

三个种群有尾和断尾丽斑麻蜥的选择体温、表面活动和摄食量*

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摘要 用2006年4–6月捕自长安(陕西)、共和(青海)、哈尔滨(黑龙江)三个地理隔离种群尾部完整的丽斑麻蜥(*Eremias argus*)成年雄体检测断尾对选择体温、表面活动(表面调温个体数)和摄食量的影响。各种群个体均分为实验和对照组,在距尾基部10 mm处切除实验组蜥尾,获得断尾个体。实验和对照组个体饲养在相同的实验室条件下收集相关数据,历时四周。表面活动的种群间差异是不同种群个体对其所处区域热环境长期适应的结果。断尾个体减少表面活动见于所有三个种群,表明尾自切能导致丽斑麻蜥活动水平的改变。同一种群断尾和有尾个体表面活动的时间格局无显著差异,不同种群表面活动的时间格局无显著差异,这些结果表明丽斑麻蜥白天活动节律具有种的特异性,不受断尾影响。丽斑麻蜥选择体温随纬度或海拔升高而降低,这种变化趋势可能是热环境制约的结果。所有三个种群断尾个体的选择体温均低于有尾个体,表明断尾可改变丽斑麻蜥的体温调定点。丽斑麻蜥摄食量存在种群间差异,长安种群蜥的摄食量显著大于共和种群蜥。三个种群断尾个体均未增加摄食以满足尾再生的额外能量需求,表明增加摄食不是该种蜥补偿断尾能量代价的对策[动物学报 54(1): 60–66, 2008]。

关键词 蜥蜴科 丽斑麻蜥 尾自切 选择体温 活动 摄食量

Selected body temperature, surface activity and food intake in tailed versus tailless Mongolian racerunners *Eremias argus* from three populations*

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Abstract Adult males of *Eremias argus* initially having intact tails were collected from three geographically separated populations (the Chang'an population in Shaanxi, the Gonghe population in Qinghai, and the Harbin population in Heilongjiang) between April and June 2006 to examine the effects of caudal autotomy on selected body temperature, surface activity (the number of individuals thermoregulating on the surface) and food intake. Lizards from each of the three populations were equally divided into experimental and control groups. We removed the tail 10 mm from the vent from each experimental lizard, thereby producing tailless lizards. Experimental and control lizards were maintained under identical laboratory conditions for four weeks to allow the accumulation of sufficient data. Surface activities differed among lizards from different populations, primarily as the consequence of long-term adaptation to local thermal environments. Reduced surface activities in tailless lizards were found in all the three

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populations, suggesting that *E. argus* is among lizard species where tail loss may modify activities. The temporal patterns of surface activity did not differ between experimental and control lizards within each of the three populations and among lizards from different populations, suggesting that there is a species-specific activity pattern in *E. argus*, and that the pattern is unaffected by tail loss. Selected body temperature increases with increase in latitude in *E. argus*, and this trend should be attributable to the constraints imposed by the thermal environment. Tailless lizards selected lower body temperatures than did tailed lizards in all three populations, suggesting that *E. argus* is among lizard species where tail loss may modify the set-point of thermoregulation. Food intake differed among lizards from different populations, with lizards from the Chang' an population ingesting significantly more food than those from the Gonghe population. In all three populations, increased energy demands associated with tail regeneration did not result in increment of food intake in tailless lizards. This finding suggests that increasing food intake is not a strategy adopted by tailless *E. argus* to compensate for the energetic costs of tail loss [*Acta Zoologica Sinica* 54 (1): 60–66, 2008].

