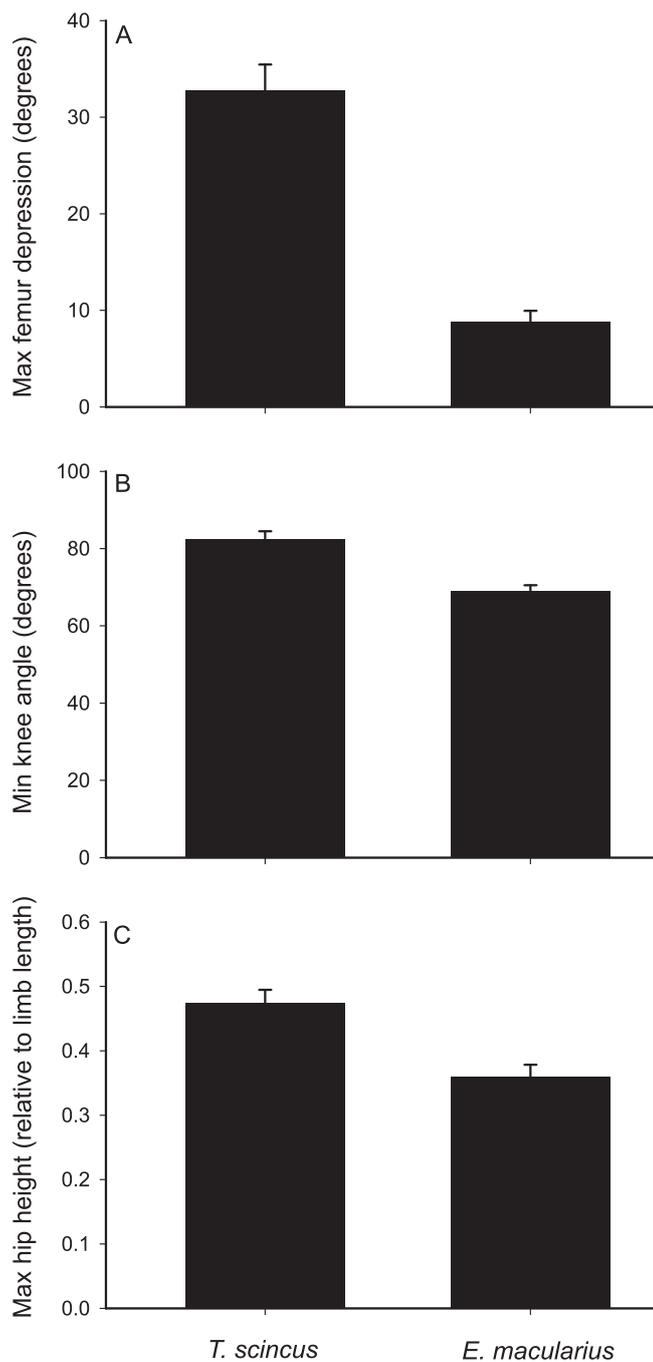


Fig. 4. Mean values of (A) maximum femur depression, (B) minimum knee angle, and (C) maximum hip height for *T. scincus* (left) and *E. macularius* (right). All three values were significantly greater for *T. scincus*.

3.3. Three-dimensional kinematics

Both species ran with a horizontal body angle with all four feet contacting the substrate. Throughout the stride cycle, *T. scincus* (Fig. 3A) maintained greater femur depression and a higher hip height than *E. macularius* (Fig. 3B). Femur depression maxima reached $32.8 \pm 2.7^\circ$ for *T. scincus*, while only $8.8 \pm 1.2^\circ$ for *E. macularius* ($p = 0.003$; Fig. 4A). Maximum hip height, when scaled to total limb length (TLL), was $0.475 \text{ TLL} \pm 0.018 \text{ TLL}$ for *T. scincus*, but only $0.358 \text{ TLL} \pm 0.015 \text{ TLL}$ for *E. macularius* ($p = 0.020$; Fig. 4C). Knee angles overlapped between *T. scincus* (Fig. 3A) and *E. macularius* (Fig. 3B) except at the minimum value. Minimum knee angle was significantly greater (more extended) for *T. scin-*

cus ($82.3 \pm 2.2^\circ$) compared to *E. macularius* ($69.0 \pm 1.5^\circ$; $p = 0.042$; Fig. 4B).

