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HOME FIELD ADVANTAGE: SPRINT SENSITIVITY TO ECOLOGICALLY

RELEVANT SUBSTRATES IN LIZARDS

by

CLINT EDWARD COLLINS

(Under the Direction of Lance McBrayer)

ABSTRACT

Effectively moving across variable substrates is important to all terrestrial animals. Much attention has been given to the effects of different substrates on locomotor performance in an attempt to link ecology and morphology. Sprint sensitivity is the decrease in sprint speed due to change in substrate. This study measures sprint sensitivity to substrate rugosity among six lizard species that occupy rocky, sandy, and/or semi-arboreal habitats. Lizards that use rocky habitats are less sensitive to changes in substrate rugosity, followed by arboreal lizards, and then by lizards that use sandy habitats. Phylogenetic analysis suggests that using rocks is highly correlated with decreased sprint sensitivity, long toes, and wide bodies. These results are discussed in the context of the adaptive significance of substrate selection, stability, and the evolution of sprint speed.

INDEX WORDS: Morphology, Performance, Lizard, Evolution, Substrate, Sprinting, Locomotion, Speed, Ecomorphology, Independent Contrasts, Habitat, Stability, Bipedal

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by

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HOME FIELD ADVANTAGE: SPRINT SENSITIVITY TO ECOLOGICALLY

RELEVANT SUBSTRATES IN LIZARDS

by

CLINT EDWARD COLLINS

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Electronic Version Approved:
May 2012

DEDICATION

I dedicate this thesis to the community of Fields, Oregon - especially Tom, Sandy, and Austin. Thank you for the delicious milkshakes, power outlets, and enthusiasm.

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INTRODUCTION

Effectively moving across variable substrates is important to all terrestrial animals. Animals ameliorate substrate incline, viscosity, obstacles, unsteadiness, and tree limb angles by kinematic adjustments, decreasing velocity, and jumping (Clark and Higham, 2011; Daley et al., 2006; Higham and Biewener, 2008; Higham et al., 2001; Higham and Jayne, 2002; Jayne and Irschick, 1999; Jayne and Irschick, 2000; Kohlsdorf and Biewener, 2006; Korff and McHenry, 2010; Luke, 1986; McElroy et al., 2007; Olberding et al., 2012; Spezzano and Jayne, 2004). Such variation suggests adaptation to varying substrate types among species (Arnold, 1983; Bock and Von Wahlert, 1965; Calsbeek, 2008; Hespenheide, 1973; Ricklefs and Miles, 1994).

Sprinting is partly dependent on effectively applying force to the substrate (Kerdok et al., 2002; Korff and McHenry, 2010; Lejeune et al., 1998). This relationship is defined by how viscous a substrate is, substrate rugosity (the amount of unevenness), and friction, as well as organismal traits related to locomotion. Because lizards sprint to escape predators and catch prey, and they use many types of habitats, they are a model system for tests of adaptation to substrate. Many lizards exhibit adaptations in toes, feet, limbs, and tails to specific substrates. A classic example of this type of ecomorphological relationship is the repeated independent evolution of toe fringes in sand dwelling lizards (Carothers, 1986; Luke, 1986). Toe fringes are laterally projecting, elongated scales occurring on the toes of some lizards that inhabit sandy substrates. It is widely believed that fringes increase the toe surface area, and thus traction, on substrates such as sand (Korff and McHenry, 2010; Luke, 1986). Another example occurs in the *Tropidurus*

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lizards. *Tropidurus* species that live on sand have long feet relative to those that live in trees, which have short tails and short legs (Grizante et al., 2009; Kohlsdorf et al., 2001). Substrate complexity varies tremendously in terrestrial environments from soft sand to increasingly rigid and rugose rocky habitats including rock faces, boulders, and paleoclastic lava fields. Although substrate complexity varies seemingly *ad infinitum* in terrestrial environments, some of the best work relating morphology, habitat, and performance has been on tree dwelling lizards.

Caribbean *Anolis* lizards partition the arboreal habitat relative to sprint sensitivity *i.e.* the decrease in sprint speed from a perch of large diameter to a perch of smaller diameter (Losos and Sinervo, 1989). *Anolis* with higher overall sprint speeds and longer legs exhibit greater sprint sensitivity (*i.e.* greater loss of performance on smaller diameter perches) and avoid perches where sprint performance is submaximal (*i.e.* smaller perches) (Irschick and Losos, 1999). However, *Anolis* with shorter limbs and slower overall sprint speeds exhibit lower sprint sensitivity values. These *Anolis* utilize a broad range of perches in the arboreal habitats (Irschick and Losos, 1999).

In rocky habitats, the distance an animal has to run to escape predation is comparatively greater than in other terrestrial habitats because vegetation and other refuges are farther apart (Goodman, 2009; Revell et al., 2007; Vitt et al., 1997). Furthermore, rocky habitats are challenging for animals to run across because they include inclines and unsteady surfaces (Goodman et al., 2008; Revell et al., 2007). Therefore, using rocks may depress locomotor performance and thus exert a strong selection pressure on locomotor morphology and performance (Farley and Emshwiller, 1996; Goodman et al., 2008; Taylor et al., 1972). Increased leg length and greater

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locomotor performance is tightly linked to using rocks in *Lygosominae* skinks (Goodman et al., 2008). In *Anolis* species, shorter limbs are needed on narrow perches to lower the center of mass and maintain balance. But specialization for climbing on narrow perches requires tradeoffs for movement on broader perches (Irschick and Losos, 1999). However, in *Lygosomine* skinks, there was no tradeoff between climbing on rocks and sprinting (Goodman et al., 2008). It is likely that climbing on rocks and climbing on trees impose similar physical constraints on locomotion (*e.g.* incline). Therefore, similar morphological and performance traits that enhance sprinting might be expected (Farley and Emshwiller, 1996; Higham and Jayne, 2002; Irschick and Jayne, 1999; Jayne and Irschick, 1999; Taylor et al., 1972). However, this pattern has not been observed (Goodman et al., 2008; Revell et al., 2007). In *Liolaemus* lizards, for example, there are no differences in sprint speeds among species that use trees, rocks, or sand (Tulli et al., 2012). Another characteristic of rocky habitats, substrate rugosity, may impose greater physical constraints than climbing. Hence, the more rugose a substrate is, the more difficult it is to run across. Here I hypothesize that living on highly rugose surfaces is correlated with the evolution of sprint performance and morphological differences between species of lizards that use different substrates.

