

1           **For running or burying—The toe fringe of *Phrynocephalus***  
2   ***mystaceus* is important**

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4   **Abstract:** Toe fringe is the most typical morphological feature of lizards  
5   adapted to sandy environments, and toe fringe is suitable for testing the  
6   adaptive convergence suggested by form-environment correlations.  
7   *Phrynocephalus mystaceus* mainly lives in dune habitats, has a developed  
8   bilateral toe fringe, and exhibits fast sand-diving behavior for predator  
9   avoidance. We tested the effects of resecting the medial and bilateral toe  
10  fringes on the locomotor performance and sand-diving performance of *P.*  
11  *mystaceus*. The results showed that the individuals that had their medial  
12  toe fringe removed exhibited significantly faster sprint speeds than the  
13  unresected and all resected individuals ( $P < 0.05$ ). The results of stepwise  
14  regression analysis show that the relative area of the toe fringe is an  
15  important morphological feature that affects locomotor performance. The  
16  sand-burial performance scores of the unresected individuals were  
17  significantly greater than those of the resected individuals ( $P < 0.05$ ). The  
18  results of stepwise regression analysis show that the relative area of toe  
19  fringe and the axilla-groin length are the main morphological features that  
20  affect the sand-diving performance of *P. mystaceus*. After the bilateral toe  
21  fringe was removed, a significant negative correlation between locomotor  
22  and sand-diving performance was observed ( $P < 0.05$ ). Taken together,

23 these results provide experimental evidence that toe fringe is positively  
24 associated with the locomotor and sand-diving performance of *P.*  
25 *mystaceus*.

26 **Key words:** Toe fringe; *Phrynocephalus mystaceus*; sprint performance;  
27 sand diving

28 Locomotion is a fundamental component of prey capture (Higham,  
29 2007). An animal's escape behavior should reflect both the cost of  
30 interrupting current activities to respond to predators and the relative risk  
31 of predation (Ydenberg and Dill, 1986; Cooper and Frederick, 2007).  
32 Some lizards escape predators by rapidly burying themselves in sand  
33 (Darwin 1962; Arnold 1995; Attum et al., 2007; Kacoliris et al., 2010).  
34 Morphological differences can explain the diversity of behavior in many  
35 species (Arnold, 1983). Similar morphological characteristics for  
36 adaptation to the desert environment have evolved in different groups of  
37 desert lizards. One of the most common morphological characteristics  
38 that has evolved is toe fringe. “Lizard toe fringes are composed of  
39 laterally projecting elongated scales and have arisen independently at  
40 least 26 times in seven families of lizards”(Luke, 1986). According to the  
41 report, lizards with toe fringe run faster than those without toe fringe on  
42 sand surfaces; nevertheless, lizards with toe fringe exhibit slow speeds on  
43 rubber surfaces compared with individuals without fringe (Carothers,  
44 1986). Except for locomotion abilities, toe fringe can also explain

45 sand-diving, a behavior used for submersion into granular substrates  
46 (Stebbins, 1944). However, it is not clear exactly what role fringe plays in  
47 the locomotor behavior of lizards. *Uma scoparia* have well-developed  
48 fringes, which are thought to improve sprinting performance over fine  
49 sand (Irschick and Jayne, 1998; Korff and McHenry, 2011). Studies have  
50 shown that the locomotor performance of lizards on sand significantly  
51 decreased after the fringes were removed. In particular, the locomotor  
52 performance of lizards was significantly decreased on the uphill sloped  
53 surfaces (Carothers, 1986). Other studies have compared *Uma scoparia*,  
54 which has fringe, to *Callisaurus draconoides*, which does not have fringe.  
55 These studies found no significant differences in the sprint speeds on the  
56 different substrates (Bergmann and Irschick, 2010; Korff and McHenry,  
57 2011; Li et al., 2012). On the other hand, with the decrease in substrate  
58 resistance, the performance of *C. draconoides* did not decrease  
59 significantly, but that of *U. scoparia* did (Qian et al., 2015). These studies  
60 indicate that fringes may perform a variety of functions.  
61 For instance, *U. scoparia* uses its fringe for fast sand-diving behavior to  
62 escape predators and extreme heat (Arnold, 1995; Attum et al, 2007).  
63 In addition, *C. draconoides* and *U. scoparia* belong to different genera  
64 and show great differences in the relative limb proportions and potential  
65 behavioral, ecological, and physiological aspects. This uncontrolled  
66 variation complicates the examination of interspecific performance

67 (Carothers, 1986).