Key words Lacertidae, *Eremias argus*, Caudal autotomy, Thermal preference, Activity, Food intake

许多蜥蜴利用尾自切作为免遭天敌致命攻击的防御机制, 这种机制在躲避、逃跑等措施均不奏效时会显得尤其重要 (Arnold, 1984, 1988; Bellairs and Bryant, 1985)。蜥蜴自然种群的断尾率不能简单地归因于捕食, 因为捕食以外的因素也能导致断尾 (Arnold, 1988; Bauer and Russell, 1994)。断尾频率的种间差异显著, 这些差异既与各种蜥蜴的尾部形态、结构和相对重要性有关, 也与蜥蜴的运动方式、生境利用、摄食行为等有关 (Vitt, 1983; Zani, 1996; Lin and Ji, 2005; Lin et al., 2006)。例如, 鬣蜥科蜥蜴未见有尾自切现象 (Ji et al., 2002; Zhang et al., 2005), 石龙子科蜥蜴则频见该现象 (Lin et al., 2006; 孙燕燕等, 2007)。自切尾个体在获得逃避天敌捕食的直接生存利益的同时, 也须为此付出代价。例如, 尾部能量丢失可减缓生长、推迟繁殖、降低繁殖输出、增加越冬死亡概率 (Dial and Fitzpatrick, 1981; Wilson and Booth, 1998), 尾自切使许多蜥蜴的运动能力受损 (Ballinger et al., 1979; Punzo, 1982; Martin and Avery, 1998; Downes and Shine, 2001; Shine, 2003; Daniels, 1983; Huey et al., 1990; Brown et al., 1995), 使得断尾个体更易被天敌捕食 (Congdon et al., 1974; Dial and Fitzpatrick, 1984; Daniels et al., 1986; Chapple and Swain, 2002)。断尾蜥蜴可通过调整活动节律、小生境利用和反捕食行为等途径降低断尾带来的不利影响, 但这些行为调整通常会降低其适合度 (Fox and Rostker, 1982; Dial and Fitzpatrick, 1984; Fox et al., 1990; Martin and Salvador, 1993; Salvador et al., 1995; Downes and Shine, 2001; Chapple and Swain, 2002)。

研究断尾对蜥蜴行为和生理表现的影响有助于揭示尾自切的进化适应意义。严重断尾可使蜥蜴蒙受显著的能量和运动代价 (Downes and Shine, 2001; Lin and Ji, 2005; Lin et al., 2006; Sun et al., 2007), 作者据此预测: (1) 断尾个体应减少表面活动以降

低被捕食的风险; (2) 断尾个体应选择较低的体温以降低维持能耗; (3) 断尾个体应增加摄食以满足尾再生的额外能量需求。作者以丽斑麻蜥 (*Eremias argus*) 为模型动物研究断尾对选择体温、活动频率和摄食量的影响。与以往所有相关工作不同的是, 作者同时用三个地理隔离种群的蜥蜴为材料开展研究, 所得的结果更有助于阐明断尾是否对特定种类的蜥蜴具有规律性的效应。

1 材料与方法

1.1 动物采集和维持

于2006年4月至6月在三个地理隔离种群捕捉体长 (Snout-vent length, SVL) 为50–66 mm的成年丽斑麻蜥, 三个种群分别为陕西长安 (CA) 种群 (34°02'N, 108°48'E)、青海共和 (GH) 种群 (36°03'N, 101°13'E) 和黑龙江哈尔滨 (HRB) 种群 (45°47'N, 126°37'E)。月平均气温显示三地热环境差异显著 (Fig. 1); 三种群 SVL 大于 50 mm 的雌体一般均能年产至少一窝卵。捕获的蜥蜴运至杭州实验室, 每 10 个一组关养在一个长 × 宽 × 高为 90 × 65 × 50 cm³、内铺潮湿沙土和瓦片的玻璃饲养缸内。饲养缸放置在气温为 23°C–28°C 的饲养室内, 缸一端悬挂一个 100 W 加热灯泡, 光照周期为 14L: 10D, 06:00 h 灯泡自动开启; 光照期间, 缸内形成从室温到 55°C 的连续温度梯度, 蜥蜴可在其中自主调温, 自由摄食面包虫 (*Tenebrio molitor*) 并饮水。饮水中添加杭州民生制药厂生产的 21 金维他和儿童钙粉, 以满足实验个体的营养需求。雌体在实验室完成当年的产卵循环, 相关数据另文报道。

