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断尾对蓝尾石龙子能量储存和运动表现的影响

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摘要:在许多蜥蜴种类中,尾自切是一种主要的逃避天敌捕食的防御性策略。虽然断尾使蜥蜴获得短期的生存利益,但同时也需为此承受多方面的代价。利用从丽水采集的117条蓝尾石龙子来评价该种动物断尾的能量和运动代价。81条(约69%)石龙子至少经历过1次尾自切。断尾个体中,原先断尾事件的发生频率在不同尾区间存在显著差别,但两性间无差别。将实验组17条具完整尾的石龙子依次切去3个尾段,然后测定断尾前后石龙子的运动表现以及每个尾段、身体各部分中的脂肪含量。另15条具完整尾的石龙子作为对照组,仅测量其运动表现。尾部的脂肪含量与尾基部宽呈正相关,说明具较粗尾部的石龙子一般具有相当较多的尾部储能。尾部脂肪含量随尾长呈非等比例分布,大部分脂肪集中于尾近基部端。断尾几乎不影响蓝尾石龙子的运动表现,仅当大部分尾部被切除时疾跑速有较小程度的降低。显示了蓝尾石龙子因遭遇天敌捕食攻击或其它因素作用而产生的部分断尾可能并不会导致严重的能量和运动代价。由于野外种群蓝尾石龙子个体的断尾情况主要发生在尾近基部或中部位置,因此可以认为自然条件下该种动物的尾自切通常会遭受明显的能量和运动代价。

关键词:石龙子科;蓝尾石龙子;尾自切;能量储存;运动表现

Effect of tail loss on energy stores and locomotor performance in the blue-tailed skink, *Eumeces elegans*

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Abstract: Tail autotomy is a major defensive strategy to escape from predation in many species of lizards. Although tail loss provides an immediate survival benefit, it may entail substantial costs. A total of 117 blue-tailed skinks (*Eumeces elegans*) were collected from a population in Lishui to evaluate energetic and locomotor costs of tail loss. Of the 117 skinks, 81 (c. 69%) had autotomized some portion of the tail at least once. The blue-tailed skink in this population showed a high tail-break frequency, and therefore may be subjected to intense predation pressure. The proportions of individuals with tail breaks located in the proximal (except for the extreme base, < 10% original tail length), middle and distal portions of tails were 47%, 36% and 11%, respectively. The frequency distribution of locations of the tail break did not differ between the sexes. Three tail segments were successively removed from each of the 17 experimental skinks (14 males, 3 females) initially having intact tails. Locomotor performance of each skink at the body temperature of 30℃ before and after each tail-removing treatment was measured by chasing them down the length of a 2 m racetrack with one side transparent, which allows lateral filmation with a digital video camera. The recorded tapes were later examined for three locomotor variables (the maximal distance, number of stops and sprint speed). All removed tail segment and body components were individually weighed and determined for the amount of lipids in each sample. Another independent sample of 15 individuals (12 males, 3 females) with intact tails was measured for locomotor performance to serve as controls for successive

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measurements taken at the time for the experimental skinks. The tail is an important storage organ for lipids in *E. elegans*. The amount of caudal lipid represented approximately 39% of the total body lipid, and was positively correlated with tailbase width, indicating that thicker tails contained relatively more lipids than did thinner tails. Caudal lipids were disproportionately stored along the length of the tail, with most lipids being concentrated in its proximal portion. Locomotor performance was almost unaffected by tail loss in this species, with a slight decrease in sprint speed until most of the tail was removed, and no significantly changes in the maximal length and number of stops after each tail-removing treatment. The degree of locomotor impairment associated with tail loss in this study (reduced by approximately 19% of the mean speed of skinks with intact tails) falls within the values reported for other species of lizards, thus *E. elegans* is among species of lizards whose tails play an important functional role in locomotion. The results from this study show that partial tail loss due to predatory encounters or other factors may not severely affect energy stores or locomotor performance in *E. elegans*. As tail breaks occurred more frequently in the proximal and middle portion of the tails in *E. elegans* collected from the field, it can be concluded that tail autotomy occurring in nature often incurs substantial energetic and locomotor costs in *E. elegans*.

