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# 生态学报 (SHENTAI XUEBAO)

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**封面图说:** 在树上嬉戏的大熊猫——大熊猫是中国的国宝, 自然分布狭窄, 数量极少, 世界上仅分布在中国的四川、陕西、甘肃三省的部分地区, 属第四纪冰川孑遗物种, 异常珍贵。被列为中国国家一级重点保护野生动物名录, 濒危野生动植物种国际贸易公约绝对保护的 CITES 附录一物种名录。瞧, 够得上“功夫熊猫”吧。

彩图提供: 陈建伟教授 国家林业局 E-mail: cites.chenjw@163.com

林植华,樊晓丽,雷焕宗,马小梅,赵丽华,马小浩. 不同基质对北草蜥和中国石龙子运动表现的影响. 生态学报, 2011, 31(18): 5316-5322.  
Lin Z H, Fan X L, Lei H Z, Ma X M, Zhao L H, Ma X H. The effects of substrates on locomotor performance of two sympatric lizards, *Takydromus septentrionalis* and *Plestiodon chinensis*. *Acta Ecologica Sinica*, 2011, 31(18): 5316-5322.

## 不同基质对北草蜥和中国石龙子运动表现的影响

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**摘要:** 动物在野外生境中的活动能力通常会受到许多方面(例如, 运动基质表面粗糙程度、遭遇障碍物的大小与形状)的影响。在特定体温(30 °C)条件下, 测量主要分布区重叠的两蜥蜴种类(北草蜥和中国石龙子)在四种不同基质表面(塑料草坪; 表面粗糙不透底的塑料地毯; 光滑具透底网格的塑料地毯和表面光滑的塑料地毯)的运动表现, 以及两者的攀附能力和最大游泳耐力。基质类型显著影响两种蜥蜴的运动表现。两种蜥蜴在粗糙表面运动时的疾跑速明显大于光滑表面(例如, 塑料草坪上北草蜥为15.7 SVL/s, 中国石龙子为8.1 SVL/s; 光滑塑料地毯上则分别为11.4 SVL/s 和3.5 SVL/s)。中国石龙子在光滑塑料地毯上具有最大的持续运动距离(10.6 SVL)和最少的停顿次数(1.9次)。北草蜥在光滑塑料地毯上具有最多的停顿次数(4.6次)。两种蜥蜴运动能力的种间差异显著。北草蜥具有较大的相对疾跑速度(北草蜥和中国石龙子; 13.5 SVL/s vs 5.8 SVL/s)和攀附能力(143.8 ° vs 101.2 °), 但较小的游泳耐力(83.5 s vs 238.5 s)。运动速度与耐力之间存在种间权衡关系而与攀爬能力无进化冲突的结论。

**关键词:** 北草蜥; 中国石龙子; 疾跑速; 攀附力; 耐力; 进化权衡

### The effects of substrates on locomotor performance of two sympatric lizards, *Takydromus septentrionalis* and *Plestiodon chinensis*

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**Abstract:** Terrestrial animals' locomotor performance can be affected by many factors (e. g., substrate size, shape and surface texture) in a structurally complex environment. In this study, we established a gradient of substrate roughness using four different substrates (artificial plastic lawn, and plastic carpet mat with rough surface, with 5 mm width of mesh, and with smooth surface) to assess their effects on locomotor performance of two sympatric species of lizards (northern grass lizard *Takydromus septentrionalis* and Chinese skink *Plestiodon chinensis*). Both lizard species are active foragers. *T. septentrionalis* primarily uses shrub and grass habitats in the hilly countryside, whereas *P. chinensis* usually uses relatively open habitats near farmlands. Locomotor performance were recorded using a digital video camera (Panasonic NV-MX3), and three locomotor variables (sprint speed in the fastest 250 mm interval, the maximal distance traveled without stopping and number of stops in the trial) were analyzed with MGI Video Wave III software. *T. septentrionalis* had smaller body size (snout-vent length, SVL, and body mass, BM), but relatively a longer tail and limbs than *P. chinensis*. In order to correct for the body size difference between the two species, relative values of sprint speed and the maximal distance (dividing each value of the variable by the SVL of the corresponding lizard) were used in statistical analyses. Cling capacity and locomotor stamina were evaluated by measuring the maximum slopes of oblique wood racetrack and the duration of exhaustive

