

## Effects of sand grain size and morphological traits on running speed of toad-headed lizard *Phrynocephalus frontalis*

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### ABSTRACT

We conducted a manipulative experiment to investigate the influential factors of locomotor ability in steppe toad-headed lizards. By using a video-base method, we measured running speed of the lizards when they run on sands of different grain sizes. We also considered body condition, tail length and sex as fixed factors to analyze their effects on running speed of the lizard. Results showed that running speed of the lizard significantly differed among different trials of sand grain size. Specifically, the peak and the nadir values of the running speed were found on sands of 0.5–1 mm and 0.075–0.25 mm grains, respectively. When lizards ran on sands of different grain size their running speed changed significantly. Body condition and tail length also had significant effects on running speed. The findings indicated that locomotor ability of lizards depended on both body condition and the external environment. We hypothesized that sand grain size is one of the factors that influence the habitat selection in steppe toad-headed lizards. Moreover, this lizard may be used as an indicator of the development of sand dunes.

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### 1. Introduction

Running speed is an important representative of locomotor ability in animals. High running speed benefits animals in chasing prey, escaping predators and achieving high social status (Blumstein et al., 2004; Dill, 1990; Garland et al., 1990; Huey et al., 1990; Husak, 2006; Perry et al., 2004; Vitt et al., 1997; Ydenberg and Dill, 1986). Therefore, running speed is commonly used as an index of whole-body performance, which is used to estimate health or survival value in animals (e.g. Blumstein, 1992; Elphick and Shine, 1998; Huey et al., 1990; Sorci and Clobert, 1997).

Morphological characteristics evolve in animals to maximize running speed during natural selection (Irschick and Garland, 2001; Van Damme and Vanhooydonck, 2001). In lizards, for instance, running speed relates to body mass and tail (Ballinger et al., 1979; Downes and Shine, 2001; Du et al., 2005; Johnson et al., 1993; Punzo, 1982). There are some arguments over the effects of body length on locomotor ability of lizards. For example, evolutionary changes in body length were not correlated with changes in sprint speed among many species of lacertid lizards (Bauwens et al., 1995) or phrynosomatid lizards (Bonine and Garland 1999). However, Zani (1996) reported a strong correlation between sprint speed and

snout-vent length in 39 lizard species. Hindlimb and toes are also considered to be indispensable elements that determine the running speed of lizards (Borges-Landáez and Shine, 2003; Vanhooydonck et al., 2002).

Beside morphological traits, the substrate of the habitat (especially microhabitat) influences running speed of lizards (Du et al., 2005; Irschick and Losos, 1999; Jayne and Ellis, 1998; Moermond, 1979). To ensure high running speed, lizards tend to either live in the habitat with the suitable surface structure or adopt different behavioral strategies to escape predators in different habitats (Irschick and Losos, 1999; Schulte et al., 2004; Van Damme et al., 1998; Vanhooydonck and Van Damme, 1999; Vitt et al., 1997). Previous studies focused on rock lizards, tree lizards and grass lizards, and considered the rock, vegetation and incline in those habitats. For example, Mcelroy et al. (2007) studied the effects of woody substrates and incline on the locomotor speed of *Urosaurus ornatus*, and dissected the effects of behavior and habitat on the locomotion. No studies have addressed the effects of sand grain size on sand lizards that lived in open field.

Steppe toad-headed lizard, *Phrynocephalus frontalis*, is a common sand lizard in central Asian deserts (Liu et al., 2008; Munkhbaatar et al., 2006; Wang and Fu, 2004; Zhao, 1997). As a runner species of reptile, the lizard lives in desert, semi-desert and grassland with low and sparse vegetations (Liu et al., 2008; Zhao, 2001). Running is the way adopted by steppe toad-headed

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lizard to capture insects and to escape predatory birds and small mammals (Zhao, 2001). However, little is known about the running speed of this sand lizard. Because locomotor ability reflects survival strategy of lizards (Tsuji et al., 1989), it would be interesting to know the running speed of this lizard and relate it to our future studies on behavior, habitat use and niche breadth of steppe toad-headed lizard.

Our study had two main aims. We wanted first to learn the relationships between the running speed and morphological traits of steppe toad-headed lizard. We also wanted to understand the effect of sand grain size on the running speed in this sand lizard. Our null hypotheses were that (1) sand grain sizes do not affect the running speed of steppe toad-headed lizard; (2) the lizards with different morphological traits show no difference in running speed. To achieve these two aims, we designed an experiment of running in our laboratory to study the relationship between running speed and sand grain size, as well as the relationship between running speed and morphological measurements. Additionally, we also tested the sexual difference in running speed of steppe toad-headed lizard.