This study quantifies differences among tree dwelling, rock dwelling, and sand dwelling lizards in sprint performance and morphology. Rock dwelling was equated to living on highly rugose substrates and thus I focused my analysis on sprint sensitivity to an increase in substrate rugosity. Increased rugosity was mimicked by increasing substrate particle size from sand to pebbles to cobbles. Sprint sensitivity was defined as the difference in sprint speed on a more rugose substrate (*e.g.* cobbles) compared to a less

rugose substrate (*e.g.* sand). It was hypothesized that as substrate rugosity increased, sprint speed would decrease. Rock dwelling lizards should exhibit lower sprint sensitivity values than their sand dwelling counterparts. Tree dwelling lizards should be intermediate along a continuum of sprint sensitivity with sand dwelling lizards at one extreme and rock dwelling lizards at the other. It is predicted that each lizard will attain its highest sprint speeds on the substrate that is uses most often; hence, each lizard should exhibit a "home field advantage".

Differences in morphology and relationships between morphology and habitat use were also quantified. It was hypothesized that rock dwelling lizards would exhibit relatively longer limb segments as was seen in *Lygosominae* skinks. This is logical because longer legs could be used to increase stride length and hip height, which would help move over highly rugose substrates (Biewener, 1990, 1991; Russell and Bels, 2001). It was also hypothesized that rock dwelling lizards would have longer tails, which aid in stability (Gillis et al., 2009; Jusufi et al., 2008; Libby et al., 2012).

To test for the adaptive significance of having different morphotypes relative to different substrates, sprint sensitivity and morphology were quantified in six species of lizards: *Aspidoscelis tigris, Crotaphytus bicinctores, Gambelia wislizenii, Sceloporus occidentalis, Sceloporus undulatus,* and *Sceloporus woodi.* These species were chosen because their relative phylogenetic positions are well known, we were able to replicate sand and rock dwelling in the phylogeny, and these species represent different body plans. *Crotaphytus bicinctores* and *G. wislizenii* represent ideal study species because they are closely related (family: *Crotaphytidae*), they are broadly sympatric, and they share a similar body plan (McGuire et al., 2007). However, *G. wislizenii* uses sandy

habitats and *C. bicinctores* uses rocky habitats (Pianka, 1967; Pianka, 1966). Therefore, differences in performance and morphology may represent adaptations to differential habitat use between these species. *Aspidoscelis tigris* is useful as an outgroup because it represents a different body plan, is distantly related to the other focal species in the study, and uses sandy substrates (Estes et al., 1988; Pianka, 1967; Pianka, 1966). *Sceloporus occidentalis* live in rocky habitats throughout much of its range and is also broadly sympatric with *C. bicinctores*. *Sceloporus woodi* is a small lizard that uses sandy substrates similar to *A. tigris* and *G. wislizenii* (Branch et al., 2003). *Sceloporus undulatus* is arboreal, though they also use rocks and other perches in portions their range (Pounds and Jackson, 1983). The population sampled for this study occurs in a locality in southeast Georgia where rocks do not occur. All *S. undulatus* were collected on the boles of pine and oak trees. The three *Sceloporus* species were chosen because they use different habitats, share a similar body plan, and are closely related. Therefore, differences in performance among these species may represent adaptations to different habitats.

This project is significant because previous research has focused on the locomotor strategies of crossing one obstacle in one or two species (Kohlsdorf and Biewener, 2006; Olberding et al., 2012) and only one other study characterized how lizards sprint over three ecologically similar substrates (Tulli et al., 2012). This study will shed light on the adaptive significance of using substrates that vary in rugosity among several species.

MATERIALS AND METHODS

Lizard Searches and Capture

Performance and morphology measurements for *A. tigris*, *C. bicinctores, G. wislizenii,* and *S. occidentalis* were collected in the Alvord Basin in southeastern Oregon (N 42.296097°, W 118.656414°). The Alvord Basin is characterized by sandy flats, hardpan, and dunes; common vegetation includes *Artemesia tridentata* and *Sarcobatus vermiculatus* (Steffen and Anderson, 2006). The Alvord Basin is surrounded by boulder fields, rocky cliff faces, and paleoclastic lava flows. *Sceloporus woodi* were collected from Longleaf Pine (*Pinus palustris*) forests and Sand Pine (*Pinus clausa*) scrub in the Ocala National Forest (N 29.257726°, W 81.778702°) and *S. undulatus* were collected from Longleaf Pine and American Turkey Oak (*Quercus laevis*) scrub in George L. Smith state park Georgia (N 32.559930°, W 82.113771°). Lizards were found by walking haphazard transects in suitable habitats for each respective study species. Sampling occurred between 830 hours and 1230 hours and between 1400 hours and 1800 hours from June 1 – July 25, 2010 for *A. tigris, C. bicinctores,* and *G. wislizenii,* from June 1 – July 25, 2011 for *S. occidentalis,* and September 5th – September 20th 2011 for *S. woodi* and *S. undulatus*. Lizards were captured by noose or hand. If possible, the temperature of each lizard was taken with a rapid reading cloacal thermometer immediately upon capture to determine field active body temperature. This was done to ensure body temperature for each species during performance trials was similar to those experienced naturally. Only adult males were used in this study to reduce the variability associated with gravidity (females) and development (subadults/juveniles). Lizards were placed in individual cloth bags and the GPS coordinates of the capture site was recorded.

Lizards were released at the point of capture after all data collection. Lizards were captured and maintained according to IACUC protocol I09009.

Performance Trials

Maximal sprinting ability in *A. tigris, C. bicinctores, G. wislizenii,* and *S. occidentalis*, was measured in the field. Three straight, level runways (5 m long x 0.25 m wide x 0.4 m high) were constructed using aluminum flashing. The first runway contained coarse sand particles ranging from 0.5 – 2.0 mm diameter. The second runway contained pebbles ranging from 10.0 – 15.0 mm diameter. The third runway contained cobbles ranging from 200 – 250 mm diameter. Substrate particles were discriminated visually according to the Wentworth particle scale. Substrates were collected from nearby areas after observing the species of lizards moving across them. Sand was collected from sites used by *A. tigris* and *G. wislizenii*. Cobbles were collected from sites used by *C. bicinctores* and *S. occidentalis*. Pebbles were used as an intermediate substrate because they are seen in both sandy and rocky habitats. Vegetation was placed at one end of each runway to serve as a refuge that could be detected by the lizard during its escape down the runway. Each quarter meter of the runway was marked to estimate distance in video recordings. For *A. tigris, C. bicinctores, G. wislizenii,* and *S. occidentalis* sprinting ability was tested 24 - 48 hours after capture. The 24 - 48 hours before trials allowed the passage of gut contents and recovery from handling stress.