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swimming inside a bath, respectively. All trials were conducted in a constant room temperature of 30 °C, which is within the optimal range of temperature for both species' locomotor performance. Nearly all the examined locomotor variables (except for the relative maximal distance in *T. septentrionalis*) were significantly affected by the substrate types in both species ( $P<0.05$ ). Sprint speed was reduced with decreasing degrees of substrate surface roughness. For example, mean sprint speed for *T. septentrionalis* and *P. chinensis* was 15.7 SVL/s and 8.1 SVL/s on the plastic lawn, but 11.4 SVL/s and 3.5 SVL/s on the plastic carpet with a smooth surface, respectively. On the plastic carpet with a smooth surface, *P. chinensis* had longer maximal distance (10.6 SVL) and fewer stops (1.9 times), but *T. septentrionalis* paused more frequently (4.6 times). Locomotor capacity (e.g., speed, stamina, and cling capacity) was significantly different between the two species. Relative sprint speed on the four different substrates was greater in *T. septentrionalis* than that in *P. chinensis* (13.5 SVL/s vs. 5.8 SVL/s). Sprinting capacity in lizards may associate with their morphological characteristics (e.g., body size, limb length). Fast-running lizard species usually have a longer limb. *T. septentrionalis* had greater relative limb length and sprint speed than *P. chinensis*, which was consistent with previous studies. Moreover, *T. septentrionalis* possessed substantially higher cling capacity, but less locomotor stamina than *P. chinensis*. Our results suggest that an evolutionary trade-off may exist between the sprinting capacity and stamina, but not between the capacity to run on a level surface and the ability to climb on the oblique surface in lizards.

**Key Words:** *Takydromus septentrionalis*; *Plestiodon chinensis*; sprint speed; cling capacity; stamina; evolutionary trade-off

不同物种、种群或者同一种群不同个体之间的形态变异与其生境利用、功能表现差异的如何相关联是生态学上的一个核心问题,围绕该问题开展研究的分支学科称之为生态形态学。原先此类工作主要依据“生境-形态-功能-适合度”的研究范例进行<sup>[1-2]</sup>,认为自然选择作用下的某一形态特征只能单独地服务于特定功能。然而,近些年一些研究显示动物某一功能特征的变化往往会引起其它功能的变化<sup>[3-7]</sup>,这些结果说明多数情况下动物的许多形态特征对功能的作用是多方向的,某一形态特征的改变可能会影响所有的功能特征。当两个或多个功能特征在同一个机体构造需求上发生冲突时,进化上的权衡作用会导致产生折中的表型<sup>[7-8]</sup>。运动表现是生态形态学研究中利用最为频繁的一个功能变量<sup>[9]</sup>。动物的某个结构能影响其运动表现的多个方面,例如,附肢的量度及肌肉组成决定蜥蜴的最大疾跑速、耐力、灵活性等<sup>[3, 6, 10-11]</sup>。当蜥蜴附肢的结构不能兼顾各运动变量的最大化时,这些变量之间则应显示为权衡关系。种间及种内水平上的比较研究多数已证实了这种权衡关系,例如不同蜥蜴种类的运动速度与稳固性、附着能力、耐力、灵活性<sup>[3, 5-7, 10, 12]</sup>等均显示为负相关关系。然而,这种关系在不同动物类群中可能并不一致。例如,疾跑速与攀爬能力之间的权衡关系在不同安乐蜥种类中显著<sup>[4-5]</sup>,但在不同蜥蜴科种类中并不明显<sup>[11]</sup>。