68 *Phrynocephalus mystaceus* is the largest species of *Phrynocephalus*,  
69 which is a genus of toad-headed agama lizards (Zhao et al., 1999;  
70 Solovyeva et al., 2018). This species is also a typical desert lizard species  
71 from central Asia to northwest China, and it mainly lives in dune habitats  
72 and has a well-developed bilateral triangle toe fringe (Luke, 1986). *P.*  
73 *mystaceus* can run quickly over fine sand substrates and exhibits fast  
74 sand-diving behavior when avoiding predators (Arnold, 1995). There is a  
75 lack of research on the morphology and locomotor performance of *P.*  
76 *mystaceus*. This species is listed as endangered on the Red List of China's  
77 Vertebrates (Jiang, 2016). Therefore, studying the locomotor behavior of  
78 this species may help us better protect *P. mystaceus*. While there have  
79 been reports of studies that have removed the toe fringes of sand-dwelling  
80 lizards to test locomotor performance (Carothers, 1986), there are few  
81 reports of studies that have removed the toe fringes of sand-dwelling  
82 lizards to test their sand-diving performance. In this study, we measured  
83 several morphological traits and analyzed the locomotor and sand-diving  
84 performance of *P. mystaceus* on sand substrates. In particular, we adopted  
85 a control test that consisted of removing the toe fringes to verify the  
86 following scientific hypotheses: (1) The presence or absence of toe  
87 fringes on *P. mystaceus* will affect its locomotor performance over sand  
88 substrates. (2) The presence or absence of toe fringes on *P. mystaceus*

89 will affect its sand-diving performance on sand substrates. (3) The toe  
90 fringes of *P. mystaceus* influence the locomotion and sand-diving  
91 performance, and there is a trade-off between the two performances.

## 92 **Materials and methods**

93 In July 2018, we collected *P. mystaceus* individuals by hand from the  
94 Tukai Desert, Huocheng County, Yili Region, Xinjiang. The selected  
95 individuals in good condition were taken back to the Zoology Laboratory  
96 of Xinjiang Agricultural University. We measured the snout-vent length  
97 ( $X_1$ : SVL), head length ( $X_2$ : HL), head width ( $X_3$ : HW), head depth ( $X_4$ :  
98 HD), mouth breadth ( $X_5$ : MB), axilla-groin length ( $X_6$ : AG), abdominal  
99 width ( $X_7$ : AW), tail base width ( $X_8$ : TBW), fore limb length ( $X_9$ : FLL),  
100 hind limb length ( $X_{10}$ : HLL) and tail length ( $X_{11}$ : TL) (Zhao, 1999). All  
101 measurements were accurate to within 0.1 mm. The toe fringes of the  
102 lizards were quantified according to the following characteristic traits:  
103 individuals' total fringe number divided by snout-vent length ( $X_{12}$ :TFN),  
104 individuals' total fringe max length divided by snout-vent length  
105 ( $X_{13}$ :TFL), and individuals' total fringe area divided by snout-vent length  
106 ( $X_{14}$ :TFA). We measured the toe fringe characteristics with a Canon  
107 digital camera and then analyzed data with image-pro Premier 6.0  
108 software. *P. mystaceus* individuals were kept in tanks for lizards. The  
109 tanks were covered with 5 cm of fine sand collected from the original  
110 habitat of *P. mystaceus*, with a 60-w bulb suspended at one end as a heat

111 source for thermoregulation. Plenty of *Tenebrio molitor* larvae and water  
112 supplemented with calcium and vitamins were provided to ensure that the  
113 animal received a full complement of nutrients. The animals were kept  
114 temporarily for 1 week before beginning the exercise test, and all tests  
115 were completed within 2 weeks. All animals were released to the original  
116 capture site after the test.

