

# Is Habitat Preference Associated with Locomotor Performance in Multiocellated Racerunners (*Eremias multiocellata*) from a Desert Steppe?

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**Abstract** Locomotor performance in lizards is strongly affected by structural habitat. Understanding this relationship allows us to predict species distributions across habitat types. However, little information is available about the ecological role of the locomotion of multiocellated racerunner (*Eremias multiocellata*) in the desert steppe ecosystem of Inner Mongolia, China. Herein, we studied the effects of habitat structure on the locomotor performance of this lizard species in the field. We found that the sprint speed of this lizard declined significantly with increasing vegetation coverage. Manipulative experiments were further conducted to examine the effects of branch barriers and surface substrates on the sprint speed of the lizard. We found that the sprint speed was significantly influenced by the surface substrates and branch barriers, and there were no interactions between them. Branch barriers impeded sprint speed, and *E. multiocellata* showed better locomotor performance on sandy rather than loamy substrates. Our results indicate that *E. multiocellata* tends to occupy open areas with sandy substrates, but its locomotor performance is not closely associated with habitat preference.

**Keywords** Habitat, lizard, locomotion, performance, substrate, barrier

## 1. Introduction

Locomotory abilities of an animal are associated with a variety of ecologically important activities, such as dispersal, mate finding, territory defense, foraging, and escape from predators (Aerts *et al.*, 2000; Husak *et al.*, 2006; Perry *et al.*, 2004; Turchin, 1998). Thus, locomotor performance directly affects the animal's fitness, and is often regarded as a relevant ecological index in fitness measuring (Higham, 2007). Furthermore, the relationship between habitat type and locomotor performance is vital for understanding fitness and the natural distribution of lizards, because the locomotor performance of lizards is strongly affected by their structural habitat (Irschick and Losos, 1999; Losos and Irschick, 1996). Therefore,

understanding the locomotor performance of lizard species is helpful in predicting their distribution across different habitat types.

The locomotor ability of lizards is correlated to morphological factors, such as body mass, tail, hindlimb, and toes (Borges-Landáez and Shine, 2003; Downes and Shine, 2001; Higham and Russell, 2010; Li C. *et al.*, 2011), and environmental factors, such as temperature, substrate type, size and incline, and surface diameter (Du *et al.*, 2005; Gilman and Irschick, 2013; Huang and Tu, 2009; Irschick and Losos, 1999; Li C. *et al.*, 2011). In addition to morphological factors, structural characteristics of the habitats (e.g. surface substrate diameter and sand grain size) are very important on the locomotor performance (Irschick and Losos, 1999; Li C. *et al.*, 2011). As a result, many lizards prefer habitats where they can maximize their locomotor performance. Previous studies have shown that habitat preference is associated with locomotor performance (Higham and Russell, 2010; Irschick and Losos, 1999). For example,

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lizards avoid habitats in which sprinting performance is submaximal (Irschick and Losos, 1999). Microhabitat use in nature may have a profound effect on the locomotor performance of lizards (Vanhooydonck *et al.*, 2005). However, besides locomotor performance, other ecological factors, including food availability, thermal environment, predation risk, and competition may also affect the habitat preference of lizards (Daly *et al.*, 2008; Du *et al.*, 2006; Lisičić *et al.*, 2012; McLaughlin and Roughgarden, 1989; Roches *et al.*, 2011). This increases the complexity of the association between habitat preference and locomotor performance.

Lizards are abundant in desert ecosystems worldwide (Pianka, 1986). However, their distributions are heterogeneous in natural habitats. The multiocellated racerunner, *Eremias multiocellata*, is a viviparous lacertid lizard, and it generally occupies arid or semi-arid regions covered by sparse vegetation (Zhao *et al.*, 1999). It is also a common lizard species in the desert steppe ecosystem of Inner Mongolia, China, and its abundance was strongly affected by the habitat structure (vegetation height, basal cover and bare ground) (Zeng *et al.*, 2014). Previous research on this species were primarily focused on variation in life history and the phenotype under different environmental conditions (Li H. *et al.*, 2011; Tang *et al.*, 2012; Yan *et al.*, 2011; Zhang *et al.*, 2010). However, the effects of habitat structure on locomotor performance and the relationship between locomotor performance and habitat preference have not yet been studied for this species.