蜥蜴类群在过去20多年间被作为生态形态学的理想模型动物开展了多方面的研究,该类群动物的文献资料亦最为丰富<sup>[7, 9, 13]</sup>,然而,这些工作中有关运动表现数据的获取主要通过实验室平坦跑道上的测量来实现。事实上,动物野外生活的自然环境通常多样化的,它们在运动过程中遭遇复杂的环境变化时应具有相应的处理能力。例如,马拉奇特绿针蜥(*Sceloporus malachiticus*)在翻越垂直障碍物时会抬高躯干和头部,前后肢分别起到牵拉和推动躯干向前上方移动的作用,躯干重心的抬升高度和后肢支撑系数随障碍物高度的增加而增加<sup>[14]</sup>。

我国蜥蜴物种多样性丰富,吸引了国内许多学者的研究兴趣,但目前涉及生态形态学的研究数据仍极少<sup>[15]</sup>。北草蜥(*Takydromus septentrionalis*)和中国石龙子(*Plestiodon chinensis*)是我国华东及华南许多地区蜥蜴区系组成的重要成分<sup>[16]</sup>。两者具有较为相似的体型,附肢无特殊构造(例如安乐蜥和壁虎趾垫),均属于活跃型捕食者,利用短时间疾跑、尾自切等策略逃避天敌<sup>[17-19]</sup>;但两者利用的生境条件明显不同,北草蜥主要栖息于山区坡地杂草堆、灌木丛等,中国石龙子则常见于开阔的农田间、路边杂草丛及乱石堆等地方<sup>[16]</sup>。本

研究以上述两物种为研究对象,检测不同基质对蜥蜴运动表现的影响以及两者不同运动变量之间潜在的权衡关系。

## 1 材料与方法

研究用北草蜥和中国石龙子于2005年4月捕自浙江丽水三岩寺。选取状态良好、尾部完整的成体带回丽水学院动物实验室,测定体重(Body mass, BM)和形态特征:体长(snout-vent length, SVL, 吻端至泄殖腔前缘间距)、尾长(Tail length, TL, 泄殖腔至尾端间距)、前肢长(Fore-limb length, FLL, 肩关节至第3指末端间距)和后肢长(Hind-limb length, HLL, 髋关节至第3趾末端间距)。两种动物分别饲养在蜥蜴专用玻璃缸(长×宽×高=0.8 m×0.4 m×0.4 m)内,每缸动物不超过15条。饲养缸放置在室温为26℃的恒温室内,缸内随机铺设树叶、草皮、瓦片等模拟野外生境,一端悬挂1只60 W灯泡作为动物体温调节的点热源,并提供足量黄粉虫(*Tenebrio molitor*)幼虫和添加钙及维生素的饮水以保证动物获得较为全面的营养。动物驯养1周后开始测试,并在2周内完成所有实验。所有动物在实验结束后释放到原捕捉地点。

运动表现在2 m长的水平跑道上测定。跑道上按实验次序分别铺设4种不同基质(1、塑料草坪,2、表面粗糙不透底的塑料地毯,3、光滑具透底网格的塑料地毯,4、表面光滑的塑料地毯),并记录动物在这些基质表面的运动表现。每隔一天完成一种基质测试。测试运动表现时,所有动物预先在(30.0±0.5)℃恒温室内适应1 h(30℃为2种动物运动表现的适宜体温<sup>[18, 20]</sup>,然后将动物移入跑道一端,毛刷驱赶使之奔跑,Panasonic NV-MX3数码摄像机记录蜥蜴在跑道中来回一次的运动表现。磁带中的数据用MGI Video Wave III软件(MGI Software Co., Canada)读出。疾跑速用动物在单位时间内跑过的距离除以体长表示,停顿次数和最大距离分别用动物在单程跑动中的停顿次数和最大不间断跑动距离除以体长表示。运动表现测试结束后,每隔3 d再分别测试动物的攀附能力和运动耐力。测试攀附能力时,先将动物置于1 m长水平木质跑道的中间,然后匀速抬升跑道一端直至动物开始滑落,记录动物滑落时跑道的倾斜角度。每一动物重复测试2次,以数值最大的单次数据作为攀附能力指标。若跑道直立时蜥蜴仍能攀附于其表面,则记录直立面攀附持续时间。运动耐力以动物在恒定温度水浴中的游泳耐力表示。测试开始前,预先将水浴锅内的水温调至30℃,将单个动物移入水浴锅,强力驱赶,使之在水中不间断游泳直至力竭,以刺激动物无反应为测试结束的判断标准,秒表记录实验个体在水中游泳时间作为耐力指标。