117 Locomotion performance was measured on a 1.4 m horizontal track,  
118 and the racetrack was covered with sand substrate from the original  
119 habitat. Before testing the locomotion performance, we conducted a  
120 preliminary test to determine the optimal temperature for the activity of *P.*  
121 *mystaceus*. A temperature gradient was designed from 0 °C to 50 °C, and it  
122 was found that the optimal temperature for the activities of the great  
123 oared lizard was approximately 34 °C; thus, before the locomotion  
124 performance test, all individuals were preconditioned for 1 h at  
125 (34.0±0.5) °C. Then, we moved the animal into the end of the track, and a  
126 brush was used to push it to sprint. A digital camera was used to record  
127 the lizard's movements on the track. Through video playback, the 1.4 m  
128 track was divided into seven segments. In addition, the frames of each  
129 segment were counted, the motion time in the video was analyzed by  
130 Adobe premiere CS6 software, and the motion velocity was calculated  
131 (Higham et al., 2010). The speed was graded by using an arithmetic  
132 sequence (to be divided by ten classes). The entire exercise test was

133 divided into three repeats: no cut fringes, single cut (removal of the  
134 medial fringes) and double cut (removal of bilateral fringes).

135 The sand-diving performance was measured in a tank covered with 10  
136 cm of fine sand from the original habitat. We used a brush to stimulate the  
137 tail, which caused the individuals to dive into the sand. The entire process  
138 was recorded with a digital camera, and sand-diving behavior was  
139 recorded through video playback. The whole sand-burying behavior was  
140 also divided into three repetitions: no cut fringes, single cut (removal of  
141 the medial fringes) and double cut (removal of bilateral fringes). The  
142 sand-burying time was graded by an arithmetic sequence.

143 The scores of sand-burying behavior were as follows: sand-burying  
144 ability score, sand-burying time score and comprehensive score. Among  
145 them, the sand-burying ability score was based on the sand-burying state  
146 of *P. mystaceus*: fully buried: 5 points, tail not buried: 4 points, head not  
147 buried: 3 points, most of the body not buried: 2 points, not buried in the  
148 sand: 1 point. The sand-burying time score was used to sort the burying  
149 time from small to large according to the arithmetic sequence and was  
150 divided into 5 grades, with the shortest burial time assigned a value of 5  
151 points, and the points were successively divided into 4 points, 3 points, 2  
152 points and 1 point according to the sorting method of the arithmetic  
153 sequence. Then, the comprehensive score was the sum of the two score  
154 types. Individuals with the best and fastest burial performance had the

155 highest the overall scores.

## 156 **Statistical analyses**

157 The data were tested by Kolmogorov–Smirnov tests for detecting  
158 normality. We log-transformed the variables to minimize the  
159 heterogeneity, where necessary (King, 2000). We used analysis of  
160 covariance (ANCOVA) to examine the differences in locomotion  
161 performance and sand-diving performance of the different states on the  
162 sand substrates with paired sample t tests (multiple comparisons). We  
163 used stepwise regression analysis to screen the morphological  
164 characteristics that could be used to determine the movement ability over  
165 sand substrate and the morphological characteristics that could be used to  
166 determine the buried sand score for sand-diving behavior. We used  
167 Fisher’s exact test to examine the differences in the probability of sand  
168 diving under different states. Spearman correlation was used to analyze  
169 the correlation between the velocity score and the comprehensive score.  
170 All analyses were conducted using R v. 3.5.1 (R Core Team, 2017).

## 171 **Results**

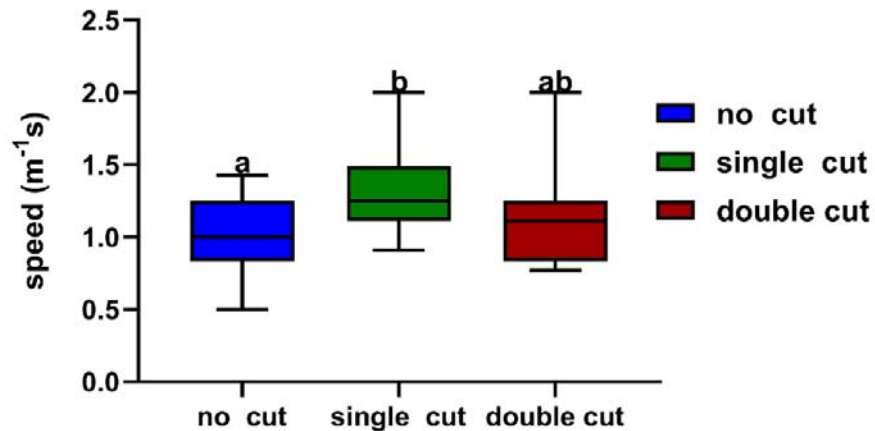
### 172 **Locomotion performance**

173 In the running trials, there were significant differences in the  
174 maximum sprint speeds on the sand substrate under the different  
175 conditions (repeated measures ANOVA,  $F_{2,8}=4.524$ ,  $P=0.02$ ). In addition,  
176 the results of multiple comparisons (the paired sample t test) showed that