Sceloporus woodi and *S. undulatus* were captured and returned to a laboratory setting at Georgia Southern University. *Sceloporus woodi* and *S. undulatus* were tested over a 3 day period after capture. Lizards were maintained separately in glass terraria with sand substrate, a water bowl, and a hide. Each terrarium was heated by UV lamp at

one end to produce a thermal gradient similar to those preferred by each species (Andrews, 1998; Crowley, 1985). Terrariums were heated and lighted from 700 to 1800 hours daily. Lizards were fed crickets to satiation every other day and were fasted 24 hours prior to sprinting trials. Three straight, level runways (4 m long x 0.25 m wide x 0.4 m high) were constructed using the same substrates described above. Similarly, each quarter meter was marked to calibrate distances in video recordings.

Prior to each run, lizards were placed in a thermoelectric cooler in individual cloth bags until their core body temperatures reached their field active body temperatures (35° - 39°C for *A. tigris, C. bicinctores, G. wislizenii, and S. woodi;* 34° - 36°C for *S. occidentalis* and *S. undulatus*). Body temperatures were measured by cloacal thermometer. All performance trials were conducted during normal lizard activity hours. Substrate temperature in each runway was closely monitored so that it was not different from the temperatures the lizards experienced while active in their habitat (min: 21.5°C; max 57.5°C). Before the first sprint trial, non-toxic correcting fluid was painted on the occiput of each lizard to use as a tracking marker in video recordings. Lizards were placed at the zero meter mark at one end of the runway and coerced to run towards the darkened end five meters away. Lizards were chased down the length of each runway and, if necessary, were lightly tapped on the dorsum, tail, and legs in order to encourage them to run with maximal effort. Cameras filming at 30 frames / second were placed one meter apart along the raceway to film the lizards as each ran through the field of view. Each camera recorded a one meter segment of the raceway. The first three meters of each run for *A. tigris, C. bicinctores,* and *G. wislizenii* were filmed. Meters 1 − 5 were filmed for *S. occidentalis, S. undulatus,* and *S. woodi.* All velocity data presented here was taken

from the third meter because analysis of videos from meters 4 and 5 indicated lizards did not increase in speed after the third meter.

Three to five trials per individual were conducted in each runway. Each individual was rested for one to three hours between trials to allow for recovery. Runs were graded on a scale of 1 – 5 with 1 being a "refusal to run", 4 representing a straight, continuous quadrupedal run, and 5 representing a straight, continuous bipedal run. Runs rated 1 – 3 were discarded; only runs rated 4 or 5 were retained to estimate maximal velocity. Only trials from lizards with at least one good run on all substrates were retained for further analysis. The fastest 0.25 meters were used for statistical analysis.

Morphology

Twelve morphological measurements were taken on each individual following all performance trials on all substrates. The measurements were chosen because they reflect variation in body form and are relevant for locomotor performance. Measurements were taken using dial calipers (or a ruler where applicable) and included: tail length, width of the body at the chest, humerus length (shoulder to the elbow), antebrachium length (elbow to wrist), manus length, length of the longest finger (IVa) measured from the manus to the tip of the claw; femur length (hip to knee), tibia length (knee to ankle), pes length, length of the longest toe (IVb), and snout – vent length (SVL).

Data Analysis and Statistics

Sprint Sensitivity

Each run rated 4 or 5 was digitized, clipped, and converted to an AVI file with Adobe Premiere© software. DLTdv3 was used to manually digitize the white marker on the lizards' occiput in each video fame (Hedrick, 2008). Velocity was estimated by

measuring the linear displacement of this marker in each frame. The $x - y$ coordinates of the digitized marker were saved in Microsoft Excel©. Displacement was calculated by measuring the distance between each $x - y$ coordinate. A scale bar of 50cm was digitized in each video to calibrate the distance traversed by the lizards in each frame. The effects of digitization error in DLTdv3 were minimized by fitting a quintic spline to the $x - y$ coordinate data using the program GCVSPL (Walker, 1998; Woltring, 1986).

Sprint sensitivity was calculated by subtracting the sprint speed on a more rugose substrate from the sprint speed on a less rugose substrate (e.g. sprint speed sand $-$ sprint speed pebbles = sprint sensitivity of sand - pebbles). Smaller values of sprint sensitivity indicated that an individual's speed was affected less by the change in substrate. Large values indicate the individual was affected more by the change in substrate. A one-way ANOVA with Tukey-Kramer post-hoc tests was used to test for differences in sprint sensitivity among species.

Morphology

To control for the size differences among and within species, a $\log -$ size component was derived by $\log_{10}$ transforming all morphological measurements, summing them, and dividing by the total number of measurements. This $\log -$ size component was then subtracted from each measurement (Mosimann, 1979). Each data point was centered by adding a value of two to each observation to create a new, size $-$ adjusted measurement.

Principal components analysis (PCA) was used to ordinate the size $-$ adjusted morphological variables into principal components. We determined the number of principal components to retain by carefully examining a scree plot and the eigenvectors

of each principal component (Jackson, 1993). A one-way ANOVA with Tukey-Kramer post-hoc tests was used to test for differences among species in principal components. To characterize relationships between substrate and morphology, principal components for each species were combined to form ecomorphs. *Aspidoscelis tigris, G. wislizenii,* and *S. woodi* were combined into the "sand" ecomorph; *C. bicinctores* and *S. occidentalis* were combined into the "rock" ecomorph; *S. undulatus* was used as the "tree" ecomorph. A one-way ANOVA with Tukey-Kramer post-hoc tests was used to test for differences among ecomorphs in principal components.

Phylogenetic analyses

Morphology and sprinting of *A. tigris, C. bicinctores, G. wislizenii, S. occidentalis, S. undulatus,* and *S. woodi* was examined in a phylogenetic context using phylogenetic independent contrasts (PIC) (Blomberg and Garland, 2002; Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Garland, 1991). Relationships were gathered from a variety of sources to generate a composite phylogenetic tree suitable for this project. Branch lengths (indicated in millions of years before present) were estimated based on morphological and molecular data. Principal comparisons are among the two *Crotaphytidae* species and *Scelporine* species, with *A. tigris* as an outgroup. (Estes et al., 1988; Leache and McGuire, 2006; McGuire et al., 2007; Townsend et al., 2011; Wiens et al., 2011) (Figure 1). We used PDAP:PDTREE in Mesquite to calculate phylogenetic independent contrasts (PIC) on all size - adjusted morphological and sprint speed data (Garland et al., 1992; Maddison and Maddison, 2006; Midford et al., 2005). Absolute values of the PIC were plotted against their standard deviations to ensure the branch lengths used adequately fit the tip data. There were no significant trends ($r^2 < 0.22$, $p >$

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0.30), so all branch lengths and tip data were retained for further analysis (Garland et al., 1992). Principal Components PIC were then regressed on sprint speed PIC to characterize evolutionary relationships between morphology and performance (Garland et al., 1999). PIC regression lines were computed and mapped back onto the original data space. One-tailed 95% confidence intervals were computed in PDAP:PDTREE. We constructed confidence intervals for all morphological and performance data to detect significant rates of evolutionary divergence in the phenotypic data (Garland and Ives, 2000).