## 2. Materials and methods

### 2.1. Materials and experimental design

All animals in this study were under animal research protocol IOZ-2006 approved by the Animal Care Committee of the Institute of Zoology, Chinese Academy of Sciences and cared for these animals in accordance with the principles and guidelines of The Ethics Committee of the Institute of Zoology, Chinese Academy of Sciences and The Chinese Wildlife Management Authority. All adult lizards were caught in field areas around Sangendalai (115°54'E, 42°38'N) which is a town in the Hunshandak Desert of Inner Mongolia, China.

We captured the steppe toad-headed lizards with pitfall-traps or by direct chasing during growing season (from June to August) in 2008. We placed pitfall-traps under the broad-leaf plants to keep the trapped lizard shaded. Wet sand and common mealworms (*Tenebrio molitor*) were provided in the traps. To make sure the trapped lizards were not eaten by predators, the traps were checked at least once every 2 h. During chasing capture, the distance we chased lizards was around 10 m, and these lizards were caught with an insect net. The captured lizards were kept in a paper box (0.5 × 0.5 m) and transported to the laboratory. In the lab, the lizards were reared in an open cage (2 × 1 m) with sand substrate under natural photoperiods. Relative humidity and temperature of the laboratory were 40%–58% and 18–26 °C respectively. Common mealworms and water were supplied to the lizards twice a day.

We collected sand from the lizards' habitat. By using a set of sieves, we sifted the sand into different size groups for four trials: Trial I: 1–2 mm, Trial II: 0.5–1 mm, Trial III: 0.25–0.5 mm, and Trial IV: 0.075–0.25 mm. We also designed another experiment for lizards running through the race tracks paved with different sand grain size of 0.5–1 mm and 0.075–0.25 mm. After entire experiment, all animals were transferred to the Beijing Zoo for further rearing. The lizards were kept in captivity for 18 days before we transported them to the zoo.

We randomly chose 14 adults (6 males and 8 non-gravid females) for our experiment. Before the manipulative experiment, we measured body mass (*W*), body length (the snout-vent lengths, *L*) and tail length (from the anterior edge of the cloaca to the tip of the tail). It is controversial to use body length to evaluate the effect of body condition on locomotor ability in lizards (Van Damme and Vanhooydonck, 2001). For instance, snout-vent length and sprint speed have evolved together in Caribbean Anolis (Losos, 1990), but

not in Costa Rican Anolis (Van Berkum, 1986). We decided that body condition index,  $CI = W(g)/L(cm)$ , is a proper parameter for evaluating the effects of body mass and body length simultaneously, and this parameter has been used to express general degree of physical status of the lizard (Ballinger, 1977; Dickinson and Fa, 2000; Plummer, 1983). We categorized the variable of body condition index into three groups: Low (range of CI was 0.20–0.30), Moderate (range of CI was 0.30–0.40) and High (range of CI was 0.40–0.50). We also categorized the variable of tail length into three groups: Short (3–4 cm), Moderate (4–5 cm) and Long (5–6 cm).

### 2.2. Measurement of running speed

Each lizard was run in a 1.5 m long, 10 cm wide race track with sand of given grain size. Before the trial, we equilibrated the lizards and the race track at an outdoor temperature of around 28 °C for an hour. All animals run a minimum of six times in each trial. We allowed the animals to rest for a minimum of 10 min between runs in the same trial and a minimum of 30 min between trials. A digital video camera (Canon XM2, video frame rate of 30 frames per second) was fastened above the race track to record the running. The vertical distance from camera lens to the race track was 1.0 m. Each lizard was placed at the beginning of the race track and collected when it finished running. If necessary, we chased the lizards with a paintbrush to encourage them to run. The mean of the six runs in each trial was used as the value for average running speed for that trial.

We replayed the videos and used a digital ruler to measure on screen the pixels of distance of each running. According to the video-base method for measuring animal movement (Poole et al., 2006), we calculated the actual distance of running and running speed with the formulas below.