1.2 实验方法

各种群 200 个尾部完整的成年雄体用作本实验材料, 长安、共和、哈尔滨种群个体的 SVL 范围分别为 50–63、50–61 和 50–66 mm。各种群个体在上述实验室热环境中驯化两周, 随后均分为实验和对照组蜥蜴。在距尾基部 10 mm 处切除实验组蜥

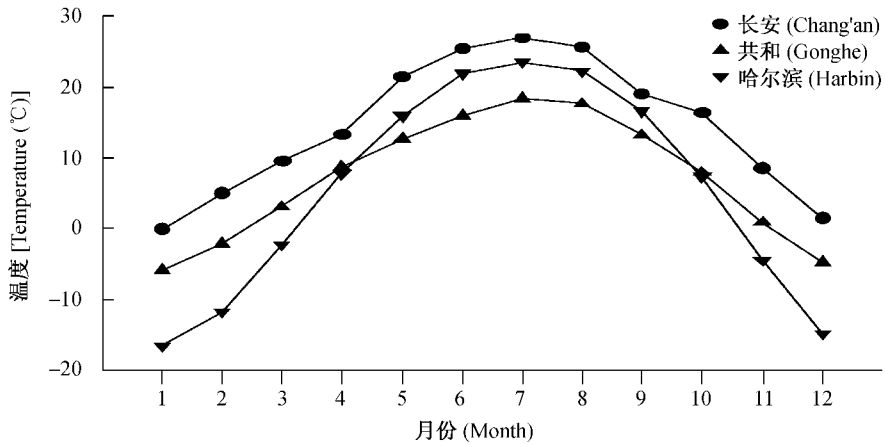


图 1 三个捕捉丽斑麻蜥成年雄体地区过去 25 (1981–2006) 年的月平均气温

Fig.1 Monthly mean air temperatures over the past 25 years (1981–2006) at the three localities where adult males of *E. argus* were collected

蜥尾部，获得断尾个体。将对照（有尾）和实验（断尾）蜥按种群来源每 10 个一组分别关养在条件完全同上的饲养缸内，次日起开始收集选择体温、表面活动个体数和摄食量数据，历时四周。

在 08: 00、10: 00、12: 00、14: 00、16: 00、18: 00 和 20: 00 h 前后 10 min 内计数各缸表面调温个体数（后称表面活动），用上海医疗仪器厂产的 UT325 数字温度计测定表面调温个体的泄殖腔温度，记作上述 7 个时刻的活动频率和选择体温。记录每缸各时刻的表面活动数据不少于 5 次，求其平均值显示该缸蜥对应时刻的活动频率；记录每个个体各时刻的泄殖腔体温不少于 5 次，求其平均值后再计算所有缸内个体 ($n = 10$) 的平均值表示该缸蜥对应时刻的选择体温。称量每日提供和剩余的面包虫重量，用减量法获得每日缸内个体 ($n = 10$) 摄入的面包虫重量。

1.3 数据分析

用 Kolmogorov-Smirnov 和 Bartlett 检验分别检验数据的正态性和均质性。选择体温数据无须转化即符合参数检验的条件，表面活动数据经 Arcsine 转化后用于参数检验。相关分析显示个体大小 (SVL) 与表面活动频率、选择体温和摄食量均无显著的相关性 ($P > 0.125$)。用种群来源和断尾处理为处理间因子、测定时间为处理内因子的重复测验方差分析 (Repeated measures ANOVA) 检验种群来源、断尾处理、测定时间及其相互作用对表面活动频率和选择体温的效应。用 2 (有尾 vs 断尾) \times 7 (每日 7 个测定时刻) 联表 (Contingency table) 和 G 检验分析同一种群有尾和断尾蜥活动节律

