

Substrate type has a limited impact on the sprint performance of a Mediterranean lizard

PANTELIS SAVVIDES^{1,*}, ELENI GEORGIU¹, PANAYIOTIS PAFILIS^{2,3}, SPYROS SFENTHOURAKIS¹

¹ Dept. of Biological Sciences, University of Cyprus, Nicosia, Cyprus. *Corresponding author. Email: savvides.pantelis@ucy.ac.cy

² Section of Zoology and Marine Biology, Dept. of Biology, National and Kapodistrian University of Athens, Greece

³ Zoological Museum, National and Kapodistrian University of Athens, Greece

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Abstract. Environmental factors may affect animal performance in diverse ways, even among different populations of a single species. Here, we assess the impact of substrate type on the sprint performance (maximum speed and acceleration) of Schreiber's fringe-fingered lizard (*Acanthodactylus schreiberi*). This species is a skillful runner that also bears micro spike-like protruding scales on its toepads (toe fringes), an adaptation for locomotion on sand. We worked with three populations living in habitats that differ in substrate type (sand, soil and rock). We measured sprint performance using a race-track with custom substrate platforms replicating the different substrate types. We formulated two hypotheses: first, we anticipated that the three populations would differ in their sprint performance due to the differences in substrate type; second, we expected that each population would perform better on its home substrate. Our results generally refuted the hypothesis that sprint performance would differ on different substrate types. Our results suggest that there is a restricted effect of substrate type on locomotion and indicate a multifactor interplay among alternative underlying parameters.

Keywords. Ecophysiology, morphology, locomotion, Lacertidae, Cyprus.

INTRODUCTION

Sprint performance is very important for all animals, as it affects most of their daily activities. Sprinting is quite common among lizards during foraging, antipredator defense and inter- and intraspecific competitive behavior (Losos and Irschick, 1996; Husak et al., 2006; McElroy et al., 2008). Speed and acceleration, the main components of sprint performance, may be crucial for the overall fitness of individuals (Jayne and Bennett, 1990; Robson and Miles, 2000; Miles, 2004). Interactions between the ecology and morphology of species act as driving factors that exert strong selective pressures leading to optimal locomotor performance (Van Damme et al., 2003; Husak et al., 2006). For instance, gekkonid and lacertid lizards were shown to adopt different locomotion patterns

because of their distinct ecology (Aerts et al., 2000). Also, Losos (1990) reported that locomotion parameters and morphological features evolved concordantly in 15 *Anolis* species.

The results of previous studies on the effects of substrate type on locomotion are puzzling (Korff and McHenry, 2011; Tulli et al., 2012; Vanhooydonck et al., 2015). The texture complexity (e.g., particle size, shape and roughness) of the substrate type is also known to affect locomotor performance (Brandt et al., 2015; Bergmann et al., 2017). The propulsive forces applied by the toes on non-solid substrates (e.g., sand) may be reduced because of insufficient grip and friction with the substrate, therefore leading to suboptimal sprint performance (Redfern et al., 2001; Korff and McHenry, 2011; Brandt et al., 2015). Stiff, rough substrates provide more

friction that enhances grip, thus allowing higher performance (Kerdok et al., 2002; Van der Tol et al., 2005; Brandt et al., 2015; Bergmann et al., 2017).

Morphological features that are often beneficial on certain substrate types include adaptations of the epidermis that covers the digits. For instance, the adhesive ability of many Gekkonidae species depends on toe pad microarchitecture (setae) that allows them to run easily on smooth and vertical surfaces such as walls or even glass (Autumn et al., 2002; Autumn et al., 2005). Also, some other taxa bear fringes on their toes (e.g. genera *Acanthodactylus*, *Basiliscus* and *Uma*) enabling them to run fast on non-solid substrates (e.g., sand or water) without ‘sinking’, as fringes increase the amount of toe surface that comes into contact with the substrate while running (Salvador, 1982; Luke, 1986; Carothers, 1986).

In this study, we aimed to evaluate the impact of substrate type on sprint performance (maximum speed and maximum instant acceleration) in Schreiber’s fringe-fingered lizard (*Acanthodactylus schreiberi* Boulenger, 1878). We worked with three Cypriot populations that reside in habitats with different substrate types (soil free from rocks, rock and sand). We formulated two hypotheses. First, we anticipated that the sprint performance of the focal populations would differ due to the presence of different substrate types in the habitats and due to the different running styles required on each one (Van Damme et al., 1998). Second, we predicted that individuals would perform better on their home substrates than those coming from other habitats (Goodman et al., 2008).