$$RD = \frac{AD \times PRD}{PAD}$$

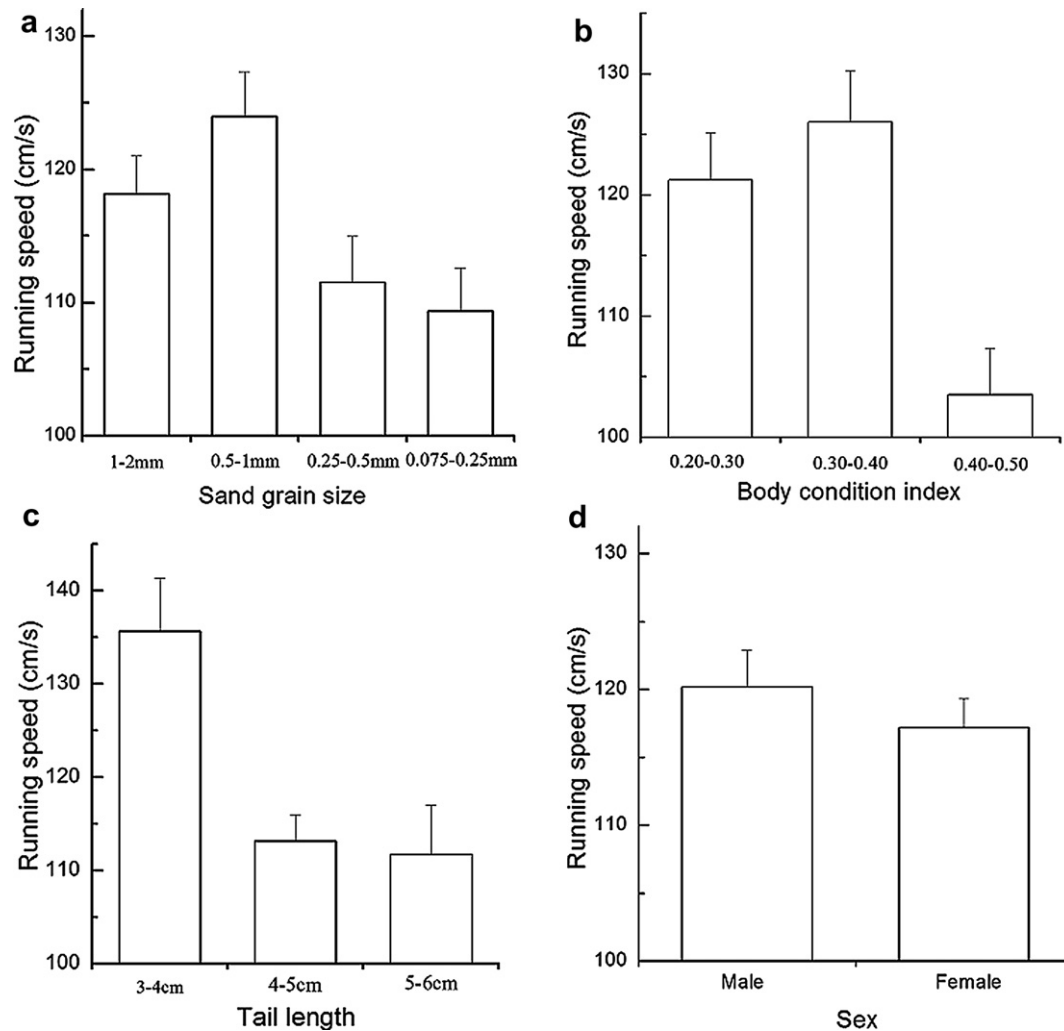
and

$$V = \frac{RD}{RT}$$

Where: *RD*: running distance, *AD*: actual distance marked on the race track, *PRD*: pixels of running distance, *PAD*: pixels of actual distance marked on the race track, *RT*: duration of each running, and *V*: running speed. The unit of running speed is cm/s.

### 2.3. Statistical analysis

Statistical analyses were conducted using SPSS-10 (SPSS, Inc. 2000). When the distribution of data accorded with the normal distribution (one sample Kolmogorov–Smirnov test,  $P > 0.05$ ), Mauchly's Test of Sphericity showed that the error covariance matrix of the orthonormalized transformed dependent variables was proportional to an identity matrix ( $P = 0.369$ ). Therefore, we used Repeated Measures of General Linear Model (GLM) to test the difference of average running speed of lizards among the trials reflecting the four sand sizes. In this statistical procedure, we also used Levene's Test to estimate the homogeneity of variances and found that those variances were equal ( $P_{\text{Trial I}} = 0.054$ ,  $P_{\text{Trial II}} = 0.337$ ,  $P_{\text{Trial III}} = 0.088$  and  $P_{\text{Trial IV}} = 0.059$ ). We also treated body condition index, tail length and sex as fixed factors to analyze their interactions in GLM analysis. To analyze the pure influence of each factor, we used a variance partitioning procedure as described by Real et al. (2003). With linear multiple regression, we obtained the total amount of variation explained by all fixed factors (sand grain



**Fig. 1.** Running speed of steppe toad-headed lizards in trials of different sand grain sizes and body measures. The peak values of the running speed were found in the group with sand grain sizes of 0.5–1 mm, in the lizards with the moderate body condition index, and in the lizards with the short tail respectively (1-a, 1-b, 1-c). There was no significant difference of running speed between two sexes (1-d).

size, body condition index, tail length and sex). Then, to specify which proportion of the variation in running speed was explained by each of these four factors exclusively, we regressed running speed on any three of the four factors simultaneously to obtain the amount of variation explained by any three factors together. Then we used subtraction to obtain the proportion of the variation explained exclusively by each factor and all interactions (see Real et al., 2003 for details). The values of the proportions were calculated and displayed as percentages (%).