Key Words: Scincidae; *Eumeces elegans*; tail autotomy; energy stores; locomotor performance

天敌的捕食行为是驱使猎物的反捕食策略及行为以多样性方向进化的一种重要的选择作用力。遭遇天敌攻击时,被捕食者采取自动脱离身体某部分器官的反捕食方式广泛见于动物界的不同类群(如棘皮动物、节肢动物、蛛形动物、甲壳动物以及脊椎动物等)。在蜥蜴类动物中,尾自切是最为常见的反捕食方式[1-2]。蜥蜴能利用断离的尾部迷惑或转移捕食者的视线以提高成功逃脱天敌捕食的机率。虽然尾自切可使蜥蜴获得的直接生存利益,但同时也直接或间接地产生多方面的代价[2, 3-6]。断尾代价在蜥蜴个体发育阶段、种间及利用不同生境条件之间常显示出一定程度的变异,这些差异可能主要与尾部功能(如社会行为、能量储存和运动作用)变化有关[3]。尾自切产生的各方面代价可能会相互影响。例如,尾部是许多蜥蜴种类的重要能量贮存器官,断尾引起的尾部贮能丢失可减缓动物的生长速率、推迟雌体繁殖、降低繁殖输出、增加越冬死亡率[7-11];断尾导致社会地位及交配成功率的降低[12-13],进而会产生较低的繁殖成功率和存活率[10, 14]。尾自切产生的另一个明显代价就是阻碍蜥蜴运动表现以及改变某些行为特征[15-20]。运动能力的下降会使断尾个体成功逃脱天敌捕食的机率减小[6,10]。

另一方面,蜥蜴断尾后能通过调整某些行为使尾自切代价得到一定程度的补偿。一些研究证实断尾和有尾个体在活动水平、反捕食行为和微生境利用等方面具有明显差异[5-6]。然而,这些行为上细小的变化进而会产生其它方面的代价。例如,降低活动水平可以使蜥蜴保存较多的能量以及增加隐蔽性,但是它同时会降低觅食效率、繁殖成功机率和社会地位[12-14]。

蓝尾石龙子为一种地栖型卵生石龙子科动物,广泛分布于我国华东、华南诸省(区)及琉球群岛[21]。到目前为止,有关蓝尾石龙子的研究涉及两性异形、繁殖输出、热生物学等方面的内容[22-25]。本文主要报道蓝尾石龙子断尾前后尾部脂肪含量和运动表现的变化,评估该种野外个体的尾自切所产生能量和运动代价的程度。

1 材料与方法

1.1 实验动物

于2006年5月在丽水白云山共捕获蓝尾石龙子117条(♀♀:♂♂ =25:92)。所有动物被带回丽水学院动物实验室,鉴定每条石龙子的性别并测定其体重和头体长(吻端至泄殖腔孔前缘间距,Snout-vent length, SVL)。检查样本断尾情况,无任何断尾痕迹的个体记录其完整尾长(Tail length, TL),至少有一次断尾痕迹的个体记录断尾位置(用泄殖腔至尾部原先痕迹的距离表示,Tail break length, BL)。利用具完整尾部的个体数据建立的TL与SVL线性回归方程,然后估算断尾个体的原始尾长(Original tail length, OTL)。用相对断尾

位置(Relative position of tail loss, BL/OTL)表示不同个体大小动物的原先断尾情况。形态数据测量后,选取部分尾部完整的石龙子用于能量及运动表现的断尾代价实验,其它个体均释放到原捕捉地点。

1.2　能量和运动表现测定

用于断尾代价测定的 32 条石龙子被分为实验组(*N* 17, ♀♀:♂♂ =3:14)和对照组(*N* 15, ♀♀:♂♂ = 3:12)。实验前动物常温饲养于模拟自然生境的玻璃缸(长×宽×高为 900 mm×600 mm×500 mm)内,每缸内动物不超过 10 条。动物在缸内能利用自然光照进行体温调节,取食黄粉虫幼虫(larvae of *Tenebrio molitor*),通过饮用添加钙和维生素的饮水获得较为全面的营养。

所有尾部完整的动物预先在(30 ±0.5) ℃恒温室内适应 1h,然后置于 2 m 长的水平木制跑道上,用毛刷刺激其尾部使之奔跑,Panasonic NV-MX3 数码摄像机记录动物在跑道上一个来回的运动过程,该数据记录为 E0 阶段。然后,每间隔 4d 人工诱导(用镊子夹紧断尾位置)实验组动物顺序断尾 3 次,使之分别保留 70 mm (E1 阶段)、40 mm(E2 阶段)和 10 mm(E3 阶段)长度的尾长。每次断尾后将动物饲养于玻璃缸内 3d 使其自行愈合伤口,然后用上述方法分别测定每一断尾阶段实验组和对照组动物的运动表现。磁带中的数据用 MGI Video Wave III 软件(MGI Software Co., Canada)读出。疾跑速为动物跑过 250 mm 的最大速度表示,最大持续跑动距离为不间断跑动的最大距离,停顿次数为在跑道中一个来回的停顿次数,回程转折点的停顿不计。