RESULTS

Sprint Sensitivity

Overall, lizards in this study exhibited a decline in sprint speed as substrate rugosity increased. However, *C. bicinctores* got faster on pebbles compared to its velocity on sand. The decline in sprint speed from pebbles to cobbles in *C. bicinctores* was significant, but it was not between sand and cobbles (Table 1; Fig 2). The other rock dwelling lizard, *S. occidentalis,* did not decrease in sprint speed between substrates (Table 1; Fig 2). All other lizards exhibited a significant decrease in sprint speed between sand and cobbles as well as pebbles and cobbles, but not between sand and pebbles (Table 1; Fig 2).

Morphology

The first two PC axes of the principal components analysis were most informative and explained 67% of the variation in morphology. Examination of a scree plot of eigenvalues indicated these two axes were most informative for interpretation. The first PC axis described 49% of the variation. High positive loadings were associated with longer tibia and feet while low loadings were associated with wide pelves and long front

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toes (Table 2; Figure 3). Principal Component 2 described 18% of the variation; positive loadings were associated with species with wide chests and longer hind toes while negative loadings were associated with species with longer intergirdle length and long tails (Table 2; Figure 3).

Sceloporus species were statistically different from the remaining species on PC axis 1. Within *Sceloporus*, *S. woodi* was different from *S. occidentalis*, while *S. undulatus* differed from neither (Table 3). On PC axis 2, *C. bicinctores* and *A. tigris* were statistically different from all other lizards. *Gambelia wislizenii, S. occidentalis, S. undulatus,* and *S. woodi* were not statistically different (Table 3).

There were significant differences among rock, sand, and tree dwelling lizards on PC axis 1 (Table 4). For PC2, rock dwelling lizards were statistically different from sand dwelling lizards, but neither sand nor rock dwelling lizards were statistically different from tree dwelling lizards (Table 4).

Phylogenetic relationships between morphology and performance

The PIC analysis revealed a strong relationship between the use of rugose substrates, morphology, and sprint sensitivity in the six focal species. This trend was marked by species with wide chests and long toes.

The relationship between morphology and the decline of sprint speed on increasing rugose substrates was best described by PC 2. While a comparison of the contrasts of PC1, PC2, and sprint speed indicated no relationship with any substrate ($p > 0.25$), a strong relationship is observed between the contrasts of PC2 and the increase in substrate rugosity from sand to pebbles ($p = 0.008$, $r^2 = 0.93$) and from sand to cobbles ($p = 0.032$, $r^2 = 0.82$) but not from pebbles to cobbles ($p = 0.91$, $r^2 = 0.003$) (Fig. 4 - 6).

Thus, variation in aspects of body shape along PC 2 is correlated with the decline of sprint speed on rugose substrates.

DISCUSSION

Sprint sensitivity was valuable in diagnosing performance capabilities among species. The lizards in this study exhibited a "home field advantage"; that is, they ran fastest on the substrate they use most often. Compared to the other species, rock dwelling lizards exhibited reduced sensitivity to increased substrate rugosity.

Substrate rugosity and sand use

While *G. wislizenii* decreased in speed between sand and pebbles and pebbles and cobbles, the closely related *C. bicinctores* increased in speed between sand and pebbles, and was not significantly different between sand and cobbles, supporting the "home field advantage" hypothesis. Why would two lizards that are closely related and that share similar body plans show such dramatic differences? Rugose and sandy substrates impose different physical constraints on lizard sprinting. If gait and posture are different between species, then a fluid substrate such as sand and a rugose substrate such as rocks would affect each lizard differently. It is plausible that *C. bicinctores*, which run bipedally, slip or sink in the sand because they are heavier, or because the shape of the toe leads to better traction on pebbles than sand (Carothers, 1986; Glasheen and McMahon, 1996; Li et al., 2011; Luke, 1986). If *G. wislizenii* run quadrupedally and have different toe morphology, then the animals' mass may be more distributed across the sand, preventing this lizard from sinking (Carothers, 1986; Glasheen and McMahon, 1996; Luke, 1986). The morphological analysis revealed *C. bicinctores* loads significantly higher than *G. wislizenii* on PC2 axis, indicating *C. bicinctores* have relatively stockier bodies than *G.*

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wislizenii (Table 3)*.* Since *C. bicinctores* have relatively wider chests and shorter limbs, then perhaps bipedal running serves two purposes for this species – raising center of mass while running, and increasing stride length; both could increase stability on rugose substrates by allowing *C. bicinctores* to contact the surface without destabilizing its center of mass and by allowing the lizards to contact the surface more efficiently (Biewener and Daley, 2007; Daley et al., 2006; Kohlsdorf and Biewener, 2006; Olberding et al., 2012). Furthermore, *C. bicinctores* are more territorial, and hence more conspicuous, than *G. wislizenii* (Cooper and Vitt, 1991; Macedonia et al., 2004). Therefore, *C. bicinctores* may live with higher predation risk than *G. wislizenii.* This increased conspicuousness and risk of predation likely plays an important role in the morphological and performance differences between these two species (Cooper and Vitt, 1991; Goodman, 2009; Husak and Fox, 2006; Husak et al., 2006; Husak et al., 2008; Macedonia et al., 2004).

Substrate rugosity vs. climbing

This study identified a positive relationship between using rugose substrates with increased body width, long toes, and reduced sprint sensitivity. Both *C. bicinctores* and *S. occidentalis* are sit - wait predators and may cling for long periods of time on relatively vertical surfaces. Since the lizards in this study lack specialized toe pads as seen in *Anolis* species, it is possible that *C. bicinctores* and *S. occidentalis* use muscular force to cling. The same muscles may be coadapted for sprinting and stability (Russell and Bels, 2001).

Differential sprint sensitivity between *S. occidentalis* and *S. undulatus* may be due to ecological differences including distance to refuge and predator evasion. If *S.*

undulatus rely more on crypsis, and/or escape by moving short distances around the bole of the tree, and are thereby less exposed to predation, then the ability to run across varied substrates may be more relevant for a rock dweller (*S. occidentalis*) compared to its arboreal counterpart (Cooper, 2009; Cooper et al., 2008).

Similarities and differences with other lizard clades

The hypothesis that rock dwelling lizards exhibit relatively longer limb segments and longer tails was accepted (Tables 2 & 4). However, the PCA analysis of the size – adjusted morphological measurements indicated that rock dwelling *C. bicinctores* exhibited short limb lengths and tail length compared to other the other focal species. If using rocks is correlated with the evolution of longer legs in *Lygosominae* skinks, then why would *C. bicinctores* exhibit short limbs? Short legs may lead to increased stability, which would be important for maintaining high speeds over rugose substrates (Channon et al., 2011; Demes et al., 1995; Irschick and Losos, 1999; Irschick et al., 2005; Kerdok et al., 2002).