MATERIALS AND METHODS

Study system

Acanthodactylus schreiberi is a medium-sized lacertid lizard (snout-vent length 73–93 mm for males and 55–76 mm for females), inhabiting various habitats all over Cyprus (Baier et al., 2009). Even though it is considered to be mostly a sand-dwelling lizard, it can be found from coastal areas to mountain pine forests (over 1,300 m a.s.l.) (Baier et al., 2009). The species is a skillful and swift runner that can use bipedalism while running (Savvides et al., 2017).

The habitats of the three focal populations vary considerably in substrate and vegetation type (Fig. 1). Geri (35°05’50”N, 33°26’21”E, elevation 183 m a.s.l.) is a sub-urban shrubland characterized by the presence of boxthorn (*Lycium ferocissimum*), thorny burnet (*Sarcopoterium spinosum*) and conehead thyme (*Thymbra capitata*). The substrate consists mostly of solid soil without any rocks. Agros (34°56’27”N, 33°00’14”E, elevation 1,348 m a.s.l.) is in a pine forest (*Pinus brutia*) with dense shrubs and has a rocky soil as its substrate. Akrotiri (34°56’27”N, 33°00’14”E, elevation 1 m a.s.l.) is a coastal dune habitat with quite sparse phrygana, where the substrate is fine-grained sand.

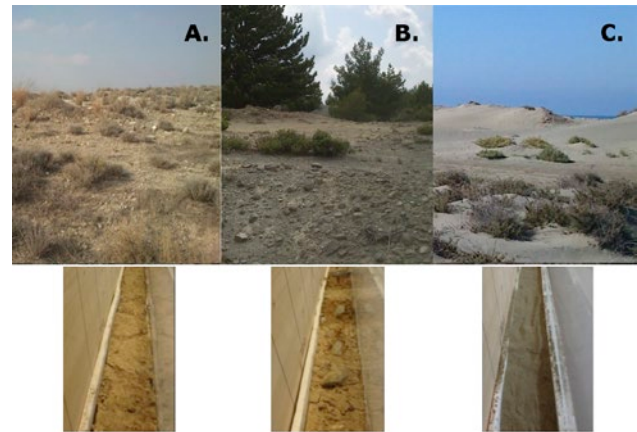


Fig. 1. The three habitats studied. A. Geri, B. Agros, C. Akrotiri and the respective platforms that were used in the laboratory to simulate the substrate of each habitat.

We captured a total of 67 adult individuals of both sexes (excluding gravid females) (Geri, N = 22; Agros, N = 22; Akrotiri, N = 23). Lizards were housed in individual terraria (30 x 30 x 30 cm) in the laboratory under a constant temperature (30 °C) and controlled photoperiod (16-h light and 8-h dark), and were provided with mealworms (*Tenebrio molitor* larvae) and fresh water *ad libitum*. All lizards were released at their sampling sites after the completion of the experiments (experimental lizards remained in the laboratory for two weeks).

Based on the substrate type of each habitat, we constructed three removable substrate platforms that were used on a custom-made wooden racetrack (240 x 12 cm²), bearing 10 cm increments on its back and clear acrylic glass on its front in order to allow video recording of each trial (Fig. 1).

Morphological measurements

Snout-vent length (SVL), hind limb length (HLL) and hind toe length (HT) were recorded with a digital caliper (Silverline 380244, accurate to 0.01 mm), before running trials. Also, the length of the largest right hind toe, the total number of fringes on it and the length of the three largest fringes from base to tip were measured using stereoscopic images of their toes (N = 60, 10 males and 10 females from each population) (Fig. 2), in order to test for correlation between toe length and fringe microarchitecture (length and number of fringes).