所有运动表现测定结束后,实验组动物随后在 -25 ℃条件下冰冻处死,解冻后将其解剖分离成躯干(包括头、四肢和除肝脏外的内脏)、肝脏、脂肪体和尾部(余下长 10 mm 的尾部作为 E4 阶段数据)4 部分,用于测定其中的脂肪含量。所有断离的尾段、躯干及肝脏单独称湿重,随后在 65 ℃干燥箱中烘干并称干重。用电动粉碎和研钵将干燥后各部分磨成粉末。各尾段和身体组分样品中的脂肪用索式提取仪在 55 ℃条件下抽提 10 h,分析纯乙醚作为抽提溶剂;样品中的脂质含量用抽提前样品干重减去抽提后样品干重来确定。

1.3　统计分析

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)。初步分析显示疾跑速和最大持续运动距离与石龙子个体大小无关。用 *G* 检验,线性回归,重复测量方差分析(repeated measures ANOVA),单因子协方差分析(one-way ANCOVA)以及 Tukey's 多重比较等分析处理相应的数据。描述性统计值用平均值 ± 标准误表示,显著性水平设置在 $\alpha = 0.05$。

2　结果

2.1　蓝尾石龙子野外断尾频率

所捕获的蓝尾石龙子中,81 条个体(约 69.2%, 17♀♀, 64♂♂)至少有一次尾自切痕迹。自然种群的断尾发生率两性之间无显著差异(♀♀:♂♂ =68.0%:69.6%, $G=0.02$, d*f* =1, $P>0.75$)。以 SVL 为协变量的 ANCOVA 分析显示蓝尾石龙子的尾长无两性间差异($F_{1,33}=1.09$, $P=0.304$),故两性数据合并后建立 TL 与 SVL 的线性回归方程(TL = 1.39 × SVL + 22.42; $R^2=0.57$, $F_{1,34}=44.42$, $P<0.0001$, 图 1)。具断尾经历的个体中,断尾位置发生在尾基部(< 10% 尾全长)约 6.2% (5/81)、近基部(10%—40% 尾全长)约 46.6% (38/81)、尾中部(40%—70% 尾全长)约 35.8% (29/81)和远基部(> 70% 尾全长)约 11.1% (9/81)。蓝尾石龙子在近基部、尾中部和远基部等区间内发生断尾的频率具有显著差异($G=10.03$, d*f* =2, $P<0.01$),大部分个体断尾发生在尾近基部和中部位置(图 2),图 2 数据的进一步 *G* 检验显示,断尾位置不同性别间差异不显著($G=5.29$, d*f* =8, $P>0.50$)。

2.2　断尾对蓝尾石龙子尾部脂肪储存的影响

实验动物首次断离的尾段平均长 55.8 mm(范围为 27.8—104.4 mm),从 E1 和 E2 动物断离的尾段长均为 30 mm。尾干重、躯干干重和肝脏干重分别约占身体总干重的 21.5%、76.1% 和 2.3%,而尾部、躯干、肝脏和脂肪体中的脂肪分别约占身体总脂肪含量的 38.6%、52.6%、5.3% 和 3.5%(表 1)。