In this study, either the highest speed for each species was attained on its native substrate, or there was no difference among substrates. Tulli *et al* (2012) found sprint speed in *Liolaemini* lizards was not the highest on each species' native substrate. Furthermore, the rock dwelling *C. bicinctores* was the fastest lizard on cobbles and pebbles, and shared the highest speed with *A. tigris* on sand. Rock dwelling *Liolaemini* lizards attained the lowest speed (Tulli et al., 2012). This highlights a fundamental difference between *Liolaemini* lizards in South America and *Iguanid* lizards and *A. tigris* in North America. Where rock dwelling *Liolaemini* lizards have evolved wide and flat body forms to hide in crevices when faced with predation, the North American rock

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dwelling species in this study have apparently evolved to sprint across open terrain, rather than hide in crevices (Bergmann et al., 2009; Revell et al., 2007; Tulli et al., 2012).

Evolution of stability

In addition to sprint speed, dynamic stability is likely important in rugose habitats (Biewener and Daley, 2007; Revell et al., 2007; Russell and Bels, 2001). It is plausible that rock dwelling animals such as *C. bicinctores* evolved upright body postures and/or bipedalism to increase dynamic stability over rugose substrates (Biewener, 2003). Clark and Higham (2011), for example, found that postural changes accounted for reduced falling over slippery surfaces in helmeted guinea fowl. A careful analysis of kinematic data could reveal why *C. bicinctores* has exhibits greater sprint speeds on rugose substrates compared to *G. wislizenii* despite their similar body plan. Furthermore, using rugose surfaces may necessitate increases in intrinsic mechanical and behavioral stability control factors. The use of increasing muscle tension to absorb additional kinetic energy may aid in attaining high velocities (Biewener and Daley, 2007; Daley and Biewener, 2011; Daley et al., 2006). Such postural, limb angle, and mechanical adjustments have been exhibited in guinea fowl and highlight the need for such kinematic data in other terrestrial vertebrates such as lizards (Daley et al., 2006). This type of data may be especially important for closely related species that use different habitats.

In summary, substrate rugosity plays an important, yet variable, role in terrestrial locomotion. Animals exhibit varied mechanisms that serve to increase sprint speed on their respective native substrates. This study reveals that there is much to be learned about how animals move over various substrates. More comparative data should be

collected to examine the evolutionary relationships between substrate, locomotion, and habitat selection in terrestrial animals.

Table 1: Sprint sensitivity values (+/- 1 SE) for each species and ANOVA summary statistics for each increase in substrate rugosity (df = 67). Each sprint sensitivity value equals the velocity attained by each lizard on a more rugose substrate subtracted from a less rugose substrate.

Species (N):	*Aspidoscelis tigris* (11)	*Crotaphytus bicinctores* (14)	*Gambelia wislizenii* (12)	*Sceloporus occidentalis* (12)	*Sceloporus undulatus* (10)	*Sceloporus woodi* (9)	F	P
Sand - Pebbles	0.40 ± 0.19	- 0.46 ± 0.14	0.13 ± 0.19	0.35 ± 0.19	0.21 ± 0.20	0.08 ± 0.20	4.18	0.0024
Sand - Cobbles	1.54 ± 0.2	0.14 ± 0.14	0.76 ± 0.19	0.50 ± 0.19	0.75 ± 0.20	0.87 ± 0.20	7.70	0.0001
Pebbles - Cobbles	1.18 ± 0.17	0.71 ± 0.12	0.63 ± 0.16	0.15 ± 0.15	0.54 ± 0.17	0.79 ± 0.17	4.00	0.0032

Table 2: Principal components factor loadings for the 12 size – corrected morphological traits measured on each lizard. For PC1, the eigenvalue is 3.84 with 49% of the variation in morphology explained. For PC 2, the eigenvalue is 2.79 with 18% of the variation in morphology explained. Factor loadings greater than 0.5 are highlighted in bold.

Morphological Trait	PC1	PC2
Chest Width	-0.27	**0.56**
Humerus	-0.48	-0.31
Antebrachium	-0.24	**-0.60**
Manus	0.19	-0.20
Front toe	**-0.84**	0.30
Pelvis	**-0.87**	0.27
Femur	0.24	**-0.63**
Tibia	**0.51**	-0.39
Pes	**0.70**	-0.39
Hind toe	-0.17	**0.54**
Intergirdle	-0.33	**-0.69**
Tail	**-0.88**	0.44

Table 3: Average principal component factor loadings (+/- 1 SE) for each species and connecting letters report ($p < 0.0001$, F > 59.00, $df = 5$, 1 − way ANOVA with Tukey − Kramer *post hoc* comparisons). Within each PC, a shared letter indicates no significant difference between species.

Species	PC1, letter	PC2, letter
Aspidoscelis tigris	-0.83 ± 0.07, C	-1.48 ± 0.12, C
Crotaphytus bicinctores	-0.82 ± 0.06, C	1.20 ± 0.11, A
Gambelia wislizenii	-0.97 ±0.08, C	0.22 ± 0.11, B
Sceloporus occidentalis	1.17 ± 0.07, A	-0.12 ± 0.11, B
Sceloporus undulatus	1.06 ± 0.08, A, B	-0.005 ± 0.13, B
Sceloporus woodi	0.74 ± 0.08, B	0.01 ± 0.14, B

Table 4: Average principal components factor loadings (+/- 1 SE) for each ecomorph and connecting letters report ($p < 0.001$, F > 16.00, $df = 2$, $1 -$ way ANOVA with Tukey $-$ Kramer *post hoc* comparisons). Within each PC, a shared letter indicates no significant difference between ecomorph.