Paired-samples *T* Test was used to check the changes in running speed of the lizards when they passed over different sand substrates. In this statistical procedure, we also used Levene's Test to estimate the homogeneity of variances (when  $P > 0.05$ , variances was equal, when  $P < 0.05$ , variances was unequal).  $P < 0.05$  was used as the definition of statistical significance in all tests.

### 3. Results

Running speed of the lizards differed significantly among trials of different sand grain sizes (Repeated measures of GLM,  $F = 4.974$ ,  $df = 3$ ,  $P = 0.003$ ; Appendix 1 electronic version only). Thus, we rejected our first null hypothesis. The peak value ( $124.00 \pm 3.35$  cm/s) and the nadir value ( $109.37 \pm 3.22$  cm/s) of the running speed were

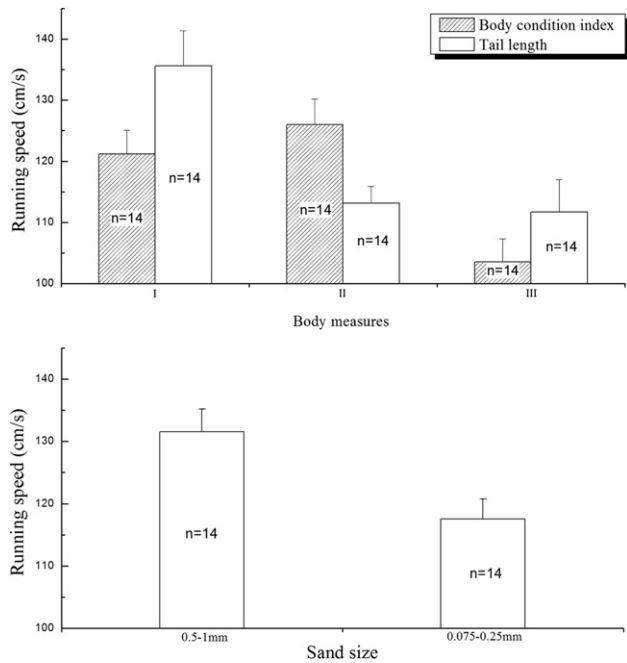
found at the groups with sand grain sizes of 0.5–1 mm and 0.075–0.25 mm respectively (Fig. 1a). The interaction effect of “sand grain size \* body condition index \* sex” was significant, whereas other interactions were not significant (see Appendix 1 for statistical parameters).

The main effects of body condition index, tail length and sex on all running speeds were listed separately in Appendix 2 electronic version only. The effects of body condition index, tail length and the interaction of “body condition index \* sex” on running speed were significant. Thus, we rejected our second null hypothesis. The peak

**Table 1**

The proportion of the variation in running speed was explained by each of those factors exclusively (Variance partitioning in linear multiple regression. sand gain size and tail length explained  $>20\%$ , whereas body condition index and sex explained  $<20\%$ , of total variations of running speed.).

Factors	Amount of variance	Proportion of the variation was explained (%)
Sand grain size	4121.14	32.56
Body condition index	1344.73	10.62
Tail length	3710.59	29.31
Sex	2274.41	17.97
All of interactions	1208.05	9.54



**Fig. 2.** Running speed of lizards on race tracks paved with sands of different grain sizes. When the lizards passed over the race tracks paved with sands of different grain sizes, their running speed changed significantly.

values of running speed ( $125.99 \pm 4.23$  cm/s and  $135.64 \pm 5.69$  cm/s) were found in the lizards with the moderate body condition index and the short tail (Fig. 1b, Fig. 1c). The sexual difference on running speed was not significant (see Appendix 2 for statistical parameters. Fig. 1d).

The variables of sand grain size and tail length explained >20% of total variations of running speed, whereas body condition index and sex explained <20% of total variation in running speed; all interaction effects explained 9.54% of the total variation (Variance partition analysis in the linear multiple regression, Table 1).