177 the maximum sprint speed after removing the medial fringes was  
178 significantly higher than that before removing the medial fringes ( $P < 0.05$ ,  
179 Fig. 1). In addition, there were no significant differences in the sprint  
180 speeds under the other states ( $P > 0.05$ , Fig. 1).  
181 Multiple stepwise regression analysis showed that under the no cut state,  
182 TFA ( $X_{14}$ ) was the major determinant of locomotion performance. Under  
183 the single cut state, TFN ( $X_{12}$ ) and TFA ( $X_{14}$ ) were the  
184 major determinants of locomotion performance. However, under the  
185 double cut state, AG ( $X_6$ ) and TBW ( $X_8$ ) were the  
186 major determinants of locomotion performance (Table 1).

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**Fig. 1** The maximum sprint speed over sand substrate of *Phrynocephalus mystaceus* under different states

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Note: Different letters indicate significant differences at the  $P < 0.05$  level

192

**Table 1** Stepwise regression analysis results of the morphological traits affecting the maximum sprint speed

193

under different states

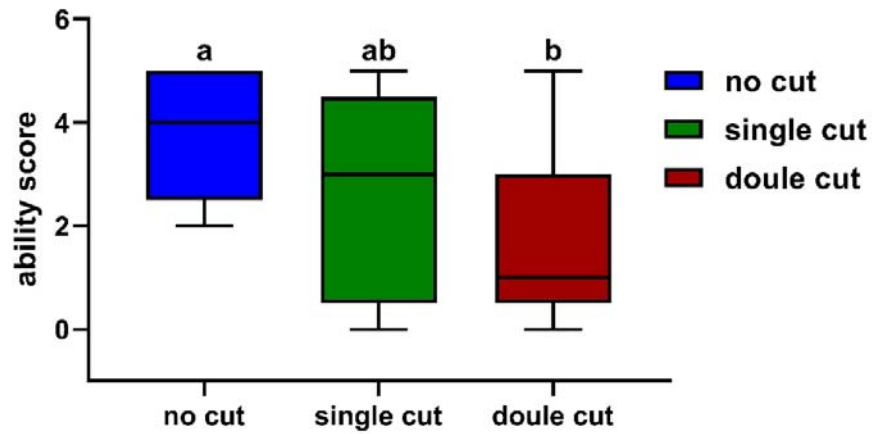
States type	Morphological	Regression	Adjusted $R^2$	$T$	$P$	Optimal regression equation
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	traits	coefficient				
No cut	TFA ( $X_{14}$ )	0.399	0.140	2.854	0.007	$Y=0.88X_{14}-0.566$
Single cut	TFN ( $X_{12}$ )	-0.777	0.220	-3.424	0.002	$Y=-0.53X_{12}+0.215X_{14}$
	TFA ( $X_{14}$ )	0.532		2.344	0.025	
Double cut	AG ( $X_6$ )	-1.629	0.217	-3.086	0.004	$Y=-3.92X_6+3.049X_8-1.353$
	TBW ( $X_8$ )	1.313		2.488	0.017	

194

### 195 **Sand-diving performance**

196 The results of the univariate repeated measures ANOVA by sphericity  
197 test show that under different states, there were no significant differences  
198 in the sand-burying ability scores on the sand substrate (repeated  
199 measures ANOVA,  $F_{2, 8}=2.057$ ,  $P=0.171$ ). However, the sand-burying  
200 ability scores after removing bilateral fringes were significantly lower  
201 than those before cutting ( $P<0.05$ , Fig. 2). In addition, there were no  
202 significant differences in the sand-burying ability scores under the other  
203 states ( $P>0.05$ , Fig. 2). There were no significant differences in the  
204 sand-burying time scores on the sand substrate (repeated measures  
205 ANOVA,  $F_{2, 8}=3.019$ ,  $P=0.077$ ). However, the sand-burying time scores  
206 after removing bilateral fringes were significantly lower than those before  
207 cutting ( $P<0.05$ , Fig. 3). In addition, there were no significant differences  
208 in the sand-burying time scores under the other states ( $P>0.05$ , Fig. 3). In  
209 terms of the probability of sand diving, there were no significant  
210 differences under the different states ( $P>0.05$ , Table 2).