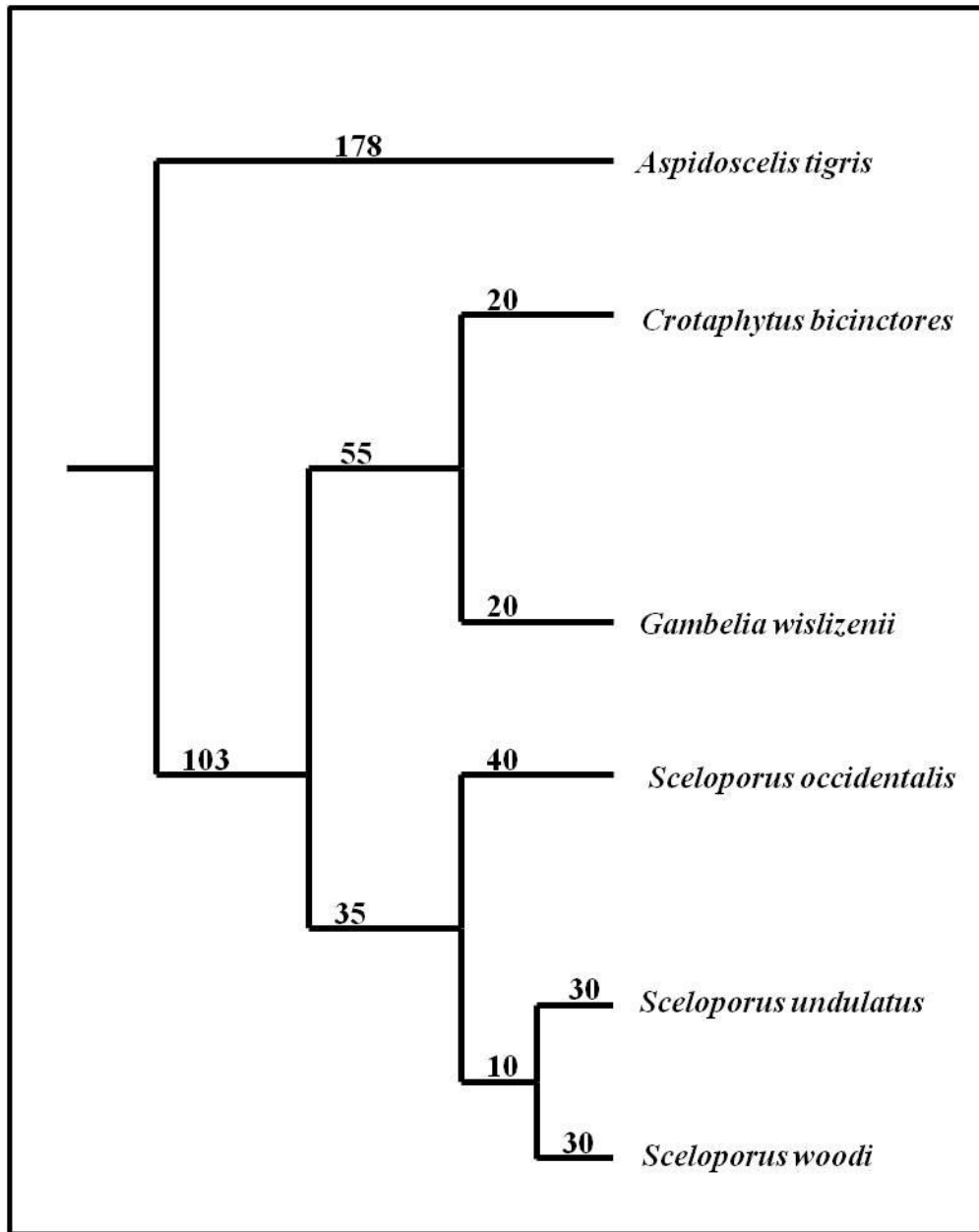| Ecomorph	PC1, letter	PC2, letter
Sand	0.11 ± 0.13, C	0.59 ± 0.13, B
Rock	-0.42 ± 0.12, B	-0.54 ± 0.12, A
Tree	1.06 ± 0.22, A	-0.005 ± 0.22, A,B