The goals of our study were: 1) to evaluate whether lizard movements changed with structural habitats in the field, 2) to determine effects of habitat structure on sprint speed of lizards by manipulating branch barriers and surface substrates in the laboratory, and 3) to test the hypothesis that habitat preference is associated with the locomotor performance of lizards.

## 2. Materials and Methods

**2.1 Field data** Our fieldwork was conducted at the Ordos Key Research Station for Field Observation of Ecological Environments by Sandy Grasslands, China. The station is located in Jungar Banner, a cold semi-arid region of Inner Mongolia (40°12'17" N, 111°07'43" E; elevation 1036 m). The mean annual temperature is 6–7°C, with an average maximum temperature of 39.1°C in July and an average minimum temperature of –32.8°C in January. Annual precipitation ranges from 300 to 380 mm, with most of the rain falling between July and September.

The study area is predominantly sandy grassland with low to moderate levels of sparse vegetation dominated by *Artemisia ordosica*. Much of the natural habitat in this region have been altered for agricultural purposes and combat desertification. These habitat alterations have increased heterogeneity since the early 2000s. Compared to the natural habitat, the altered habitat is generally either vegetatively: 1) sparser and dominated by *Ephedra sinica*, or 2) more dense and dominated by *Hedysarum leave*. In total, three distinct habitat types with different vegetation coverage (sparse, natural, and dense) were selected in our study (Zeng *et al.*, 2014).

A raceway (L × W × H: 300 × 30 × 30 cm<sup>3</sup>) through the vegetation of the three habitats was set up in the field to evaluate the effect of habitat structure (mainly including surface substrates and branch barriers) on the locomotor performance of field-caught adult lizards. A total of 20 adults *E. multiocellata* (12 males and 8 females) were used in the locomotor performance test. We measured snout-vent length and tail length with a ruler to 1 mm, brachium length, antebrachium length, metacarpus and fore-foot length, thigh length, crus length, and metatarsus and hind-toe length with a caliper to 0.1 mm. We measured body mass with an electronic scale (KL-928; Dongguan Sincerity and Success Electronic Manufactory, Guangdong, China) to 0.01 g at the beginning of the test, and then placed the lizards in individual wooden containers (L × W × H: 55 × 32 × 38 cm<sup>3</sup>) and left them undisturbed for at least 30 min to acclimate to the ambient temperature prior to each trial. The locomotor performance of lizards is dependent on body temperature, but it is difficult, if not impossible, to precisely control the body temperature of lizards in a field experiment. To minimize temperature effects, we initialized all trials at 1400 and finished before 1600 on sunny days from 20–28 July 2012, during which the fluctuations in ambient temperatures were relatively small. In addition, we measured the body temperature of each lizard just before the locomotor performance test so that we could account for any influence in our statistical models. We assessed locomotor performance by chasing the lizards along the raceway with a paintbrush. Each lizard was tested twice with a rest period of at least 30 min between two trials. The running speed was calculated by dividing the length of racetrack (3 m) with the cumulative time taken by lizards to cross the end of the raceway. The fastest speed for each individual was then used to evaluate the locomotor capability of each lizard in each habitat. We tested for the effects of body temperature on sprint speed using Pearson's correlation test. Correlation

analysis indicated that the sprint speed of lizards was not significantly related to their body temperature ( $r = -0.031$ ,  $P = 0.816$ ,  $n = 60$ ). Accordingly, body temperature was not included in our statistical model to test for the among-habitat difference in the sprint speed of lizards.