(即表面活动时间格局) 的异同；用 3 (种群) \times 7 联表和 G 检验分析不同种群蜥活动节律的异同。用种群来源和断尾处理为因子的双因子方差分析检验种群来源、断尾处理及其相互作用对摄食量的效应。描述性统计值用平均值 \pm 标准误表示，多重比较均采用 Tukey 检验，显著性水平设置为 $\alpha = 0.05$ 。

2 结果

共和及哈尔滨种群表面调温个体数显著大于长安种群，断尾组个体表面调温个体数显著大于对照组；08: 00–12: 00 h 表面调温个体数最多且无显著差异，随后逐渐减少；因子相互作用是表面活动个体数的显著变异来源 (图 2, 表 1)。三种群个体均在调温期间 (08: 00–20: 00 h) 显示一定的活动节律，但相同种群的断尾和有尾个体的活动节律无显著差异 ($G_{CA} = 0.916/G_{CH} = 0.424/G_{HRB} = 0.386$, $df = 6$, $P > 0.975$)。合并同种群断尾和有尾蜥的表面活动数据后发现，不同种群的活动节律相同 ($G = 3.530$, $df = 12$, $P > 0.975$)。

长安种群选择体温 (34.2°C) 显著大于共和种群 (33.5°C)，共和种群选择体温显著大于哈尔滨种群 (32.5°C)；有尾个体选择体温 (33.6°C) 显著大于断尾个体 (33.2°C)；14: 00–20: 00 h 时间段选择体温总体上大于 08: 00–12: 00 h 时间段 (图 3, 表 1)。除断尾处理和测定时间相互作用对选择体温有显著的效应外，其它因子相互作用均不是选择体温的显著变异来源 (表 1)。