所有被处理的数据在作进一步统计检验前,用Kolmogorov-Smirnov和F-max分别检验数据的正态性和方差同质性(Statistica统计软件包)。用单因子方差分析或协方差分析(one-way ANOVA or ANCOVA)比较动物形态特征的种间差异,用t检验(t-test)、重复测量方差分析(repeated measures ANOVA)和Tukey's多重比较等分析比较功能变量的种间及处理间差异。描述性统计值用平均值±标准误表示,显著性水平设置为α=0.05。

## 2 结果

北草蜥和中国石龙子形态特征的描述性统计值见表1。研究用北草蜥个体(SVL)显著小于中国石龙子。而当去除个体大小的影响后,北草蜥的尾长、前后肢长均显著大于中国石龙子。

两种蜥蜴在水平跑道上的运动表现具有显著的种间差异。在不同基质表面测试的运动表现,北草蜥停顿次数(除表面粗糙地毯)、持续运动距离(除表面光滑地毯)和疾跑速的平均值均大于中国石龙子(图1)。基质类型显著影响两种蜥蜴的运动表现(表2)。2种蜥蜴在塑料草坪和粗糙地毯上运动时的疾跑速大于具网格和光滑的塑料地毯上的疾跑速;中国石龙子在表面光滑的塑料地毯上运动一次来回的停顿次数最少、持续运动距离最大,而北草蜥则在具网格的塑料地毯上停顿次数最少,在粗糙及具网格的塑料地毯上持续运动距离最大。种间和基质效应的交互作用对停顿次数和持续运动距离的影响显著,而对疾跑速的影响不显著(表2,图1)。

北草蜥的攀附能力显著大于中国石龙子( $t=27.71$ ,  $df=38$ ,  $P<0.001$ )。在攀附能力测试过程中,北草蜥约20%的个体具攀附于直立跑道的能力,平均持续时间为(11.0±5.3)s;而中国石龙子仅1个体出现攀附直

立面的情况,持续时间约8 s。北草蜥的游泳耐力显著小于中国石龙子( $t=9.82$ ,  $df=38$ ,  $P<0.001$ )(图2)。

表1 北草蜥和中国石龙子形态特征的描述性统计值

Table 1 Descriptive statistics of morphology traits of the northern grass lizard (*Takydromus septentrionalis*) and Chinese skink (*Plestiodon chinensis*)

	北草蜥 <i>T. septentrionalis</i>	中国石龙子 <i>P. chinensis</i>	统计结果 Results of statistical analyses
N	20	20	
体长	$66.0 \pm 0.7$	$105.8 \pm 2.3$	$F_{1, 38} = 405.14$ , $P<0.001$
Snout-vent length/mm	58.5—70.5	92.5—123.0	TS<PC
尾长	$206.3 \pm 6.8$	$123.1 \pm 6.4$	$F_{1, 37} = 6.84$ , $P<0.02$
Tail length/mm	139.0—257.0	58.5—167.5	TS > PC
前肢长	$25.2 \pm 0.4$	$29.1 \pm 0.7$	$F_{1, 37} = 10.45$ , $P<0.003$
Fore-limb length/mm	23.0—29.5	22.0—34.0	TS > PC
后肢长	$32.4 \pm 0.3$	$39.8 \pm 0.7$	$F_{1, 37} = 7.49$ , $P<0.01$
Hind-limb length/mm	30.5—35.0	36.0—46.0	TS > PC
体重	$5.7 \pm 0.2$	$25.5 \pm 1.7$	
Body mass/g	4.0—7.4	18.0—40.3	$F_{1, 37} = 2.83$ , $P=0.101$