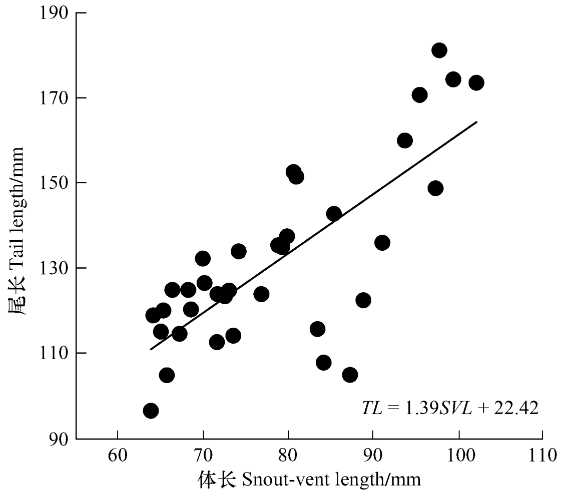

图1 体长与尾长的直线回归

Fig. 1 The linear regression of tail length against snout-vent length

图中数据基于野外采集的36条具完整尾的蓝尾石龙子个体

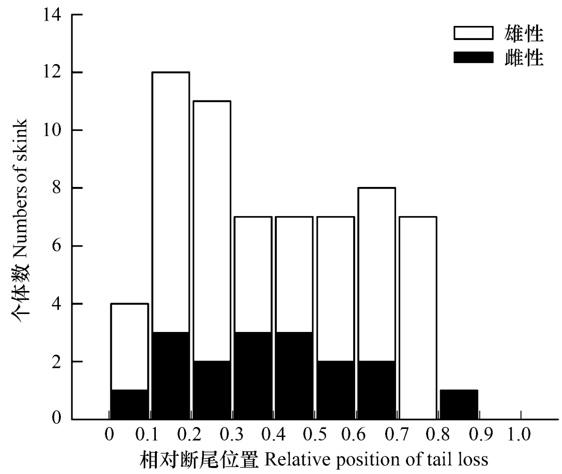

图2 野外蓝尾石龙子个体断尾位置的分布

Fig. 2 Frequency distribution of locations at which caudal autotomy occurred

图中数据基于野外采集的117条蓝尾石龙子个体中的81条断尾个体

表1 用于检测断尾对能量储存和运动表现影响的17条实验组蓝尾石龙子的描述性统计值

Table 1 Descriptive statistics of the 17 experimental individuals of *Eumeces elegans* used to examine the effects of tail loss on energy stores and locomotor performance

项目 Item	平均值 Mean	标准误 SE	范围 Range
体长 Snout-vent length / mm	91.24	1.75	79.86—102.14
体湿重 Body wet mass / g	14.55	0.79	9.80—21.00
尾长 Tail length / mm	125.76	6.21	97.79—174.35
尾基部宽 Tailbase width / mm	7.84	0.10	7.12—8.69
尾湿重 Tail wet mass / g	2.65	0.14	1.98—4.03
尾干重 Tail dry mass / g	0.92	0.05	0.64—1.42
躯干干重 Carcass dry mass / g	3.25	0.21	2.01—4.99
肝脏干重 Liver dry mass / g	0.10	0.01	0.06—0.16
尾部脂肪含量 Lipid content in the tail / g	0.088	0.004	0.063—0.117
躯干脂肪含量 Lipid content in the carcass / g	0.120	0.007	0.083—0.177
肝脏脂肪含量 Lipid content in the liver / g	0.012	0.001	0.007—0.020
脂肪体脂肪含量 Lipid content in the fatbody / g	0.008	0.002	0—0.030

尾部脂肪含量与尾基宽呈显著正相关($R^2=0.43$, $F_{1,15}=11.24$, $P<0.01$,图3),但与尾长不相关($R^2=0.01$, $F_{1,15}=0.17$, $P=0.690$)。实验组动物四次断离的尾段干重($F_{3,48}=57.61$, $P<0.0001$)和脂肪含量($F_{3,48}=105.62$, $P<0.0001$)有显著差异。基部(0—10 mm)、近基部(10—40 mm)、中部(40—70 mm)和远基部尾段(70 mm至尾尖)的干重分别约占尾总干重的24.0%、41.1%、21.7%和13.2%,而脂肪含量分别约占尾部总脂肪含量的22.6%、52.1%、16.8%和8.5%(图4)。

2.3 断尾对蓝尾石龙子运动表现的影响

重复测量方差分析显示总体上3个所检测运动变量(最大运动距离、停顿次数和疾跑速)无显著的组间差异,但断尾显著影响蓝尾石龙子的疾跑速(表2)。单独分析实验组的疾跑速数据时发现E3阶段的平均值显著小于E0和E1阶段($F_{3,48}=4.07$, $P<0.02$)。依次断尾后蓝尾石龙子在跑道上的运动显示出停顿次数增加而最大运动距离减小的趋势,但统计上差异并不显著(表2,图5)。