Sprint performance

All individuals were allowed to thermoregulate for an hour in a specifically designed terrarium (Van Damme et al., 1986) before each trial, so as to perform at the highest level possible (Irschick and Losos, 1998). After this period, lizards were placed in the racetrack. We triggered motion with a brush touching the lizard’s tail base. Each individual performed five trials on each substrate type in a single day. Between trials on

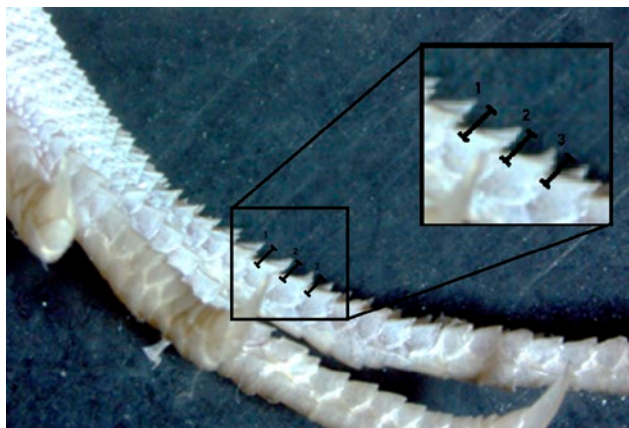


Fig. 2. Stereoscopic image of the toes and an example of how we measured the three largest toe fringes.

different substrate types, lizards were left to rest for a day and were then tested on the new type (in total, 15 trials per individual within five days). Trials were recorded with a video camera (Olympus SH-60) viewing the racetrack from the side (covering all the distance from start to finish), at a rate of 240 frames per second. Sprint performance was estimated from the video recordings (Martin and Avery, 1998; Kaliontzopoulou et al., 2012; Vanhooydonck et al., 2015; Savvides et al., 2017).

Maximum speed was calculated for all trials, based on the number of frames needed to cover a distance of 20 cm within a known time interval (Savvides et al., 2017). We chose the highest values for each individual to represent its best trial. Maximum instant acceleration was calculated by digitizing the position of the lizard's snout in every frame, for all trials, on x- (movement) and y- (gravity) axes (MATLAB DLTdataviewer3; Hedrick, 2008). In each frame, we estimated the displacement of the snout and converted it from pixels to meters. We filtered the curve of the instantaneous displacement of the snout over time (i.e. instantaneous velocity) using a fourth-order zero phase shift Butterworth low-pass data noise filter (40Hz; VBA application in Office Excel). The time differential of the instantaneous velocity yields the instantaneous acceleration and we chose the highest value (i.e. peak) for each individual's best trial (Van Wassenbergh, 2007). We only used trials during which lizards ran continuously for at least 50 cm.

Using the Pearson product moment correlation coefficient, we found that the length of the largest hind toe correlated strongly with the length of the three longest fringes in all populations (all r values > 0.6 and P values < 0.05), so we used this measurement as a proxy of fringe size to detect possible fringe effects on sprint performance.

Statistical analyses

We used the Shapiro – Wilks and Levene's tests to check for data normality and homogeneity of variance, respectively. All data were log-transformed based on the results of these

tests. Log-transformed data for the morphological characters were compared between sexes for each population using one-way MANCOVA and taking SVL as covariate. One-way MANCOVA was also used to search for differences among populations in relation to the transformed data for the morphological characters (HLL and HT), using again SVL as a covariate. One-way MANOVA was used to compare their sprint performance among different substrate types and populations. A post-hoc Tukey test was used in order to determine the differences among populations. The Friedmann test and the Bonferroni correction were used to compare the performance of each individual on the three types of substrate. The effects of the log-transformed values of morphological characters (HLL and HT) on sprint performance were identified independently, using linear regression.

RESULTS

Morphological characters showed significant differences between the sexes in each population, with female individuals having relatively smaller hind limbs and hind toe length than male individuals (one-way MANCOVA: Geri, $F_{2,18} = 9.965$ Roy's largest root = 1.107; Agros, $F_{2,18} = 29.373$ Roy's largest root = 3.264; Akrotiri, $F_{2,18} = 5.517$ Roy's largest root = 0.613; all P values < 0.05). Thus, hind limbs and hind toes length were therefore compared among populations separately for males and females (Table 1), but no significant differences were found (all P values > 0.05).