3.4. Limb excursions

Overall limb movements of *T. scincus* differed from those of *E. macularius* (Fig. 5). The lateral (x and y coordinates) path of knee, ankle, and metatarsal (base of the fourth toe) overlapped for *T. scincus* (Fig. 5A) but not for *E. macularius* (Fig. 5B), indicating that the distal limb elements were farther from the midline of the body for *E. macularius*. Also, the knee of *T. scincus* (Fig. 5C) reached a more ventral position, compared to *E. macularius*, relative to the hip during the stance phase when the foot was on the ground. Interestingly, the knee was above the hip for a considerable portion of the stride in *E. macularius* (Fig. 5D).

3.5. Regressions with speed

Increases in stride length (Fig. 6A) and stride frequency (Fig. 6B) corresponded with increases in speed for both *T. scincus* and *E. macularius*. Femur depression (Fig. 7A) was not correlated with speed for either *T. scincus* ($p = 0.485$, $r^2 = 0.0261$) or *E. macularius* ($p = 0.751$, $r^2 = 0.000$). For *T. scincus*, maximum hip height ($p = 0.003$, $r^2 = 0.372$; Fig. 7B) and maximum ankle angle ($p = 0.002$, $r^2 = 0.400$; Fig. 7C) increased with speed. However, no such correlation occurred for *E. macularius* (hip height: $p = 0.751$, $r^2 = 0.006$; Fig. 7B; ankle angle: $p = 0.313$, $r^2 = 0.068$; Fig. 7C). Also, speed was marginally correlated with maximum knee extension for *E. macularius* ($p = 0.029$, $r^2 = 0.264$), but not for *T. scincus* ($p = 0.817$, $r^2 = 0.003$).

4. Discussion

Our study addressed the kinematic differences between two species of padless geckos that occupy desert habitats. One of our key findings is that the species living in more open areas, *T. scincus*, exhibits a more erect posture and runs faster than *E. macularius*, which lives in more structured habitats. We discuss the mechanisms underlying the differences in speed and posture below.

4.1. Performance

Several morphological and physiological factors can influence locomotor speed. In terms of morphology, *T. scincus* exhibited a longer fourth toe relative to *E. macularius*, although the rest of the hindlimb was comparable in proportion (Table 1). Limb length can limit maximum step length and floating distance (Vanhooydonck et al., 2002), so the longer toes of *T. scincus* may account for its slightly longer stride length. However, stride frequency for *T. scincus* was approximately three times that of *E. macularius* (Fig. 2B), suggesting that frequency modulation was the more influential mechanism of increased speed.

Previous work examining speed modulation in lizards has found that both stride length and stride frequency can be increased to increase speed (e.g., White and Anderson, 1994; Reilly and Delancey, 1997; Fieler and Jayne, 1998; Van Damme et al., 1998; Zaaf et al., 2001). Zaaf et al. (2001) also found that stride frequency modulation was used more than changes in stride length to control speed in *E. macularius* and *Gekko gekko*. Maximum stride frequency is likely limited by hindlimb muscle physiology and morphology. For example, larger fast-twitch, type II muscle fibers would likely permit faster skeletal muscle contractions, facilitating faster speeds (Widrick et al., 1996). A greater proportion of fast-twitch fibers would likely increase maximum shortening velocity (Rome et al., 1990), which would likely lead to higher maximum stride frequencies. Muscle fiber types have not yet been studied in relation to