211

212

**Fig. 2 Ability scores for sand diving by *Phrynocephalus mystaceus* under different states**

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**Note: Different letters indicate significant differences at the  $P < 0.05$  level**

214

**Table 2 Descriptive statistics of the ability score frequencies for sand diving by *Phrynocephalus mystaceus***

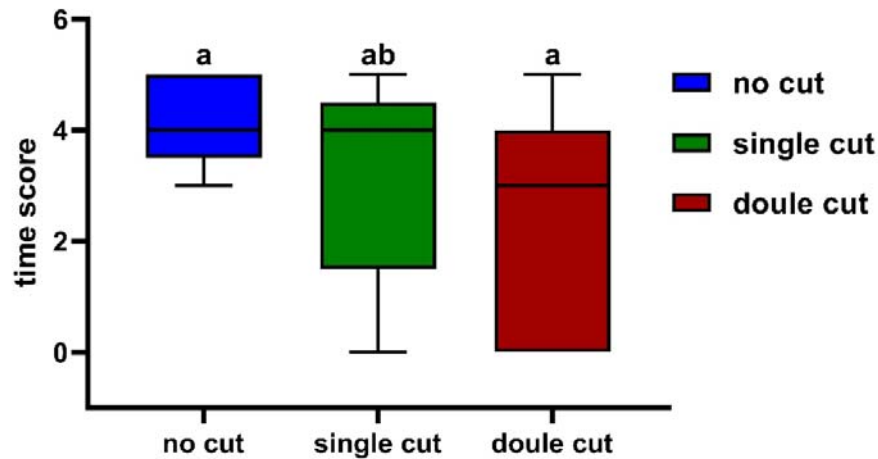
215

**under different states**

States	Sand diving (Total)	No sand diving (Total)	Grouping	$X^2$	$P$
No cut	9 (9)	0 (9)	No cut vs Single cut	2.25	0.235
Proportion	100	0			
Single cut	7 (9)	2 (9)	No cut vs Double cut	2.25	0.235
Proportion	77.8	22.2			
Double cut	7 (9)	2 (9)	Single cut vs Double cut	0	0.712
Proportion	77.8	22.2			

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219 **Fig. 3 Time scores for sand diving of *Phrynocephalus mystaceus* under different states**

220 **Note: Different letters indicate significant differences at the  $P < 0.05$  level**

221 In terms of the score type, TFA ( $X_{14}$ ) was the major determinant of the  
 222 sand-burying ability score, and AW ( $X_7$ ) was the major determinant of the  
 223 sand-burying ability time. In terms of the type of composite score, AG ( $X_6$ )  
 224 and TFA ( $X_{14}$ ) were the key factors (Table 3).

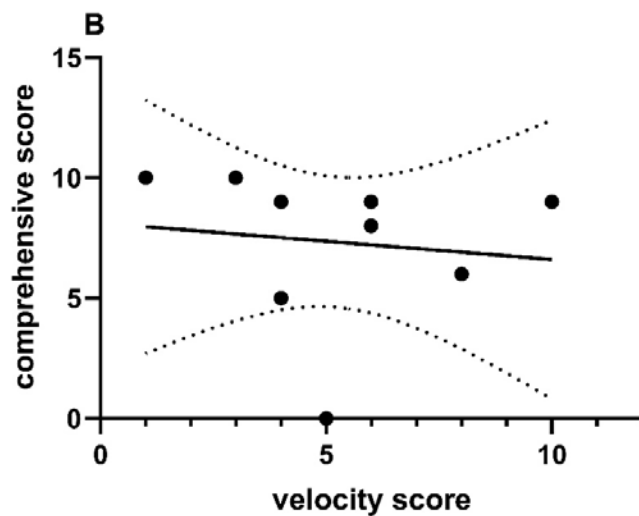
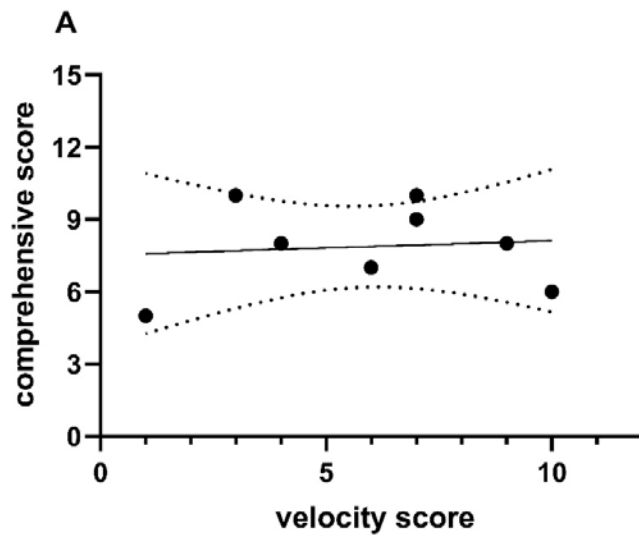
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226 **Table 3 Stepwise regression analysis results of the morphological traits affecting the different score types**