When comparing sprint performance among populations, we observed that the Agros males (home habitat with rocky substrate) were significantly faster than the other populations (one-way MANOVA: $F_{6,26} = 4.072$, Roy's largest root = 0.940, $p = 0.005$). They achieved the highest maximum speed (Post hoc Tukey HSD: Agros vs. Geri, $P = 0.012$; Agros vs. Akrotiri, $P = 0.002$) and maximum instant acceleration (Post hoc Tukey HSD: Agros vs. Geri, $P = 0.001$; Agros vs. Akrotiri, $P = 0.002$) on soil

Table 1. Mean values for morphological characters between males and females from the three populations. SVL: snout-vent length, HLL: hind limb length, HT: longest hind toe length. Values are in cm.

Character		Geri		Agros		Akrotiri	
		Mean	SD	Mean	SD	Mean	SD
SVL	♂♂	7.10	0.43	6.90	0.64	6.35	0.40
	♀♀	6.45	0.41	6.50	0.34	6.00	0.44
HLL	♂♂	4.60	0.23	4.65	0.14	4.49	0.43
	♀♀	4.00	0.28	4.00	0.16	3.96	0.22
HT	♂♂	1.29	0.14	1.24	0.12	1.22	0.10
	♀♀	1.13	0.22	1.10	0.09	1.00	0.10

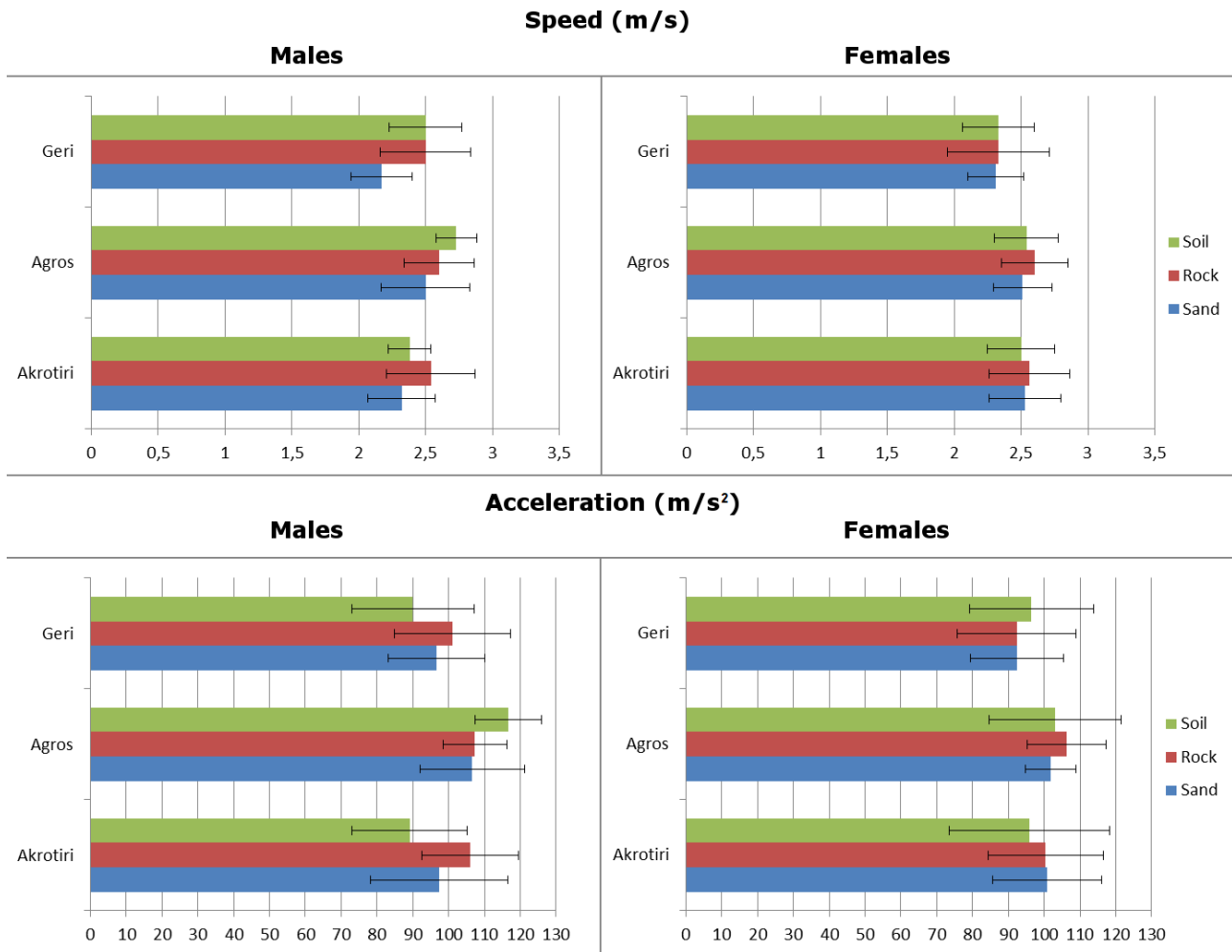


Fig. 3. Mean values for speed and acceleration on each substrate within populations and for males and females.