**2.2 Controlled experiments** In September 2014, we collected another 10 adult *E. multiocellata* (4 males and 6 females) from the field and transferred them back to the Institute of Zoology, Chinese Academy of Sciences, for experiments. The lizards were housed in plastic terraria ( $L \times W \times D$ :  $600 \times 300 \times 400$  mm<sup>3</sup>) filled with 50 mm of moist sand. These terraria were kept in a room with a temperature of  $24 \pm 1^\circ\text{C}$  and a 12 h:12 h light:dark cycle. Food (mealworm, *Tenebrio molitor*, and crickets, *Acheta domestica*, dusted with mixed vitamins and minerals) and water were provided *ad libitum* for the adult lizards. The experiment was performed within three weeks after capturing. Body variables of these lizards were measured at the beginning of the experiment by using the aforementioned methods.

Experimental trials were conducted using a wood runway ( $L \times W \times H$ :  $150 \times 20 \times 20$  cm<sup>3</sup>), with a transparent glass panel for lateral filming. The bottom of the runway was covered by 5 cm soil substrate with two treatments (sandy substrate and loamy substrate). The sandy substrate was derived from sandy soil on the surface of the sparse habitat, and the loamy substrate was from sandy loam on the surface of the dense habitat. The surface soil from the natural habitat was not considered because it was similar to that from the sparse habitat. In addition, a barrier gradient, ranging from no, low, to high branch barriers, was designed by placing some chopsticks on the substrate. The chopsticks were distributed in diamond shapes with 30 cm long diameter and 4 cm or 8 cm short diameter. The former with 4 cm short diameter and the latter with 8 cm short diameter were regarded as treatments of high and low branch barriers, respectively. Therefore, we used a total of six treatments (2 surface substrates  $\times$  3 branch barriers) in our controlled experiments.

We quantified the locomotor performance (sprint speed) of the lizards by racing each individual down the racetrack (marked at 20 cm intervals) and encouraged with a soft paintbrush. Individuals were raced 3 times for each treatment at  $30 \pm 1^\circ\text{C}$ , with 1 h of rest between each consecutive race. We recorded the running with a video camera from a lateral perspective. For each individual in each treatment, we used the fastest 20 cm from each of the three races to calculate sprint speed and quantify locomotor performance.

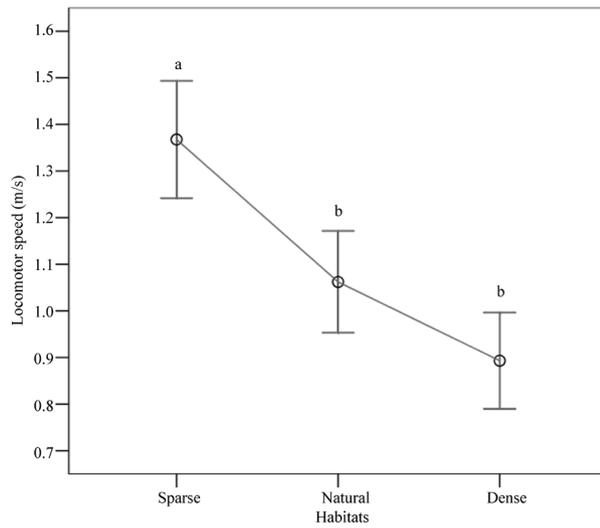
**2.3 Data analysis** One-way repeated-measures analysis of variance (ANOVA) was used to determine the among-habitat difference in the sprint speed of *E. multiocellata* with sex as the between-subjects factor and sprint speed in each habitat as the repeated measure. Two-way repeated-measures ANOVA was used to test the effects of surface substrates and branch barriers on the sprint speed. Partial correlation analyses was used to test for the effects of body variables on the sprint speed of lizards with habitat type in the field data and surface substrates and branch barriers in the experiment data as control variables. To remove the effects of some body variables on locomotor performance, univariate analysis of covariance (ANCOVA) was used to determine differences among habitats (or among surface substrates and branch barriers) in the sprint speed with body variables as the covariates. All data were analyzed by the software package of SPSS 19.0.