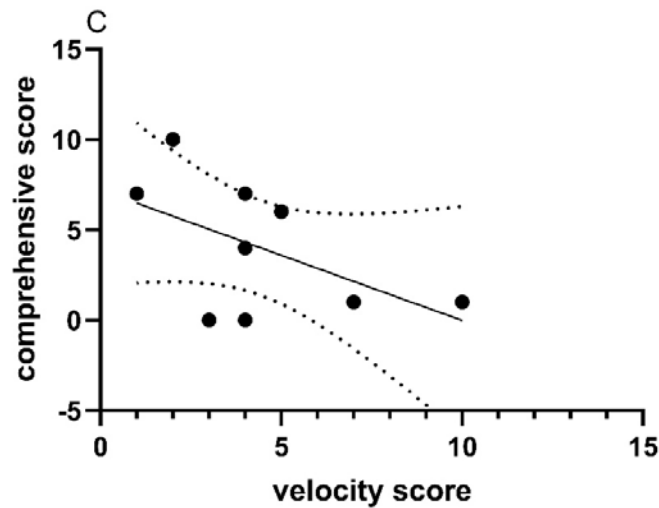
Score types	Morphological traits	Regression coefficient	Adjusted $R^2$	$T$	$P$	Optimal regression equation
Ability	TFA ( $X_{14}$ )	0.534	0.251	2.892	0.009	$Y=0.441X_{14}+2.183$
Time	AW ( $X_7$ )	-0.425	0.141	-2.150	0.043	$Y=-0.189X_7+4.677$
Comprehensive	AG ( $X_6$ )	0.623	0.387	3.602	0.002	$Y=-0.675X_6+0.885X_{14}+6.949$
	TFA ( $X_{14}$ )	-0.447		-2.581	0.018	

227 In the case of no cutting, no significant correlations were observed  
 228 between the velocity score and the comprehensive score ( $r^2=0.03$ ,  
 229  $P=0.943$ , Fig. 4A). After removing the medial fringes, there was a

230 negative correlation between the velocity score and the comprehensive  
231 score, but the correlation was not significant ( $r^2=-0.509$ ,  $P=0.197$ , Fig.  
232 4B). However, in the case of double cutting, there was a significant  
233 negative correlation between the velocity score and the comprehensive  
234 score ( $r^2=-0.853$ ,  $P=0.015$ , Fig. 4C).



236



237

238 Fig. 4 The correlation between the speed score and the comprehensive **sand-diving** score for *Phrynocephalus*  
239 *mystaceus* under three states

240 Note: A no cut ; B: single cut ; C: double cut. curve indicate means with 95% confidence intervals

## 241 Discussion

242 The morphological characteristics of animals have evolved through  
243 natural selection to maximize sprint speed (Irschick and Garland, 2001;  
244 Van Damme and Vanhooydonck, 2001). For example, the sprint speed of  
245 a lizard is related to body mass and tail size (Ballinger et al., 1979;  
246 Downes & Shine, 2001; Du et al., 2005; Johnson et al., 1993; Punzo,  
247 1982). Hind limb length and toe length are also thought to be  
248 indispensable factors for a lizard's sprint speed (Borges-Landáez and  
249 Shine, 2003; Vanhooydonck et al., 2002). Natural selection acts on  
250 individual variations in locomotor performance in a given environment,  
251 thereby altering the trajectory of evolution in the variety of underlying  
252 traits governing locomotion (Arnold, 1983; Darwin, 1859; Losos, 2010;