3 讨论

蓝尾石龙子尾部的脂肪含量占身体总脂肪含量的1/3 以上,仅次于躯干脂肪含量,因此尾部是其重要的能量贮存器官。与其它许多石龙子科蜥蜴种类相似[19, 26-27],蓝尾石龙子尾部脂肪沿尾纵长呈非等比例分布,较为集中地分布于近尾基部的部分。虽然 E1 阶段断尾使蓝尾石龙子失去近一半尾长(约 44% 尾全长),但仍能保留 90% 以上的尾部脂肪;E2 阶段断尾使其失去累积约 68% 尾长,但仍保留约 75% 左右的尾部脂肪(图 4)。不同蜥蜴种类尾部脂肪主要集中于尾基部,这可能代表了一种为抵消高尾自切频率的能量保存机制,使发生在尾远基部位置的尾自切不会导致蓝尾石龙子的能量储存严重损失。而自然种群中蓝尾石龙子尾远端断尾的概率较低,这可能与少量断尾并不足以吸引天敌的注意力从躯干部分转移到断落尾段有关。而另一方面,该种个体发生接近完全断尾的频率也极低,这与其尾椎骨解剖学上的特性有关[28],因为绝大多数蜥蜴种类在发生尾自切时,尾基部的尾椎通常无法形成断裂面[1]。此外,较大程度的尾自切可能会显著影响断尾个体的适合度,使其付出难以承受的生存代价。一般认为特定蜥蜴种类的断尾程度应取决于尾自切的利益 和代价之间的权衡[2]。蓝尾石龙子自然种群个体的尾自切主要发生在近基部和中部尾段之间(10%—

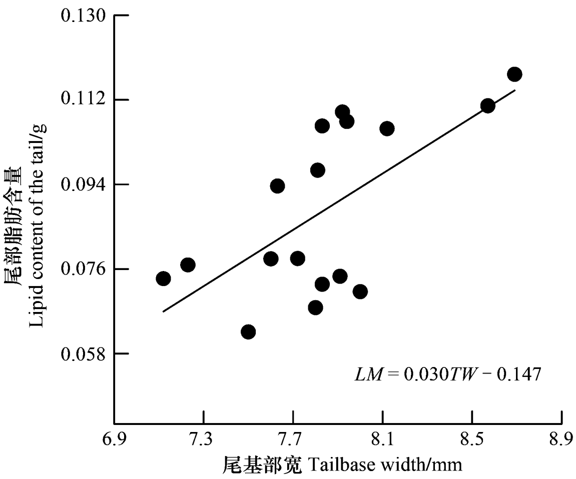

图 3　蓝尾石龙子尾部脂肪含量与尾基部宽的直线回归

Fig. 3　The linear regression of lipid content of the removed tail against the tailbase width in *Eumeces elegans*