数据用平均值±标准误(范围)表示;种间比较用单因子方差分析(对体长)或以体长为协变量的单因子协方差分析(对其余变量);TS:北草蜥;PC:中国石龙子

表2 基质类型对北草蜥和中国石龙子运动表现的影响

Table 2 The effects of substrate type on locomotor performance of the northern grass lizard (*Takydromus septentrionalis*) and Chinese skink (*Plestiodon chinensis*)

	停顿次数 Number of stop	最大距离 The maximal distance	疾跑速 Sprint speed
物种 Species	$F_{1, 38} = 9.76$ , $P<0.01$	$F_{1, 38} = 16.31$ , $P<0.001$	$F_{1, 38} = 185.49$ , $P<0.0001$
基质 Substrate	$F_{3, 114} = 3.62$ , $P<0.02$	$F_{3, 114} = 3.36$ , $P<0.05$	$F_{3, 114} = 24.75$ , $P<0.0001$
交互 interaction	$F_{3, 114} = 11.80$ , $P<0.001$	$F_{3, 114} = 10.97$ , $P<0.001$	$F_{3, 114} = 0.09$ , $P=0.966$

表中显示运动表现(停顿次数、最大距离、疾跑速)的重复测量方差分析结果

### 3 讨论

基质表面粗糙程度影响两种蜥蜴的运动表现。实验室研究主要利用木质或粗糙橡胶跑道来测量不同动物的运动表现,以期望获得能反映动物最佳功能表现的数据,然而由此得出的结果可能与动物在自然生境中的功能表现存在偏差。两种蜥蜴在粗糙表面均具有较快的速度,这可能与相对较大的摩擦和支撑有关。基质效应对其它两个运动变量的作用具有种间差异。不同基质表面的跑动一次来回中,北草蜥的最大距离无显著差异(repeated measures ANOVA,  $F_{3, 57} = 2.42$ ,  $P=0.076$ );在光滑表面北草蜥停顿次数最多,中国石龙子的持续运动距离最大(图1)。这些结果可能说明基质条件影响蜥蜴的运动方式和行为<sup>[21-22]</sup>。自然环境中的动物当在未知基质上活动时,可能会增加停顿的次数和时间以应对陌生的环境。例如,生活于半干旱沙丘的蜥蜴(*Procellosaurinus tetradactylus*)在硬纸板上的停顿时间增加,另一种利用开阔生境的蜥蜴(*Vanzosaura rubricauda*)则在沙质表面的停顿时间增加<sup>[23]</sup>。灌木丛中生活的北草蜥在光滑表面停顿较为频繁的结果与之相符,而中国石龙子利用生境较为复杂,光滑表面停顿次数减少、单次移动距离增加则可能受其它因素的影响,例如反捕食行为的改变等。基质效应不仅影响地栖蜥蜴的运动方式与行为,亦可影响树栖种类。例如,栖木的直径大小影响安乐蜥的疾跑速、加速以及跳跃能力<sup>[4, 24]</sup>;基质结构影响锯尾蜥虎(*Hemidactylus garnoti*)的加速能力及瞬时速度<sup>[25]</sup>。

蜥蜴的运动能力通常与其微生境利用、形态特征相关联<sup>[15, 26-29]</sup>。理论模型预测具较长附肢的蜥蜴运动时因较大步伐长度而具有较快的疾跑速。这种附肢长度与疾跑速之间的正相关关系在许多蜥蜴种类中已得到证实<sup>[7, 27, 30-33]</sup>。与大多数研究的结果一致,北草蜥的相对附肢长度和疾跑速显著大于中国石龙子。然而,