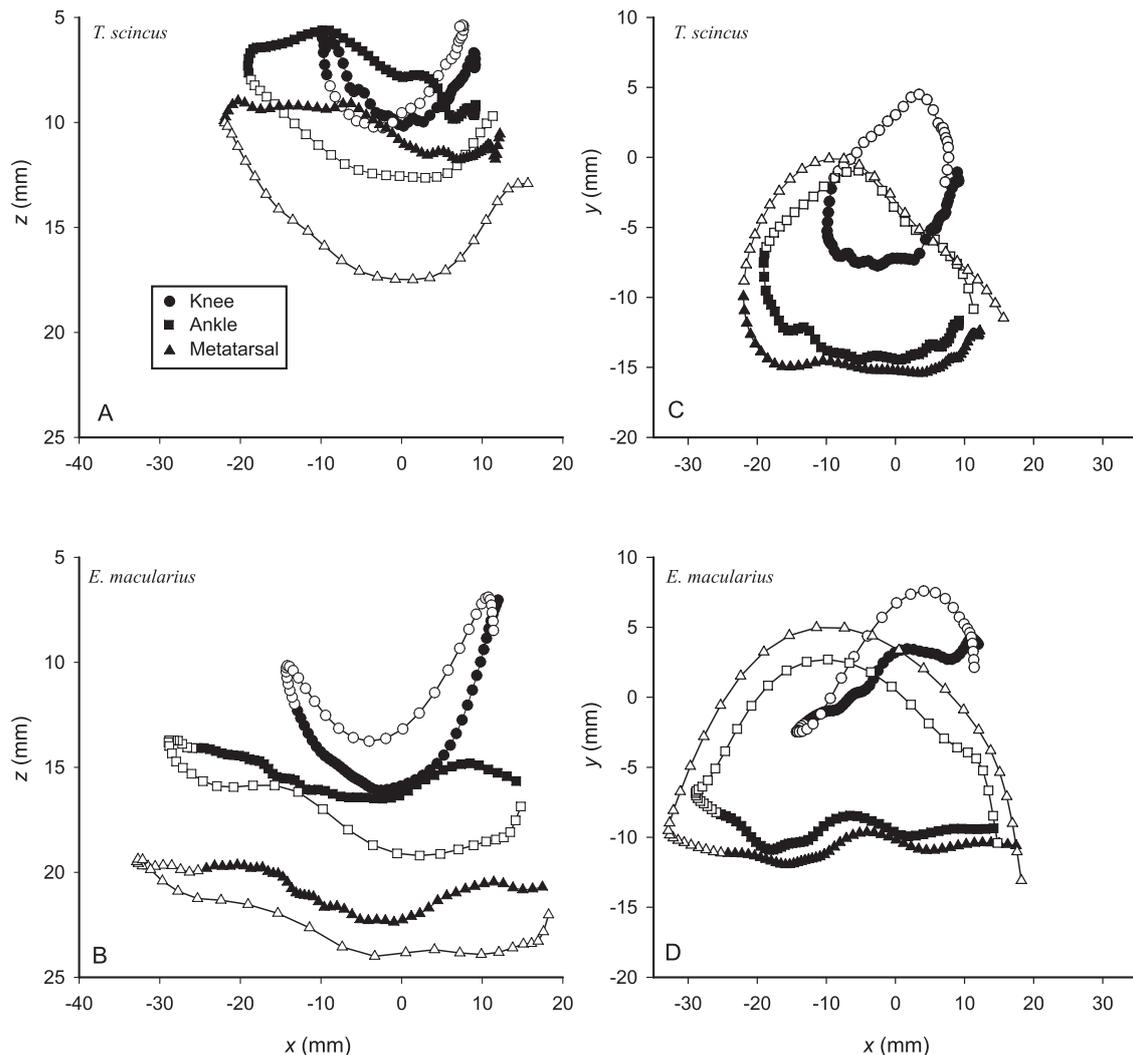


Fig. 5. (A and B) Dorsal (z versus x) and (C and D) lateral (y versus x) paths made by the knee, ankle and metatarsal during a complete representative stride. (A) and (C) are for *T. scincus* and (B) and (D) are for *E. macularius*. The open and filled symbols represent swing and stance, respectively. All plots are relative to the hip (0,0). The directions of the loops are counterclockwise (A and B) and clockwise (C and D). The average locomotor speeds for *E. macularius* and *T. scincus* in these representative strides were 0.13 m s^{-1} and 0.61 m s^{-1} , respectively.

speed for either of these species, but this information would be very valuable.

T. scincus may exhibit faster running speeds than *E. macularius* because of habitat differences between the two species. Higher sprint speeds or faster acceleration to avoid predators may be factors affecting selection for many lizards when moving and exploiting their habitats (Vanhooydonck et al., 2006; Bonine, 2007). Faster speeds may be associated with evolutionary pressures to avoid fast predators or to catch motile prey (Husak, 2006). In habitats with little cover and a broad substrate, faster individuals which are able to reach cover more quickly than their counterparts would likely be better at avoiding predation (Bauwens et al., 1995; Bonine and Garland, 1999; Irschick and Losos, 1999; Melville and Swain, 2000; Husak, 2006; Calsbeek and Irschick, 2007). However, faster speeds demand greater oxygen consumption than slow speeds during locomotion and necessitate rest periods after each burst of activity (Kramer and McLaughlin, 2001). According to the description of native habitat for *E. macularius* (Szczerbak and Golubev, 1996), they have a high availability of cover nearby and may be capable of remaining under cover constantly. In thick cover such as dense vegetation, the ability to maneuver is likely to outweigh the ability to reach high speeds (Melville and Swain, 2000; Goodman et al., 2008). In contrast, *T. scincus* lives in relatively open habitats

(Szczerbak and Golubev, 1996; Seligmann et al., 2007), which suggests that faster running speeds would benefit this species.