(Fig. 3). We did not observe further differences in the sprint performance among other populations on the other substrates.

The sprint performance of all lizard populations (for both sexes) did not differ among the three types of substrate (all P values > 0.05) (Fig. 3).

The length of hind limbs and toes showed no significant effects on performance among populations and substrates (all regression P values > 0.05).

DISCUSSION

Locomotion patterns may change in response to endogenous or extraneous factors (Vanhooydonck and Van Damme, 2003; Sathe and Husak, 2018). Among the latter, the type of substrate is known to affect locomotion in lizards. In some cases, specific substrate types

favor higher performance (e.g., solid substrates like rock), while others restrict locomotion (e.g., substrates not providing sufficient grasp, e.g., sand or mud) (Vanhooydonck et al., 2005; Tulli et al., 2012). In our study, we did indeed see certain differences in sprint performance among conspecific populations of Schreiber's fringe-fingered lizard. However, these differences followed a rather unclear pattern and indicated a limited effect of substrate type on locomotion.

Interestingly, when we analyzed sprint performance taking into account the effect of hind limb length, we did not find any significant effects for any type of substrate. Also, the multiple regression analyses did not show a beneficial effect of toe fringes (using the hind toe as a proxy). Hind limbs have been repeatedly reported to affect lizard locomotion (Vanhooydonck et al., 2001; Herrel et al., 2002; Savvides et al., 2017). The absence of such effects in our study might indicate an interplay among

other morphological features (e.g., fore limbs, tail length, etc.) involved in locomotion in response to substrate type requirements (Herrel et al., 2002). On the other hand, we cannot rule out the possibility that despite our best efforts, lizards might have underperformed and have failed to achieve their maximum performance levels.

Contrary to our first hypothesis regarding sprint performance on different substrates, no differences emerged from the comparison among the three populations, save the single case of the Agros males (rock substrate) that were the fastest sprinters. However, subsequent analysis based on morphological features, failed to provide an underlying reason for this finding. In our initial hypothesis, we considered the three types of substrate to be of different quality. We presumed that sand would be the more challenging substrate because of its grainy texture that “sinks” under the weight of a running lizard (Clemente, 2014; Sathe and Husak, 2015). As such, we expected that sprint performance therein would be the lowest. On the other hand, solid substrates are known to provide high traction and thus facilitate locomotion (Lejeune et al., 1998; Claussen et al., 2002; Brandt et al., 2015; Bergmann et al., 2017). Apparently, these predictions were not valid in our study system, as we failed to find any significant deviations. It seems that there is no ideal substrate type for *A. schreiberi* locomotion and all populations are well adapted in their home habitat.

According to our second hypothesis, lizards should have performed at higher levels on their home substrate. However, we did not find such a pattern in our study system. All populations performed at similar levels on all substrate types, indicating that the species conserves generalized running capabilities that allow a high level of performance on various types of substrate. The rejection of the specialized populations hypothesis, might be due to overlapping genetic pools or mixed habitat characteristics, leading the lizards in similar directions regarding their kinematics and their interactions between morphology, biomechanics and environmental factors. We also have to highlight the fact that long periods of draught in Cyprus can change abruptly to rainy periods (especially during late spring and early summer). This would cause the substrate to change its properties, such as its roughness and its potential to provide grip and would thus favor the generalized pattern we observed in this study.

This study will enhance the growing body of literature on saurian locomotion, as it examines some of the widely accepted principles in the field. According to our findings, the type of substrate has a limited impact on sprint performance, and at least for Schreiber’s fringe-fingered lizard, there were no strict patterns observed. Further research including more species will shed light

on the fascinating interplays taking place in lizard locomotion.

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