摄食量种群间差异显著 ($F_{2, 54} = 3.91$, $P = 0.026$)，但断尾对摄食量无显著影响 ($F_{2, 54} =$

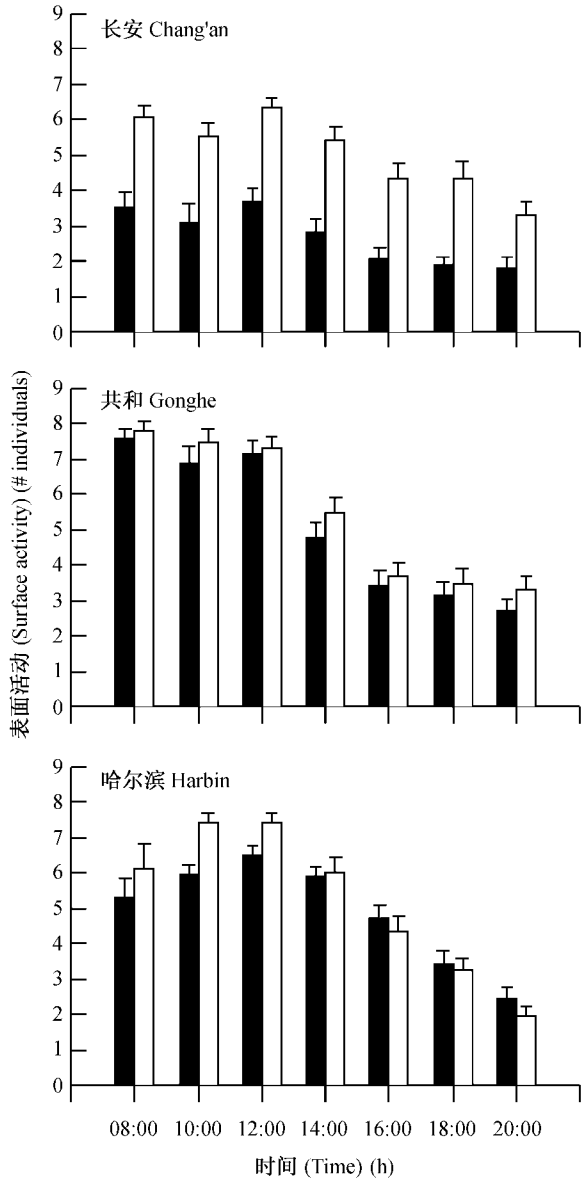


图 2 光照期间不同时间观测到的表面活动
数据用平均值 + 标准误表示。实柱：实验组。空柱：对照组。

Fig.2 Surface activities observed at different times during the photophase

Data are expressed as Mean + SE. Black bars: experimental group.
Open bars: control group.

0.02, $P = 0.878$), 种群来源和断尾处理的相互作用对摄食量无显著影响 ($F_{2, 54} = 0.47$, $P = 0.626$)。Tukey 检验发现：长安种群摄食量显著大于共和种群，与哈尔滨种群无显著差异；共和种群摄食量与哈尔滨种群无显著差异 (图 4)。

3 讨论

本研究中三个地理隔离种群的个体饲养在相同

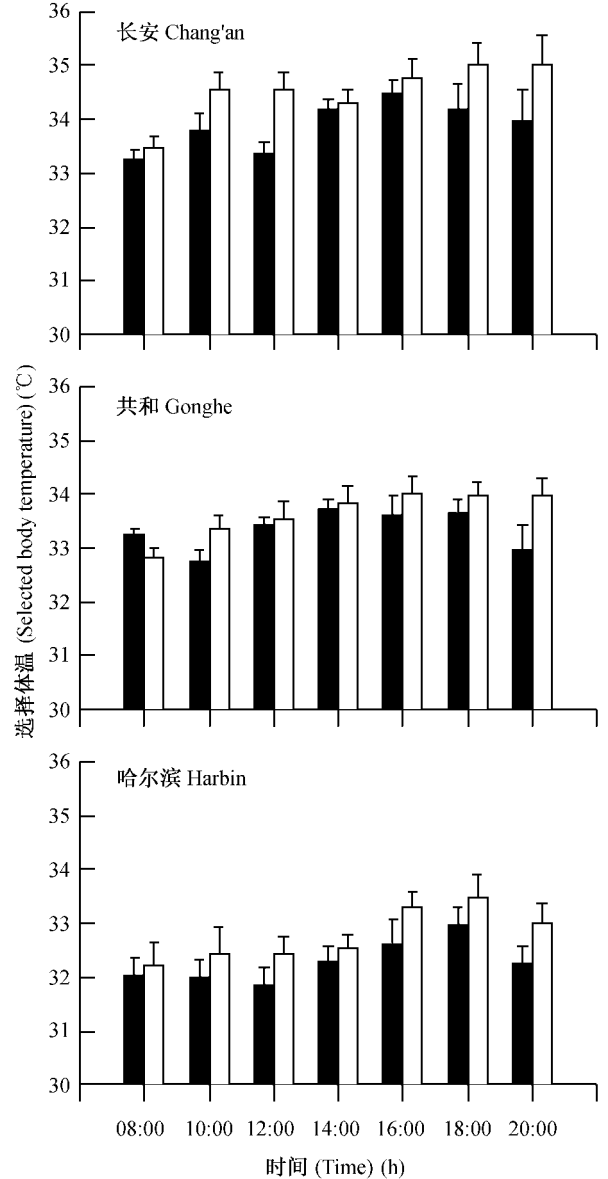


图 3 光照期间不同时间测到的选择体温

数据用平均值 + 标准误表示。实柱：实验组。空柱：对照组。

Fig.3 Selected body temperature measured at different times during the photophase

Data are expressed as mean + SE. Black bars: experimental group.
Open bars: control group.