The speeds recorded for *E. macularius* in our study are lower than those previously recorded by Zaaf et al. (2001). However, in this previous study, the individuals were run on a motorized treadmill in order to increase the range of locomotor speeds. We did not use a treadmill in our study, which might explain why our speeds are lower. It is important to note, however, that many strides in the study by Zaaf et al. (2001) exhibit comparable speeds to those observed in our study. In addition, we were not attempting to elicit maximum performance from the individuals in our study. In a more recent study, McElroy et al. (2008) observed an average speed of 0.24 m s^{-1} , which is almost identical to what we found (0.18 m s^{-1}). Thus, the speeds elicited in our study are probably representative of the species as a whole.

4.2. Posture

In contrast to the assertion that both *E. macularius* and *T. scincus* assume a more erect posture (Werner and Broza, 1969; Zaaf et al., 1999), our observations indicate that *E. macularius* maintains a more sprawled posture than *T. scincus* during locomotion (e.g., Fig. 5C and D). The body of *E. macularius* did remain elevated above

the substrate, but these individuals were less erect than *T. scincus* as evidenced by a highly elevated femur, a low hip height, and a flexed knee. This posture keeps the body closer to the ground with a center of gravity staying well within the bounds of its leg supports (Rewcastle, 1983; Van Damme et al., 2003). As discussed above, it appears that the elevated femur is the key kinematic factor contributing to the hyper-sprawled posture of *E. macularius*. Whether other lizards exhibiting hyper-sprawled postures also exhibit this mechanism is something that will have to be revealed by future research.

Body height and limb angles may indicate trade-offs for desert-dwelling lizards such as *T. scincus* and *E. macularius*. *T. scincus* operates with a more erect posture, possibly at the expense of balance. Werner and Broza (1969) hypothesize that a more erect posture may help species such as *T. scincus* to increase their field of vision by seeing over low visual obstructions such as sand ripples. Being able to see over these low obstructions will allow *T. scincus* to spot predators earlier, giving individuals more time to react and escape. Modulating body height and limb angles may also improve the efficiency of *T. scincus* while negotiating small inconsistencies at high speed over open ground. However, *T. scincus* may be at a disadvantage compared to lizards with a more sprawling posture when moving within cover-rich areas or moving over large obstacles that have variable inclines. In these types of desert habitats, selection may favor the more stable sprawling posture of *E. macularius* for negotiating within and around cover. In addition, an erect posture would not likely provide a visual advantage when obstructions are large, as, e.g., rocks or bushes. Both species appear to exhibit relative trade-offs favoring functional advantages in the context of their respective habitats.

4.3. Comparisons with other lizard taxa

Several studies have examined posture and three-dimensional kinematics in lizards (Reilly and Delancey, 1997; Irschick and Jayne, 1998; Jayne and Irschick, 1999; Blob and Biewener, 2001; Higham and Jayne, 2004; McElroy and Reilly, 2009). For example, Higham and Jayne (2004) found that the veiled chameleon (*Chamaeleo calypttratus*) held its foot in a more medial position relative to the desert iguana (*Dipsosaurus dorsalis*). They observed that increased knee flexion (acute angle at mid-stance), rather than increased femur depression (maximum values approximating 30°), was the mechanism underlying this medial foot position. Thus, the femur of chameleons was not particularly erect (also confirmed by Fischer et al., 2010), as suggested by other qualitative descriptions (e.g., Peterson, 1984). However, Fischer et al. (2010) note that, because chameleons are arboreal, they exhibit some degree of parasagittal limb posture for at least part of the stride.

Jayne and Irschick (1999) described the influence of speed and incline on postural kinematics for the morphologically generalized desert iguana, *D. dorsalis*, and found that three-dimensional knee and ankle angles changed with speed. More notable was the significant correlation of both femur depression and hip height at footfall with changes in speed. Although we found significant differences in knee angle, hip height, and femur depression between the two species, there was no correlation of femur depression with speed for either species. *T. scincus* did show a positive trend for both hip height and ankle angle when regressed against speed, and *E. macularius* had a marginally significant correlation between knee angle and speed. It appears that changes in speed yield different changes in kinematics across diverse groups of lizards. It is, however, important to note that the range of speeds (including the maximum speed obtained) was much lower for the species in this study than for *D. dorsalis* in the study by Jayne and Irschick (1999).