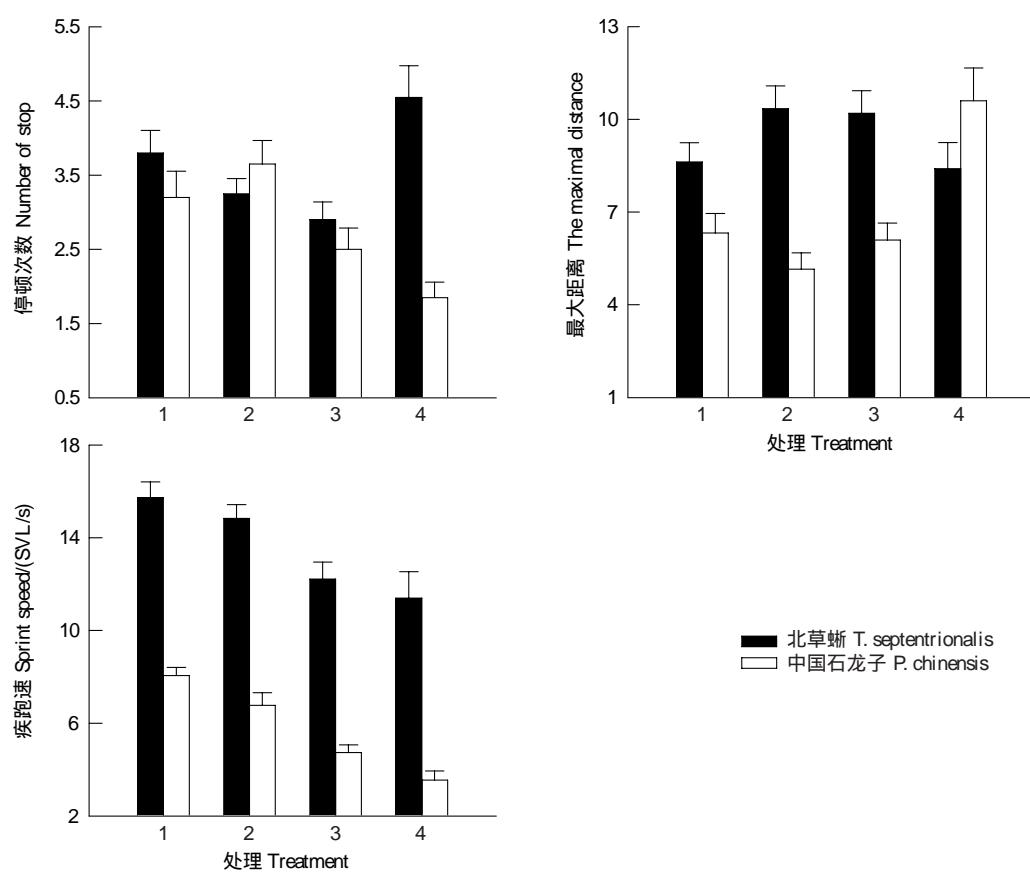


图1 北草蜥和中国石龙子在不同基质上的运动表现

Fig. 1 Locomotor performances of *Takydromus septentrionalis* and *Plestiodon chinensis* on different substrate types