253 Ricklefs & Miles, 1994). In some cases, novel morphological structures  
254 have evolved that increase the performance of ecologically relevant tasks  
255 (Dornburg et al., 2011; Vermeij, 2006). For example, *R. afer* deploys  
256 adhesive toe pads to increase its speed on a level surface (Collins and  
257 Higham, 2017). Our results reveal that when *P. mystaceus* is in the no cut  
258 or single cut state, the locomotor performance of *P. mystaceus* is related  
259 to TFA and TFN (Table 1). In particular, the locomotor performance of  
260 lizards on sand significantly increased after the medial fringes had been  
261 removed (Fig. 1). However, the locomotor performance of lizards on sand  
262 showed a downward trend after the bilateral fringes had been removed  
263 (Fig. 1). In addition, the locomotor performance of lizards on the sand did  
264 not significantly differ between the no cut and double cut states (Fig. 1).  
265 Further explanation is needed for why the outside fringes are one of the  
266 main factors that affect the locomotor performance of *P. mystaceus*.

267 Fringes are often thought to be an adaptation of lizards to allow for  
268 sand diving. In *Uma* species, the fringes affect not only the movement of  
269 the sand but also the sand-diving ability (Stebbins, 1944). Sand-diving  
270 behavior is not only an antipredation behavior (Evans et al., 2017) but  
271 also an adaptive behavior that is used to avoid environments that cause  
272 water loss and overheating (Halloy et al., 1998; Arnold, 1995). Our  
273 results show that under the condition in which sand diving was likely to  
274 occur, there were no significant differences under the different states

275 (Table 2). The sand-diving performance when no fringes were cut was  
276 significantly higher than when the bilateral fringes had been removed.  
277 However, the performance of *P. mystaceus* under the single cut condition  
278 was in the intermediate state. This finding further proves that the fringes  
279 significantly affected the sand-diving performance. In terms of fringe  
280 characteristics, the relative TFA was selected by the regression model of  
281 the sand-diving ability score and the comprehensive score for *P.*  
282 *mystaceus*, and these scores were significantly positively correlated  
283 (Table 3). This result demonstrates that TFA promotes the sand-diving  
284 performance of *P. mystaceus* in terms both scoring types. This is the first  
285 time that a control test has been used to confirm that fringes affect  
286 sand-diving performance. In addition, there was a significant negative  
287 correlation between the sand-diving time score and AW, showing that  
288 individuals with larger AW tend to spend more time burying into sand. In  
289 some cases, *Phrynosoma* rarely use sprinting as an antipredation strategy,  
290 but static antipredation mechanisms such as shape (flat body) and color  
291 (body color changes with background color) changes are  
292 employed(Stankowich et al., 2016).

293 At this point, sprint speed is not the deciding factor. The flat body shape  
294 of *Phrynocephalus* species is an important antipredation adaptation  
295 characteristic, and it is beneficial the hiding ability of the species.  
296 However, a larger AW can affect the sprint speed, which may be the result



297 of a trade-off between hiding and escape strategies (zheng et al., 2019).  
298 The results of our study on *P. mystaceus* suggest that AW has a negative  
299 effect on sand-diving performance and may reflect a trade-off between  
300 concealment and sand-diving strategies.

301 When multiple phenotypic traits perform multiple functions, phenomena  
302 such as functional redundancy, tradeoffs, and promotion are ubiquitous  
303 (Edwards et al., 2016; Bergmann et al. 2017). Sand diving is a  
304 comprehensive antipredation behavior that is related to the escape  
305 distance of *P. mystaceus* (Evans, 2017). When confronted with danger in  
306 the wild, the lizards that exhibit sand-burying behavior tend to prefer  
307 smooth surfaces and soft sand, which may be because it saves energy  
308 (Arnold, 1990). However, the antipredator behavior of running is much  
309 simpler than sand diving (Arnold, 1990). The trade-off between running  
310 and sand diving may be related to the predation pressure. The  
311 antipredation strategy is related to the fringe state. When the fringes were  
312 not resected, the correlation between the comprehensive score and the  
313 velocity score was not obvious. The decision to run or bury in the sand in  
314 the face of danger may be related to the flight distance and habitat of *P.*  
315 *mystaceus*. On smooth, soft sand, lizards might be more inclined to bury  
316 in the sand. Conversely, the lizards might be inclined to run under  
317 different conditions (Evans, 2017). However, after the bilateral fringes  
318 were removed, there was a significant negative correlation between

319 running and sand diving, and the sand-diving performance of *P.*  
320 *mystaceus* decreased significantly compared with the locomotor  
321 performance. Our results indicate that after removal of the bilateral  
322 fringes, *P. mystaceus* preferred to run rather than dive into the sand. It is  
323 suggested that the toe fringes of *P. mystaceus* may be important for  
324 sand-burying behavior.