In our study, the femur of *T. scincus* exhibited a very large degree of maximum femur depression compared to *E. macularius* (33°

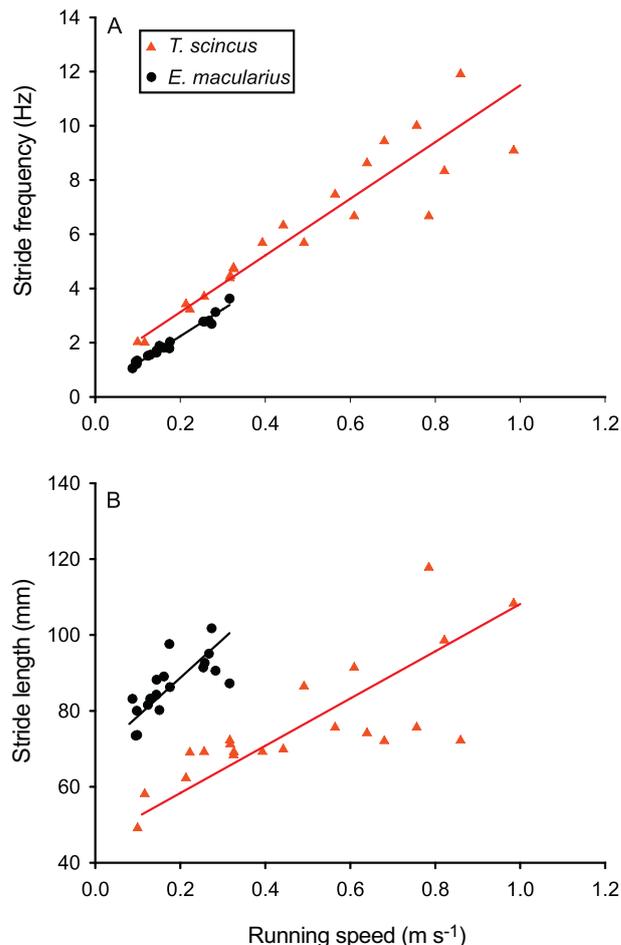


Fig. 6. Reduced major axis regressions of (A) stride frequency versus running speed and (B) stride length versus running speed for *T. scincus* and *E. macularius*. The r^2 values are 0.85 (A) and 0.59 (B) for *T. scincus*, and 0.98 (A) and 0.53 (B) for *E. macularius*.

versus 9°). The degree of femur depression in *T. scincus* falls in line with other sprawled lizards (Irschick and Jayne, 1999; Jayne and Irschick, 1999; Blob and Biewener, 2001; Russell and Bels, 2001; Higham and Jayne, 2004). Interestingly, the femur of *E. macularius* is highly elevated compared with all other sprawled lizards, suggesting they exhibit a 'hyper-sprawled' posture. Why is *E. macularius* different from other lizards? One explanation for this posture in *E. macularius* is that most lizards previously studied are fast-running terrestrial species, such as *Callisaurus draconoides*, *Uma scoparia*, *D. dorsalis*, and *Cnemidophorus tigris* (Irschick and Jayne, 1999). *E. macularius*, in contrast, likely moves slowly through its natural habitat and potentially moves on rocks that have inclination. The benefits of a hyper-sprawled posture on an incline, as previously discussed, may supersede the benefits of postures associated with faster lizards on open ground.

4.4. Future work

It is currently unclear whether the postures of *T. scincus* and *E. macularius* are a result of selection or simply evolutionary history. A comparative study that would facilitate ancestral reconstructions would potentially explain how *E. macularius* and *T. scincus* have inherited their respective modes of locomotor behavior. The habits of recent ancestors may have a lasting effect on successive species, such as the selection for cryptic escape habits in *Liolaemus* iguanas (Schulte et al., 2004). In addition to evolutionary analyses, extensive field observations are needed to understand how these two species