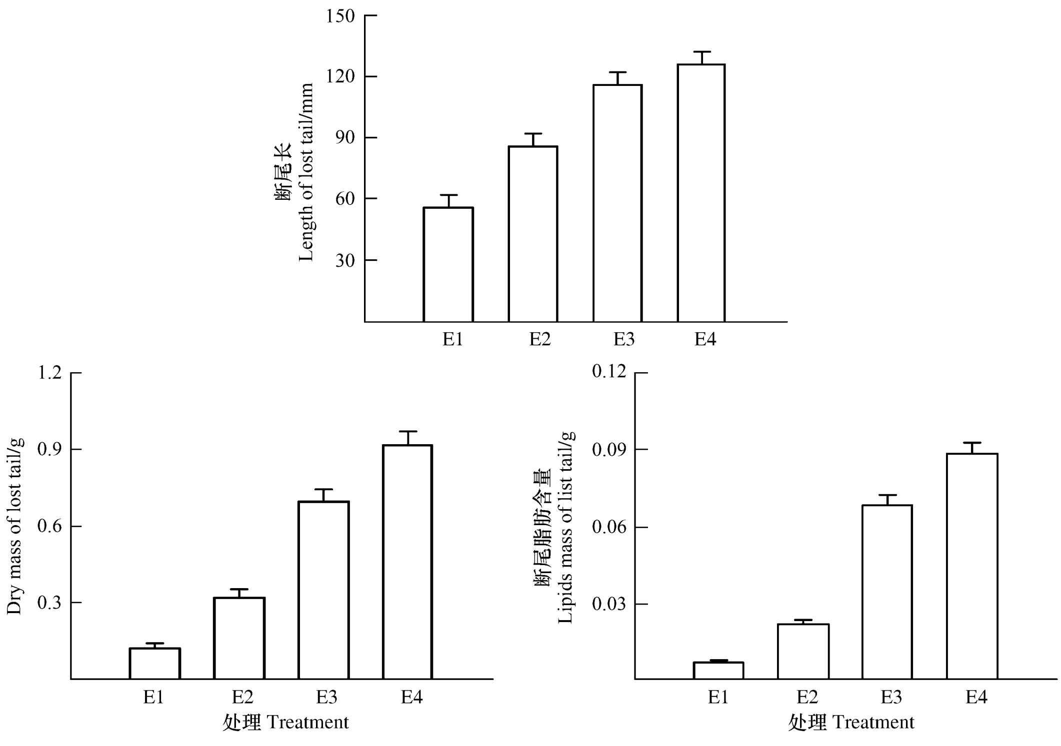

图 4　实验组石龙子依次切除的四尾段长度、干重和脂肪含量的累积值(平均值 ± 标准误)

Fig. 4　Mean values (± SE) for accumulative values of the length, dry mass and lipid content of the four tail segments successively removed from each of the 17 experimental skinks

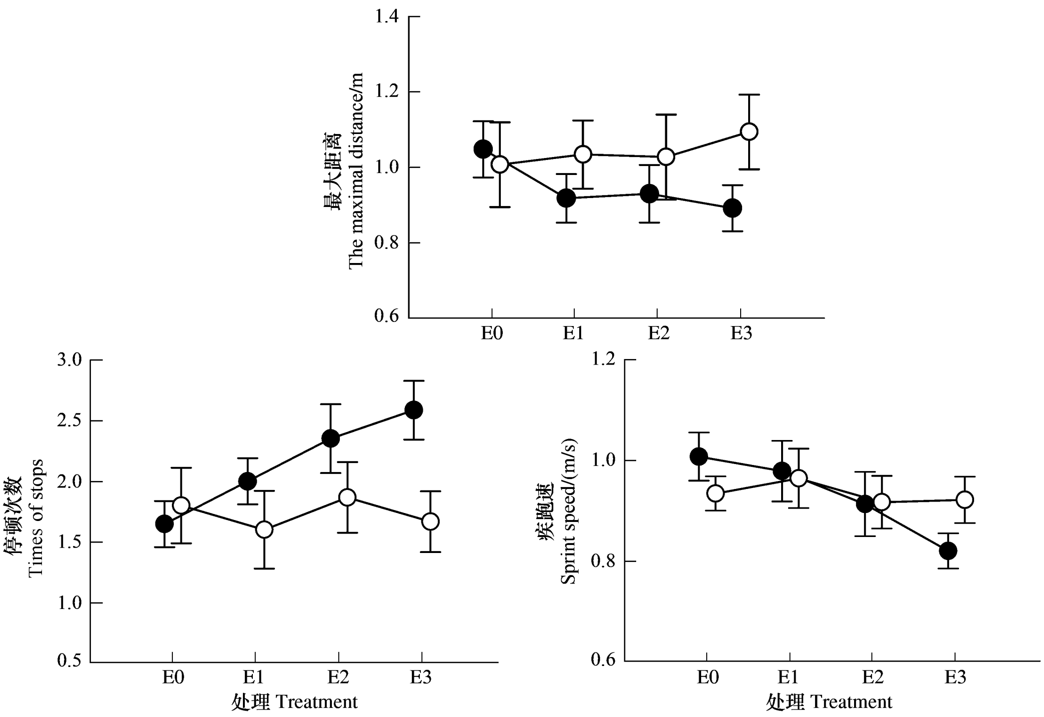

图5 断尾前后蓝尾石龙子各运动指标的平均值(±标准误),实心点代表实验组;空心点代表对照组

Fig. 5 Mean values (±SE) for locomotor variables before and after tail removing treatments in *Eumeces elegans*. Solid circles: experimental skinks; Open circles: control skinks

表2 断尾对蓝尾石龙子运动表现的影响

Table 2 The effect of tail loss on locomotor performance in blue-tailed skink, *Eumeces elegans*