### 3. Results

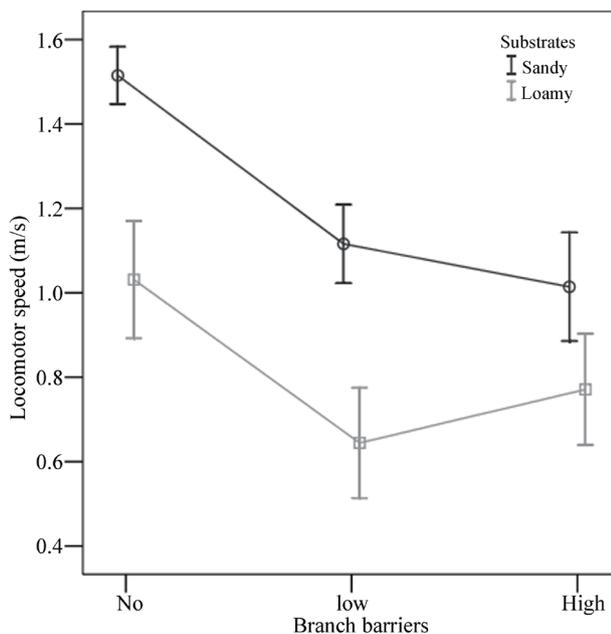
The sprint speed of the lizards differed among habitats ( $F_{2,36} = 29.58$ ,  $P < 0.0001$ ), and a significant interaction was not found between habitat and sex (habitat  $\times$  sex:  $F_{2,36} = 0.03$ ,  $P = 0.967$ ), indicating that *E. multiocellata* performed differently in each habitat. Partial correlation analyses indicated that the sprint speed of the lizards in the field was significantly related to body mass ( $r = 0.499$ ,  $P < 0.0001$ ,  $n = 57$ ), snout-vent length ( $r = 0.437$ ,  $P = 0.001$ ,  $n = 57$ ), brachium length ( $r = 0.504$ ,  $P < 0.0001$ ,  $n = 57$ ), and thigh length ( $r = 0.474$ ,  $P < 0.0001$ ,  $n = 57$ ). After the effects of these four body variables on locomotor performance had been statistically removed, the sprint speed significantly declined with increasing vegetation coverage in the habitats ( $F_{2,53} = 24.67$ ,  $P < 0.0001$ ) (Figure 1).

Surface substrates and branch barriers had apparent effects on the locomotor performance of *E. multiocellata* in the controlled experiments (Figure 2). The sprint speed of the lizards decreased by branch barriers ( $F_{2,18} = 12.81$ ,  $P < 0.001$ ), and the lizards had faster sprint speed on the sandy than loamy substrates ( $F_{1,9} = 16.46$ ,  $P = 0.003$ ). The interaction between the surface substrates and branch barriers had no significant effect on the sprint speed (surface substrates  $\times$  branch barriers:  $F_{2,18} = 1.20$ ,  $P = 0.324$ ). Partial correlation analyses indicated that the sprint speed of the lizards in the controlled conditions was significantly related to snout-vent length ( $r = 0.315$ ,  $P = 0.016$ ,  $n = 56$ ) and crus length ( $r = -0.296$ ,  $P = 0.024$ ,  $n = 56$ ). After the effects of these two body variables on

locomotor performance had been statistically removed, the sprint speed significantly decreased with increasing branch barriers ( $F_{2,52} = 8.49$ ,  $P = 0.001$ ), and the sprint speed was still faster on the sandy than loamy substrates ( $F_{1,52} = 20.36$ ,  $P < 0.0001$ ). *E. multiocellata* showed better locomotor performance on sandy rather than loamy substrates (Figure 2).