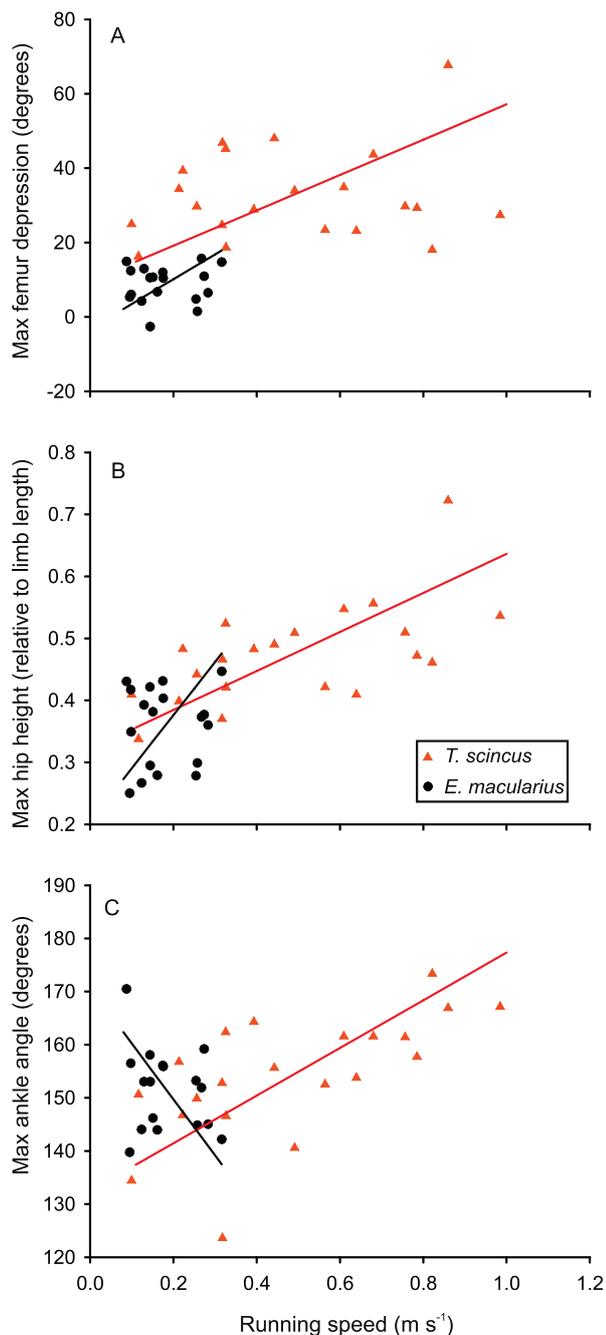


Fig. 7. Reduced major axis regressions of (A) maximum femur depression versus running speed, (B) maximum hip height versus running speed, and (C) maximum ankle angle versus running speed for *T. scincus* and *E. macularius*. The r^2 values are 0.03 (A), 0.40 (B), and 0.37 (C) for *T. scincus*, and 0.01 (A), 0.07 (B), and 0.03 (C) for *E. macularius*.

actually move in their natural environment. *E. macularius* lives in the desert, but likely moves on rocks and in bushes rather than in open sandy areas. However, quantitative descriptions are necessary given that little information is available about their ecology or habitat preference (Szczerbak and Golubev, 1996). To assess the potential benefits of a semi-erect posture in *T. scincus*, field studies are needed to assess the degree to which the field of view expands in response to an increase in body height. As Werner and Broza (1969) suggest, increasing the field of view may improve chances of prey or predator detection. A larger field of view may be possible in the open, sandy habitat of *T. scincus*, but field observations are necessary to determine if the slight increase in body height

is enough to allow *T. scincus* to significantly improve its field of view.

Lizard shape and flexibility of the backbone might also influence kinematics and selection in different environments (Van Damme and Vanhooydonck, 2001; Bergmann and Irschick, 2010). A more flexible backbone may help lizards negotiate tight bends such as crevices, while a stiffer backbone can increase efficiency for running (Van Damme and Vanhooydonck, 2001). Future studies analyzing the number and flexibility of vertebrae could reveal further morphological differences influencing the postures and kinematics of these two species.

Future studies of physiology can also clarify how and why *T. scincus* moves faster than *E. macularius*. Leg muscle fiber types are likely to vary between the two species. Also, the tail of *T. scincus* appeared to stay elevated during running (Fuller and Higham, personal observation), while the tip of the tail of *E. macularius* often touched the track surface during each stride. *T. scincus* may benefit from a functional advantage for having a raised tail while running; Nelson and Jayne (2001) revealed a connection between a raised tail, stretching of the caudofemoralis muscle, and a resulting increase in speed in the lizard *D. dorsalis*.

Our study revealed interesting differences in locomotion between two species of padless geckos that occupy desert habitats. Future work utilizing these species could elucidate potential mechanisms and origins of functional diversity among geckos.

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