Figure 1: Phylogenetic relationships among focal species. Numbers indicate branch lengths in millions of years before present. Phylogenetic positions were derived from, and branch lengths were based on, Estes, de Queiroz et al. 1988, McGuire, Linkem et al. 2007, and Wiens, J. J., C.A. Kuczynski, et al. 2011.
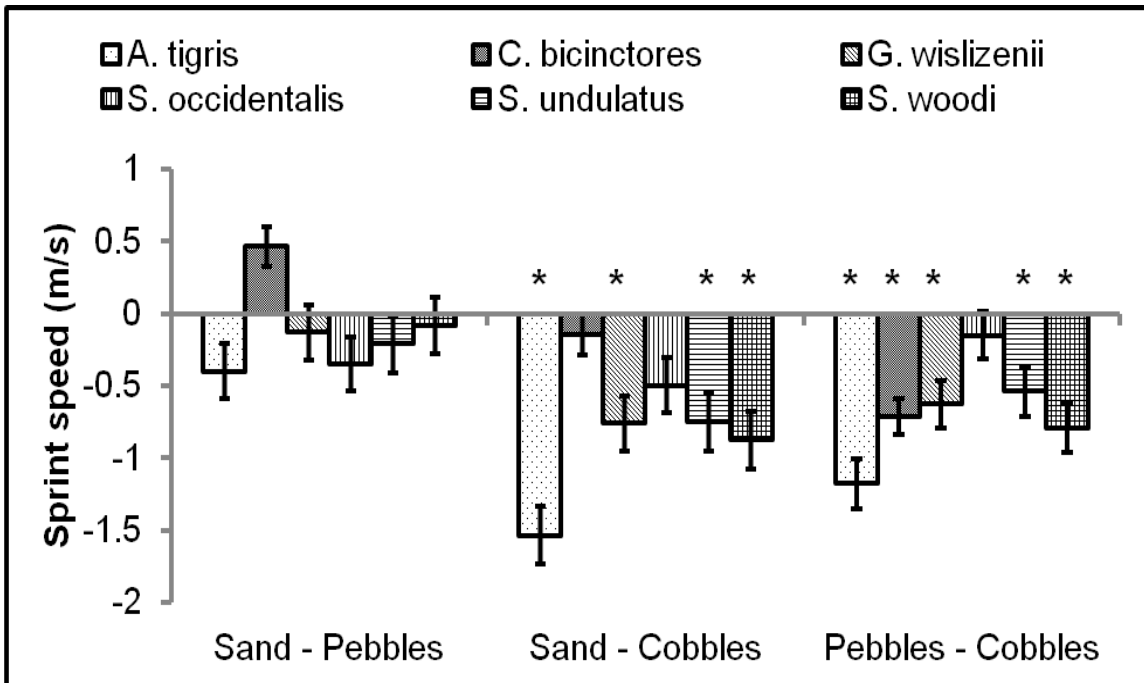
Figure 2: Mean values (+/- 1 SE) of sprint sensitivity between each substrate for each species. *Crotaphytus bicinctores* increased in velocity from sand to pebbles while all other lizards decreased in velocity. The two rock dwelling species, *C. bicinctores* and *S. occidentalis* did not exhibit a significant decline in velocity from sand to cobbles as in all other species did. *Sceloporus occidentalis* did not exhibit significantly lower sprint speeds from pebbles to cobbles although all other species did. Asteriks indicate a significant decline in sprint speed (*p > 0.001, df = 5*, two − way ANOVA with Tukey-Kramer *post hoc* comparisons*).
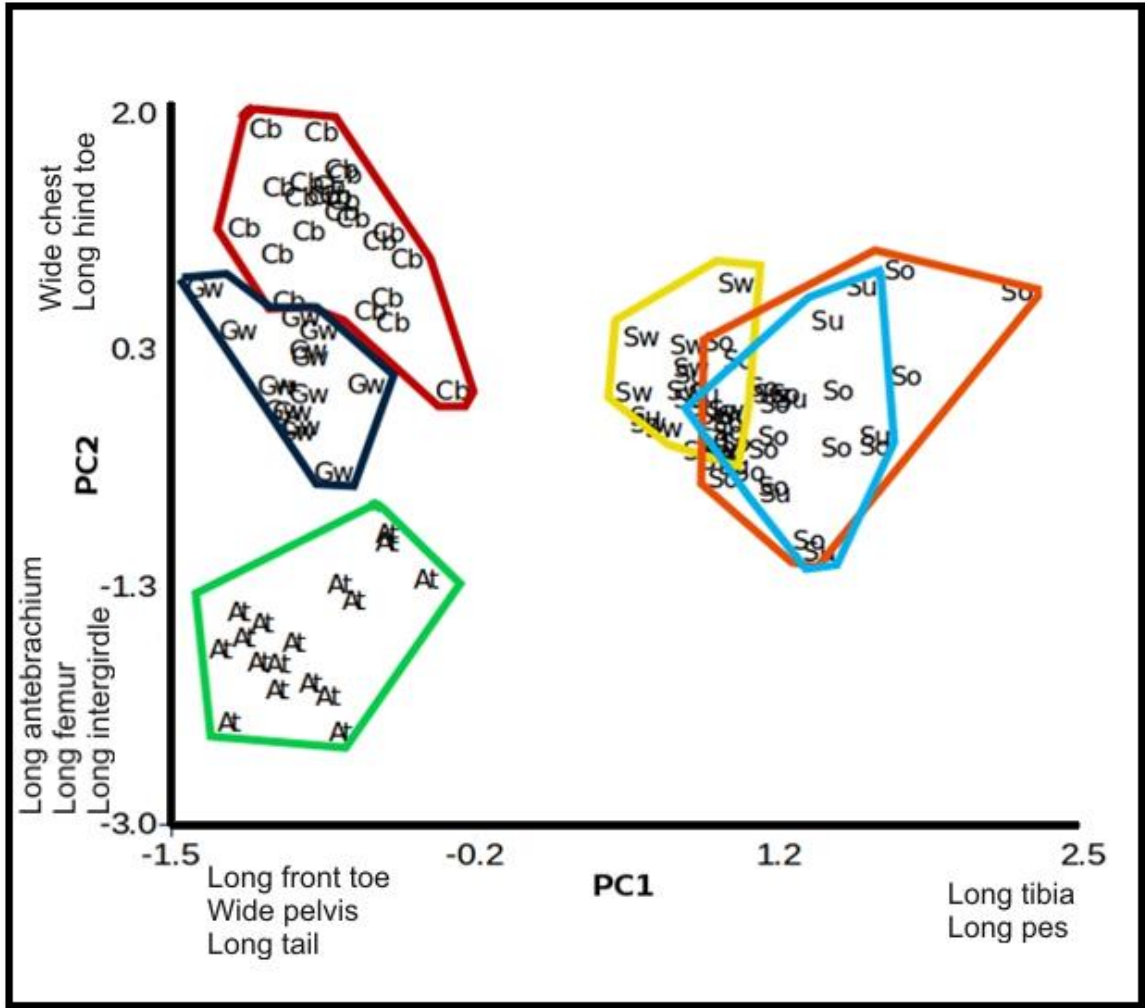
Figure 3: Scatterplot of PC1 scores vs. PC2 scores for 12 morphological variables across six species of lizards. *Sceloporus* species are characterized by having relatively long tibia and long feet. *A. tigris* is characterized as having long front toes, long antebrachium and femur as well as long bodies and tails. *C. bicinctores* is characterized as having wide chests and long hind toes. *G. wislizenii* occupies intermediate morphological space between *C. bicinctores* and *A. tigris* on PC component 2.

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Figure 4: Correlation between Sand – Cobbles sprint sensitivity and PC2 (morphology). The figure shows the correlated evolution of sprint sensitivity contrasts with a wide chest and long hind toes phenotype.