**Figure 1** Locomotor performance of the lizard *Eremias multiocellata* in sparse, natural, and dense habitats in the desert steppe of Inner Mongolia, China. Data are expressed as means  $\pm$  1 SE. Means with different letters above the error bars are statistically different (Tukey's test). Sample sizes were 20.



**Figure 2** Locomotor performance of the lizard *Eremias multiocellata* under different controlled conditions. Data are expressed as means  $\pm$  1 SE. Sample sizes were 10.

#### 4. Discussion

In this study, we measured the ecological performance of multiocellated racerunners moving through their natural environment and highlighted the differences in their locomotor performance in different structural habitats. We found that the locomotor performance of *E. multiocellata* declined markedly with increasing vegetation coverage in the structural habitats. Our experiment results indicated that surface substrate and branch barrier are two important components of habitat structure influencing the lizard's locomotor performance. Previous studies have shown that natural habitats had higher abundance of *E. multiocellata* than structurally sparse and dense vegetation (Zeng *et al.*, 2014). Obviously, our studies both in the field and laboratory supported that locomotor performance of *E. multiocellata* is not closely associated with habitat preference, despite the significant effects of habitat structure on locomotion. Similar results were found in two sand lizard species (*Uma scoparia* and *Callisaurus draconoides*) in the Mojave Desert, their differences in habitat distribution are not closely related to locomotor performance (Korff and McHenry, 2011). Furthermore, our experiments show that *E. multiocellata* performs better on sandy rather than on loamy substrates. Thus, this lizard species is expected to occupy primarily open areas with sandy substrates.

The locomotor performance measured under our controlled conditions was very close to that measured under natural conditions for *E. multiocellata* in our studies. Field speeds of *E. multiocellata* in the sparse, natural, and dense habitats were about 92%, 95% and 108% of controlled trackway speeds that measured under corresponding controlled conditions, respectively (Figures 1, 2). In contrast, larger discrepancies in locomotor performance usually occur between field- and laboratory-based measures in other lizards. For example, some lizards have been recorded in the field to run at about 78%–90% of the maximum speed measured under controlled experiments (Higham and Russell, 2010; Irschick and Losos, 1998), whereas others run at higher (about 118%) velocity in the field than in the laboratory (Higham and Russell, 2010; Jayne and Ellis, 1998). Therefore, we concluded that maximum performance was accurately measured under our controlled conditions for *E. multiocellata*. More importantly, the pattern of habitat effects on locomotor performance was the same in the field and laboratory tests, suggesting that the relationship between locomotor performance and habitat structure is relative constant with little effects from other ecological

factors. The consistency of our results from the field and laboratory tests provides solid evidence to test for the hypothesis that habitat preference is associated with locomotor performance in lizards.

Previous studies suggest that habitat structures influence the locomotor performance of lizards (Du *et al.*, 2005; Irschick and Losos, 1999). Some attributes of habitat structure may impede locomotion when lizards move through their natural environment. Structurally, habitats become more complex with increasing vegetation coverage, so lizards may frequently encounter more branch barriers located along their traveling routes. Consequently, lizard movements change with structural habitats in the field, and *E. multiocellata* obviously showed an impeded locomotor performance in a denser habitat. This may be an important factor that influences its distribution in a dense habitat where *E. multiocellata* is rarely found (Zeng *et al.*, 2014), because some lizards avoid structural habitats in which their maximal sprinting abilities are impaired (Irschick and Losos, 1999). However, a great mismatch between the locomotor performance and population density of the lizards occurred in the field study. *E. multiocellata* is more abundant in natural rather than dense habitats (Zeng *et al.*, 2014), but the locomotor performance was similar between these two habitats. *E. multiocellata* is more abundant in natural rather than sparse habitats (Zeng *et al.*, 2014), but the locomotor performance was better in the sparse than natural habitats. These results suggest that locomotor performance is not closely associated with habitat preference in this lizard species. Other than the effects of locomotor performance, ecological factors such as soil, temperature, predators, competition, and prey may all interact to affect the distribution of lizards (Daly *et al.*, 2008; Du *et al.*, 2006; Lisičić *et al.*, 2012; McLaughlin and Roughgarden, 1989; Sun *et al.*, 2014; Zaady and Bouskila, 2002). The habitat preference of *E. multiocellata* may be associated with some other ecological factors to a greater extent. For example, we found that *E. multiocellata* had a higher predation risk from birds in sparse habitats than in dense habitats (unpublished data). Habitat structure affects predation risk (López and Martín, 2013). This lizard species is especially vulnerable to predators while moving across relatively open habitats. Therefore, sparse habitats, where *E. multiocellata* showed the best locomotor performance, are not dominantly occupied by the lizard species.