的实验室条件下，尽管获得的数据不一定代表野外受生物和非生物因子制约条件下的真实情况，但具有可比性。显然，丽斑麻蜥的表面调温个体数 (图 2)、选择体温 (图 3) 和摄食量 (图 4) 存在种群间差异，这些差异与断尾与否无关。共和及哈尔滨种群表面调温个体数大于长安种群，可能与前两个种群所处的纬度 (HRB) 或纬度及海拔 (GH) 较高有关。高纬度、高海拔地区全年及每日适合调温

表 1 用种群来源和断尾处理为处理间、测定时间为处理内因子对表面活动（表面调温个体数）和选择体温进行重复测验方差分析的结果

Table 1 Results of repeated measures analysis of variance on surface activity (the number of lizards thermoregulating on the surface) and selected body temperature, with population source and tail-removing treatment as the between subject factors and measuring time as the within subject factor

效应 Effects	表面活动 Surface activity	选择体温 Selected body temperature
种群来源	$F_{2, 54} = 12.96, P < 0.0001$	$F_{2, 54} = 27.92, P < 0.0001$
Population source (P)	CA ^b , GH ^a , HRB ^a	CA ^a > GH ^b > HRB ^c
断尾处理	$F_{1, 54} = 16.26, P < 0.0002$	$F_{1, 54} = 6.57, P = 0.012$
Tail-removing treatment (TR)	E < C	E < C
测定时间	$F_{6, 324} = 207.91, P < 0.0001$	$F_{6, 324} = 11.73, P < 0.0001$
Measuring time (T)	T08 ^a , T10 ^a , T12 ^a , T14 ^b , T16 ^c , T18 ^d , T20 ^e	T08 ^c , T10 ^{bc} , T12 ^{bc} , T14 ^{ab} , T16 ^a , T18 ^a , T20 ^{ab}
种群来源 × 断尾处理	$F_{2, 54} = 5.41, P < 0.008$	$F_{2, 54} = 0.26, P = 0.775$
P × TR		
种群来源 × 测定时间	$F_{12, 324} = 19.16, P < 0.0001$	$F_{12, 324} = 1.15, P = 0.316$
P × T		
断尾处理 × 测定时间	$F_{6, 324} = 3.47, P < 0.003$	$F_{6, 324} = 2.03, P = 0.061$
TR × T		
种群来源 × 断尾处理 × 测定时间	$F_{12, 324} = 1.61, P = 0.088$	$F_{12, 324} = 0.47, P = 0.932$
P × TR × T		

CA: 长安, GH: 共和, HRB: 哈尔滨; T: 测定时间; E: 实验组, C: 对照组。上标不同的平均值差异显著 (Tukey 多重比较, $\alpha = 0.05$: $a > b > c$)

CA: Chang'an, GH: Gonghe, HRB: Harbin; T: measuring time; E: experimental group, C: control group. Means with different superscripts differ significantly (Tukey's *post hoc* test, $\alpha = 0.05$; $a > b > c$.)

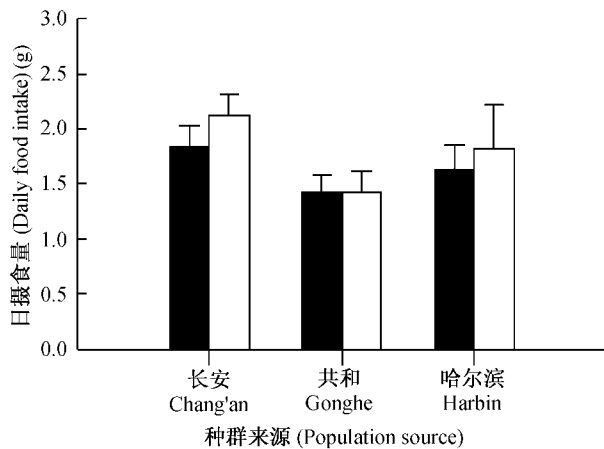


图 4 三个种群实验 ($n = 10$) 和对照 ($n = 10$) 个体摄食量的描述性统计值

数据用平均值 + 标准误表示。实柱: 实验组。空柱: 对照组。

Fig. 4 Descriptive statistics of food intake for experimental ($n = 10$) and control ($n = 10$) lizards from the three populations

Data are expressed as mean + SE. Black bars: experimental group.