项目 Item	运动表现 Locomotor performance		
	最大距离 The maximal distance	停顿次数 Number of stops	疾跑速 Sprint speed
组间效应 Animal category	$F_{1,30}=1.65$, $P=0.209$	$F_{1,30}=4.12$, $P=0.051$	$F_{1,30}=0.01$, $P=0.930$
断尾效应 Tail loss	$F_{3,90}=0.17$, $P=0.913$	$F_{3,90}=1.37$, $P=0.258$	$F_{3,90}=2.75$, $P<0.05$
交互作用 Interaction	$F_{3,90}=0.79$, $P=0.504$	$F_{3,90}=1.53$, $P=0.212$	$F_{3,90}=1.52$, $P=0.214$

70%尾全长),这一结果与原先报道的一些种类相似[19, 27-29]。野外蓝尾石龙子的尾自切通常会导致其损失一定程度的尾部能量储存。

蜥蜴野外自然种群尾自切的发生频率及程度在不同类群甚至不同种群间可存在明显的差异。一些研究显示不同蜥蜴种类的尾自切发生率范围为3%—82%,尤其是石龙子科蜥蜴的尾自切发生频率较高,平均值约45%[1]。本研究采集的蓝尾石龙子样本断尾个体所占比例约69.2%,该比值明显大于石龙子科的平均值,而略低于主要分布区重叠的其它两种石龙子科蜥蜴(中国石龙子约73%[19],印度蜓蜥约77%[27])。蜥蜴自然种群的断尾率通常反映了当地捕食者的密度[1, 30]。以上3种同域分布的石龙子所面临的捕食者应是相似的,蓝尾石龙子相对略低的野外断尾率可能与其选择易于躲避的微生境有关。在丽水地区,蓝尾石龙子常见于山区路旁草丛、石缝、乱石堆中;而中国石龙子和印度蜓蜥主要生活于平原或低海拔山区的灌木丛、杂草丛等地方。

与许多蜥蜴种类一样[15, 17-19, 28, 31],尾自切显著降低蓝尾石龙子的运动速度。本研究中E3阶段断尾个体的平均运动速度比具完整尾(E0阶段)时约低19%,处于其它蜥蜴种类断尾导致运动速度下降程度的范围(12%—48%)之内。与E0阶段相比,E1和E2的平均速度分别约低3%和9%,但统计上差异并不显著(图5)。本研究的样本中仅约6%个体的相对断尾程度大于实验组E3阶段,41%个体大于E2阶段(图2),因此

可以推测野外蓝尾石龙子大部分断尾个体运动能力的变化可能并不大。尾自切对蜥蜴运动表现的影响在不同蜥蜴类群中存在显著差别,从已有文献来看,石龙子科种类中断尾均导致运动速度下降(范围为 22%—35%[16-19, 28];少数蜥蜴科和鬣蜥科种类无明显变化[29-30, 32],而绝大多数壁虎科种类无影响或增加运动速度[20, 33-34]。断尾效应的种间及类群间差异可能主要与尾部功能和形态的差异有关。尾部对蜥蜴的运动起推动及平衡作用的种类中,断尾通常会导致这些动物的运动速度下降;而尾部的运动功能不明显的种类中,断尾并不影响其运动速度[20, 34]。一些壁虎科种类具有较大或扁平的尾部,其断尾可能消除尾部与基地面之间摩擦作用从而减小了运动时的阻力,因此,也有少数种类尾自切反而可能会引起运动速度的增加[33]。

实验组动物断尾后的运动显示出持续运动距离减小而停顿次数增加的趋势,这部分地反映了蜥蜴断尾可能会影响其运动耐力。已有的文献中涉及直接测量断尾对运动耐力影响的蜥蜴种类仅 2 种石龙子(*Niveoscincus metallicus*[16]和 *Eulamprus quoyii*[35]),而一些物种运动耐力的断尾效应主要从某些运动指标(例如持续运动距离、停顿次数和时间)间接地反映[19, 29, 34]。生物力学研究显示断尾对蜥蜴运动的影响主要是减小其步伐长度。当步伐长度减小时,动物需要增加步伐频率以维持同等的运动速度,单位时间内的能量消耗则随之增加[15]。此外,蜥蜴尾部可能为其持续运动提供一定的能量支持,断尾导致运动能力的下降也可能部分与能量上的限制有关。

总之,发生于远尾基部的尾自切对蓝尾石龙子的能量储存和运动表现的影响较弱,而近基部的尾自切可能会显著降低动物的适合度。野外采集的蓝尾石龙子样本断尾主要发生于近基部至中部区间位置,据此可以认为野外蓝尾石龙子尾自切通常会使断尾个体蒙受一定程度的能量代价和较少的运动代价。

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