Locomotor performance depends on a mechanical interaction between the feet of the lizard and the surface substrate. Effects of this interaction may be

substrate-specific and species-specific because of their different locomotor morphologies. For example, *Callisaurus draconoides* without toe fringes ran with a faster maximum speed than *Uma scorparia* with toe fringes on dune sand, but not on wash sand (Korff and McHenry, 2011). This effect was also substrate-specific for *E. multiocellata* in our experiments. We found that the locomotor performance of this lizard species was significantly different among surface substrates from different structural habitats, and the surface substrates had no significantly interactive effects with the branch barriers. Substrate type affects the maximum instantaneous speed of animals: the gecko *Hemidactylus garnoti* attains higher maximum instantaneous speeds on wood surfaces than on metal or cloth surfaces (Vanhooydonck *et al.*, 2005). For the sympatric toad-headed lizard *Phrynocephalus frontalis* in the desert steppe, substrate (i.e., sand grain size) also has significant effects on its running speed, and it is a factor that influences its habitat selection (Li C. *et al.*, 2011). Obviously, locomotor ability is important for a lizard species, especially when escaping from predators or capturing prey (Irschick and Losos, 1999; Pounds, 1988). When natural selection acts on locomotor performance, substrate choice of the lizard species could influence its fitness. Consequently, lizards may dominantly use and inhabit a preferred sandy substrate with a locomotory advantage. Therefore, only a few *E. multiocellata* are distributed in dense habitats with loamy substrates (Zeng *et al.*, 2014).

Effects of habitat structure, especially habitat substrates and physical structure, on locomotor performance have been extensively studied and well documented in lizards (Irschick and Losos, 1998; Mattingly and Jayne, 2004; Mcelroy *et al.*, 2007; Vanhooydonck *et al.*, 2005; Vanhooydonck and Van Damme, 2003). However, the ability of these animals to move through branch barriers has received much less attention. Animals often encounter different barriers along their traveling routes in their natural environment. The ability of reptiles to negotiate different barriers is likely to be under strong selection because habitats with dense vegetation impose spatial challenges for ecologically relevant activities, such as foraging and escape from predators (Irschick and Losos, 1999; Pounds, 1988). Therefore, understanding the effects of habitat barriers on the locomotion of lizards is very important.

Working on the relationship between maximal locomotor performance of lizards and the obstacles of habitat structures such as perch height and incline, some scientists found that locomotor speed significantly

decreases with increasing perch height or when lizards run on steep inclines (Irschick and Jayne, 1998; Jayne and Irschick, 2000; Mcelroy *et al.*, 2007). Kohlsdorf and Biewener (2006) also studied the kinematics of lizard locomotion when animals move over obstacles encountered along traveling routes. However, few studies have considered the effects of branches as physical barriers in structural habitats. Our experiments showed that branch barriers significantly impeded the locomotor performance of *E. multiocellata*. Lower sprint speeds when negotiating branch barriers are likely associated with a movement deceleration to evade the obstacle.

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