325 Wind-blown debris is the nutritional basis of sand slipface  
326 communities (Robinson and Barrows, 2013). Male *P. mystaceus*  
327 individuals spend considerable time looking around and sunbathing at the  
328 top of sand dunes (personal observation) to defend the field by showing  
329 threats and fighting to chase away intruders. In the face of threats from  
330 natural enemies, *P. mystaceus* can choose to run or bury themselves in the  
331 sand to avoid the enemy. Studies have shown that sand-burying behavior  
332 can reduce the risk associated with the occupation of exposed areas  
333 (Attum et al., 2007; Stelatelli et al, 2015). Therefore, the effect of fringes  
334 on the sand-diving performance of *P. mystaceus* has adaptive value. The  
335 repeated evolution of fringes among different groups of lizards and their  
336 relationship to specific environments (Luke, 1986; Halloy et al., 1998;  
337 Irschick and Jayne, 1998; Korff and McHenry, 2011) strongly support  
338 adaptive explanations involving movement (and burying) in sandy  
339 environments. In addition, toe fringe has been derived in the *Uma* genus  
340 (Etheridge and de Queiroz, 1986), which is probably due to adaptations to

341 sand-bearing environments (Carothers, 1986). Molecular phylogenetic  
342 studies based on mitochondrial gene fragments have shown that *P.*  
343 *mystaceus* belongs to the primitive group in *Phrynocephalus* (Pang et al.,  
344 2003; Guo and Wang, 2007). Sand-diving behavior may be a primitive  
345 feature. Other *Phrynocephalus* species (with less developed fringes) can  
346 show sand-burying behaviors, but they have difficulty completing the  
347 task (Arnold, 1995). However, recent studies based on nuclear genes  
348 (nuDNA) suggest that the location of the base position of *P. mystaceus* is  
349 the result of interspecific hybridization and ancient mitochondrial gene  
350 infiltration. The common ancestor of *Phrynocephalus* probably preferred  
351 sandy substrates with the inclusion of clay or gravel. Climate change in  
352 the middle Miocene led to the migration of *Phrynocephalus* lizards into  
353 the desert, specifically the diffusion and adaptive evolution of large  
354 wind-blown dune habitats (Solovyeva et al., 2018). If this is the case, then  
355 the fringes of the *Phrynocephalus*, similar to those of *Uma*, are also the  
356 result of convergent evolution to adapt to the sand environment.

### 357 **Conclusion**

358 The fringes of *P. mystaceus* play a significant role in its antipredation  
359 behavior in terms of maximum sprint speed. The presence of lateral  
360 fringes is more conducive to running in *P. mystaceus*. However, the  
361 species exhibits better sand-diving performance under the bilateral fringe  
362 state. Moreover, TFA can promote the burying performance of *P.*

363 *mystaceus*. The fringes also play an important role in the selection of  
364 antipredation strategies. In the three fringe states, the predator avoidance  
365 strategy of *P. mystaceus* gradually shifted from sand diving to locomotor.  
366 It also shows that the fringes play a great role in sand-burying behavior.

### 367 **Animal Ethics**

368 The following information was supplied relating to ethical approvals  
369 (i.e., approving body and any reference numbers): Specimens were  
370 collected following Guidelines for Use of Live Amphibians and Reptiles  
371 in Field Research (the Herpetological Animal Care and Use Committee  
372 (HACC) of the American Society of Ichthyologists and Herpetologists,  
373 2004). This study was conducted in compliance with current laws on  
374 animal welfare and research in China and the regulations set by the  
375 Xinjiang Agricultural University. After the research was completed, the  
376 lizards were released where they were captured.

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### 383 **Competing interests**

384 The authors declare no competing or financial interests.

385 **Author contributions**

386 Conceptualization: P.Z., T.L., S.L. Methodology: P.Z., T.L., S.L. Formal  
387 analysis: P.Z. Investigation: P.Z., T.L., J.A., S.L. Writing - original draft:  
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