When the lizards passed over the race tracks paved with sands of different grain sizes of 0.5–1.0 mm and 0.075–0.25 mm, their running speed was decelerated significantly from  $131.53 \pm 3.69$  cm/s to  $117.54 \pm 3.20$  cm/s (Paired-samples *T* Test,  $t = 4.490$ ,  $n = 14$ ,  $P = 0.000$ . Fig. 2).

#### 4. Discussion and conclusions

In our study, maximum running speed in the lizards was found when they ran on sand of 0.5–1 mm. Moreover, when the lizards passed over the race tracks paved with sands of different grain sizes, their running speed changed significantly. Although we didn't explore the optimum sand size for the lizards to achieve their highest running speed, we demonstrated that running speed of steppe toad-headed lizards was affected by sand grain size. Similarly, previous studies in other habitat types suggest that habitat structures influence running speed of lizards (Du et al., 2005; Irschick and Losos, 1999). Steppe toad-headed lizards tended to live in moving sand dunes with low and sparse vegetations rather than stabilized sand dunes (Liu et al., 2008; Zhao, 2001). It was reported that the composition of moving sand dunes are grains with the size of 0.25–1 mm, whereas the composition of stabilized sand dunes are grains with the size of 0.001–0.05 mm (Wang et al., 2006; Zhang et al., 2004). Therefore, higher running speed could be a factor that influences steppe toad-headed lizards in selecting sand

habitat with certain grain size to live in. Indeed, many lizard species tend to select the habitat with the most useful structure or they change their behavioral strategy to respond to different habitat (Irschick and Losos, 1999; Irschick and Garland, 2001; Schulte et al., 2004; Vanhooydonck et al., 2002; Vitt et al., 1997; Zaady and Bouskila, 2002).

Running speed of steppe toad-headed lizards was also influenced by morphological traits. Based on our data, the lizards with the moderate body condition index ran faster than others. The same result of the effect of body condition index on running was found in teiid lizard species (White and Anderson, 1994). As an indicator of body condition, body mass is considered as a factor that influences locomotor ability. For example, running speed of agama (*Stellio stellio*) increased as their body mass increased (Huey and Hertz, 1982). However, running speed of the lizard *Dipsosaurus dorsalis* decreased with body mass (Johnson et al., 1993). Because of the different effects of body mass on running of lizards, body condition index could be a proper parameter when we study the relationships between locomotor ability and body mass (e.g. Dickinson and Fa, 2000; White and Anderson, 1994).

The tail is considered as an important organ affecting locomotor ability of lizards. Many classical studies suggested that the tail of lizards serves as a counterbalance during running and is genetically related to locomotor performance (Sukhanov, 1968; Tsuji et al., 1989). Experimentally-reduced tails resulted in a decrease in running speed and confined locomotor performance of lizards (Ballinger et al., 1979; Downes and Shine, 2001; Formanowicz et al., 1990). We didn't cut tails of steppe toad-headed lizards in our experiment; we didn't know what would happen when the lizards lost their tails. We only focused on the intact animals with whole tails, and found that lizards with short tails ran faster than those with long tails. Garland (1985) classified the lizard species into two categories according to their running pattern: bipedal lizards that ran with hindlimbs and quadrupedal lizards that ran with forelimbs and hindlimbs, and suggested that long tail benefits the locomotor performance of bipedal lizards, whereas the short tail benefits the quadrupedal lizards (Garland, 1985).

Indeed, the effects of tail on running speed may relate to the usage of tails for counterbalance in lizards. For instance, Punzo (1982) found that tail autotomy occurred more frequently in lizards which utilize tail-breakage as a principal means of escaping predators. Steppe toad-headed lizards are the lizards that never autotomize tails to escape predators and usually raise their tails up while running (Zhao, 2001). Together with our present study, a short tail could benefit the locomotor ability of a quadrupedal lizard that relies on running speed to escape predators (Garland, 1985).

Our data also found that there was no sexual difference of running speed in steppe toad-headed lizard.

Over all, our findings indicate that, together with morphological traits, sand grain size affected running speed of steppe toad-headed lizards. The proportion of running speed variation was most explained by sand grain size, then tail length and finally body condition. Moreover, maintaining a high running speed could be one of the factors that influence the habitat selection in steppe toad-headed lizard (our unpublished data). Van Damme and Vanhooydonck (2001) suggested that differences in sprint speed reflected phylogeny rather than ecology of lizards, which probably reflects inter-species rather than intra-species effects. Within the context of one animal species, successful survival depends on oneself and the chosen habitat. Further study is needed to answer the question if steppe toad-headed lizards could be used as an indicator of the development of sand dunes according to the lizards' tendency of habitat selection.

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## Appendix. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.jaridenv.2011.06.015.

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