Open bars: control group

的时间较短, 生活在这些地区的蜥蜴在适合体温调节的时间段内增加表面活动频率有利于其通过体温调节维持相对较高且稳定的体温, 使得调温个体具

有较好的行为表现, 并能较高水平地表达其生理功能。因增加表面调温活动会增加被天敌捕食的几率, 蜥蜴须通过权衡调温的利益和代价关系来决定表面活动的强度。相对于共和及哈尔滨种群, 长安种群所处的地区相对较为温暖且全年及每日适合调温的时间较长。长安种群表面活动个体数较少是一个可预见的结果, 这不仅因为该种群野外调温机会较多, 还因为地表下温度平均值较高且较稳定, 后者物理性地使该地区蜥蜴更有可能维持相对较高且稳定的体温。因此, 表面活动个体数的种群间差异是不同种群个体对其所处区域热环境长期适应的结果, 具有一定的遗传基础, 相同的实验室经历无法完全去除这一差异。

三个种群断尾个体表面活动频率总体上均低于有尾个体 (图 2), 与作者预测的结果一致。断尾降低表面活动频率见于所有三个种群, 该结果表明丽斑麻蜥同其它已被研究的蜥蜴一样, 尾自切能导致活动水平的改变 (Martin and Salvador, 1993; Salvador et al., 1995)。降低表面活动频率能增加断尾个体的隐蔽性, 从而降低被天敌捕食的几率。同一种群内断尾和有尾个体活动频率的时间格局无显著差异, 不同种群活动频率的时间格局无显著差

异。这些结果表明丽斑麻蜥昼日活动节律具有种的特异性，不受断尾影响，上午活动相对更为频繁（图 2）。

爬行动物的体温显著影响其生理和行为表现（Huey and Kingsolver, 1989）。同其它变温动物一样，爬行动物主要通过改变活动时间、穿梭移动于冷（阴）热（阳）斑块之间和调整身体姿势等行为机制在异质热环境中维持相对较高且稳定的体温（Cowles and Bogert, 1944; Avery, 1982; Huey, 1982）。爬行动物体温调节的精度和调定点决定于调温的利益-代价关系，也受热环境的强烈制约（Huey and Slatkin, 1976; Van Damme et al., 1987; Kearney and Predavec, 2000）。丽斑麻蜥选择体温随纬度或海拔升高而降低，这种变化趋势可能反映了热环境制约的结果。所有三个种群的蜥蜴上午均选择相对较低的体温但表面活动更为频繁。这些观察结果不仅显示了丽斑麻蜥选择体温存在时间变化，还说明了表面和表层覆盖物下活动的丽斑麻蜥均能进行体温调节；此外，这些结果还进一步证实了丽斑麻蜥白日活动节律具有种的特异性。断尾个体的选择体温低于有尾个体，这与作者预测的结果一致。断尾个体选择低体温有利于降低维持能耗，但这是否能在一定程度上补偿断尾的能量（丢失）代价待进一步论证。然而，所有三个种群断尾个体均选择较低体温的结果说明断尾能改变丽斑麻蜥的体温调定点，并可能会改变与体温有关的生理和行为表现。

丽斑麻蜥摄食量存在种群间差异，但目前尚无足够的证据对导致这种差异的原因展开讨论并做出相关推测。与作者预测结果不同的是，三个种群断尾个体均未增加摄食来满足尾再生的额外能量需求。对野外个体而言，惟有通过增加活动才有可能增加摄食量，但活动能耗和被捕食风险会对动物增加活动产生强烈的制约作用。实验室饱和给食条件下并未发现断尾个体增加摄食量，表明增加摄食不是丽斑麻蜥补偿断尾能量代价的对策。

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