数据用平均值±标准误表示

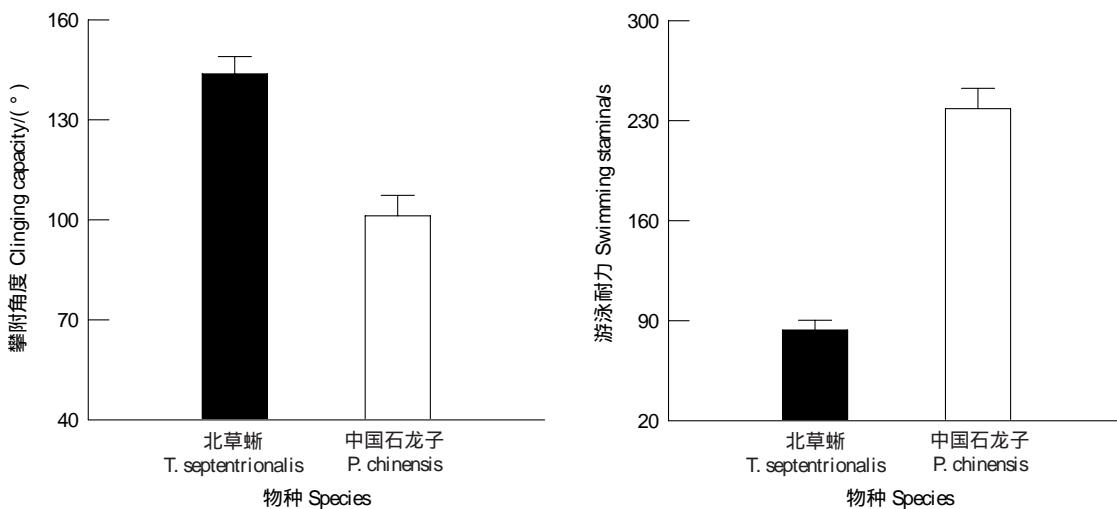


图2 北草蜥和中国石龙子的攀附能力和游泳耐力

Fig. 2 Clinging capacity and swimming stamina of *Takydromus septentrionalis* and *Plestiodon chinensis*

数据用平均值±标准误表示

特定物种的疾跑能力会受到许多因素(例如,环境温度、年龄、激素水平、食物摄入量、断尾及繁殖状态等)的影响<sup>[18, 34-36]</sup>。上述关系在其它一些研究中并不明显,例如,西班牙壁蜥(*Podarcis hispanica*)大陆亚种的最大

运动速度大于岛屿亚种,但两者的附肢长度无显著差异<sup>[37]</sup>。北草蜥比中国石龙子具有较大的攀附能力是可以预见的,这与其主要在灌木丛中生活关系密切,北草蜥较长的指和趾更能稳定地抓握细小叶片和枝条<sup>[15]</sup>。

本研究显示北草蜥比中国石龙子具有相对较大的运动速度(平均相对疾跑速分别为13.5 SVL/s和5.8 SVL/s)和攀附能力(平均攀附角度分别为143.8°和101.2°),但具较小游泳耐力(平均持续游泳时间为83.5 s和238.5 s)(图1,图2)。在种间水平上,运动速度与耐力之间似乎存在进化权衡关系,而与攀附能力之间无此种关系。当动物运动器官的结构不能同时满足不同功能特征的最适表达时,这些功能特征之间可能显示为负相关关系。较长附肢可以使蜥蜴获得较大运动速度,但导致能量消耗的增加而降低运动耐力<sup>[30,37]</sup>。此外,附肢肌肉的类型和组成也可能是导致蜥蜴运动速度与耐力权衡的一个重要原因<sup>[38]</sup>。蜥蜴运动速度与耐力之间的权衡也见于其它研究<sup>[7]</sup>。本研究亦显示北草蜥和中国石龙子的运动速度与攀附能力之间无权衡关系,这与仅包括蜥蜴科物种的研究结果相似<sup>[39]</sup>,但与仅包括树栖种类—安乐蜥不同<sup>[4-5]</sup>。较长附肢的安乐蜥在宽木板表面运动时具较快疾跑速度,在窄栖木上运动时具较差攀爬能力;而较短附肢种类的情况则相反。通常认为较长附肢不有利于树栖种类在树枝上的活动,这样导致身体重心与树枝表面的距离增加而降低攀爬时的稳固性<sup>[4-5]</sup>。但上述效应对主要栖息于灌木丛的草蜥或细小枝条的树栖种类的影响不大。这些物种可能倾向于加大附肢的侧向弯曲程度以保持身体重心接近于基质表面并提高其稳固性<sup>[39]</sup>。当它们在较宽、具较多抓握点的基质表面活动时,较长附肢可能更有助于动物的抓附和攀爬。

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3	植物生态学报	4384	3	应用生态学报	1.733
4	西北植物学报	4177	4	生物多样性	1.553
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6	植物生理学通讯	3362	6	西北植物学报	0.986
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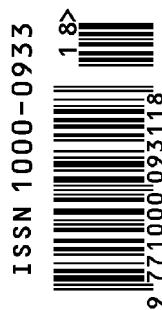
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