Figure 5: Correlation between Sand − Pebbles sprint sensitivity and PC2 (morphology). The figure shows the correlated evolution of sprint sensitivity contrasts with a wide chest and long hind toes phenotype.
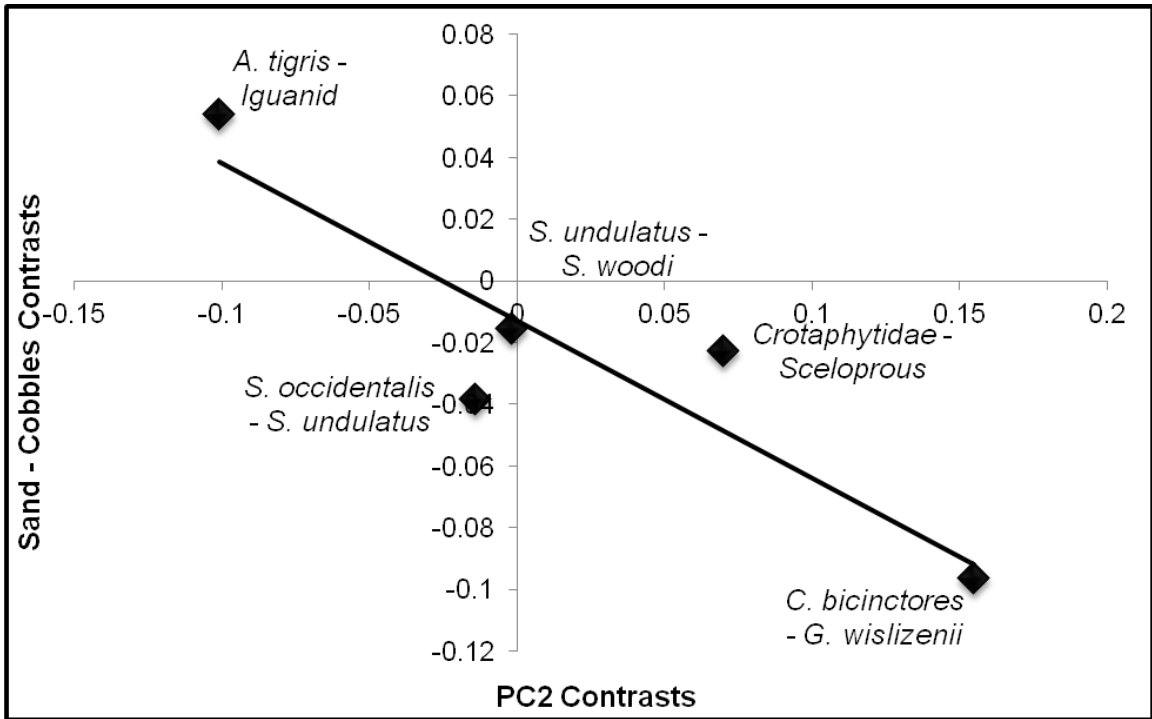
Figure 6: Correlation between Pebbles - Cobbles sprint sensitivity and PC2 (morphology). The figure shows the correlated evolution of sprint sensitivity contrasts with a wide chest and long hind toes phenotype.
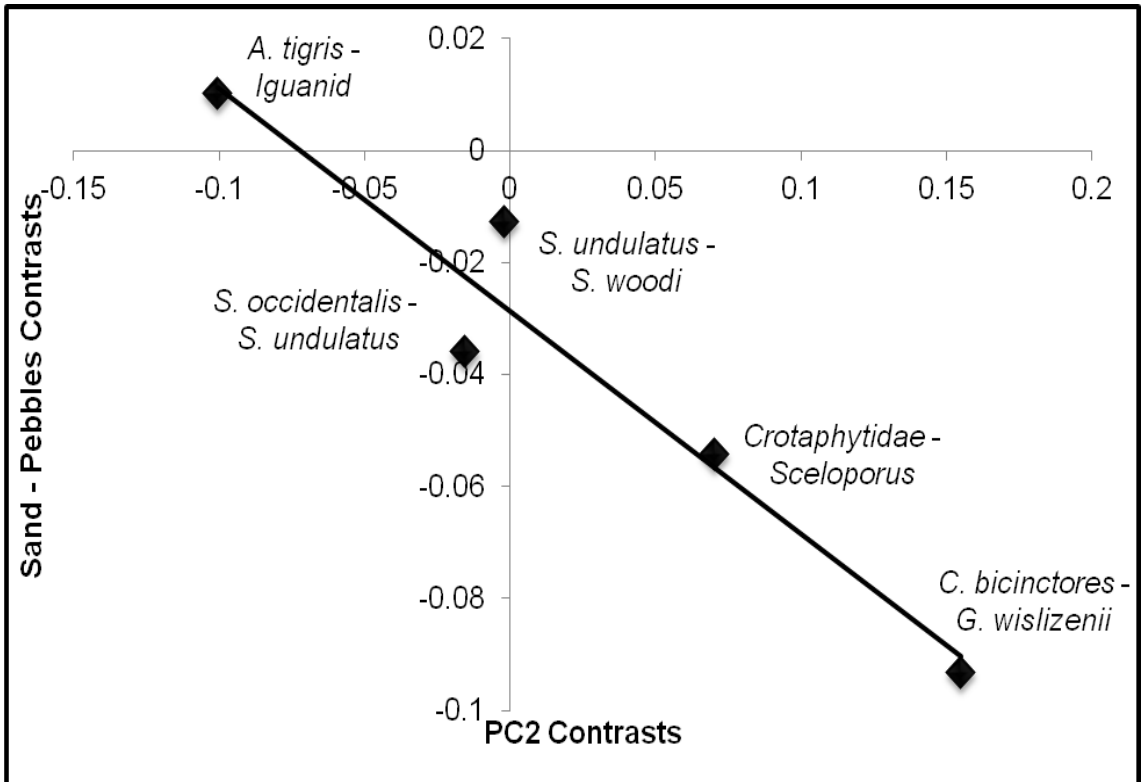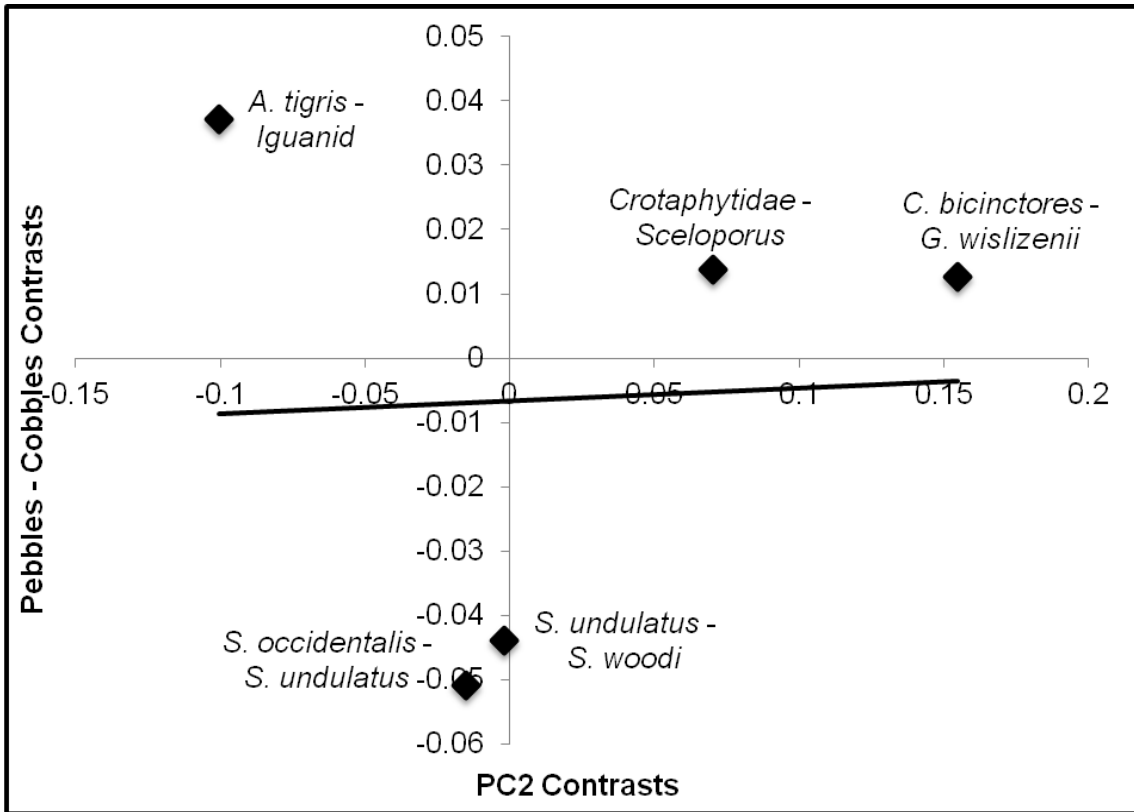
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