

北草蜥禁食期间喜好体温的漂移*

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Northern grass lizards *Takydromus septentrionalis* (Lacertidae) shift thermal preferences when fasted*

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Abstract We used *Takydromus septentrionalis* as a model animal to examine whether lizards shift thermal preferences when fasted. The experiment was conducted in March 2007. Thirty-six adults collected from Shengsi, Zhoushan Islands, were equally assigned to experimental (fasted) and control (fed) groups, with nine housed together in a 0.6 m × 0.2 m × 0.5 m glass cage with moist soil (10 cm in depth), debris and grasses. A 100-W light bulb suspended above one end of each cage created a thermal gradient ranging from room temperatures (15°C – 24°C) to 60°C for 12 h daily, so that lizards could thermoregulate during the photophase. Prior to the experiment, lizards were allowed to feed on mealworms (larvae of *Tenebrio molitor*) for 10 days. Thereafter experimental lizards were fasted for 20 days, and were measured for thermal preferences on Day 1 – 10, Day 15 and Day 20 since fasting. We found in fasted lizards that selected body temperature (Tsel, a measure of thermal preference) gradually decreased from 32.4°C to 30.9°C in the first four days, and then increased to a level similar to that (32.9°C) recorded in the controls. Lizards fasted for 9 days or longer did not differ from controls in Tsel. Our study is the first to demonstrate that lizards fasted for a prolonged time may shift thermal preferences in a pattern well fitting to a Gaussian peak curve [Acta Zoologica Sinica 54 (4): 739 – 743, 2008].

Key words Lacertidae, northern grass lizard, *Takydromus septentrionalis*, Fast, Thermal preference, Gaussian peak curve, Thermoregulation

关键词 蜥蜴科 北草蜥 禁食 喜好体温 高斯峰曲线 体温调节

爬行动物在异质热环境中能通过行为调温将体温调节到相对较高且稳定的水平, 以较好地表达行为和生理功能 (Avery, 1982; Bartholomew, 1982; Huey, 1982)。爬行动物不同行为和生理功能的最适温度存在差异, 无任何特定的体温可使所有行为和生理功能都达到最高水平的表达 (Huey and Berrigan, 1996; Xu and Ji, 2006)。因此, 爬行动物

的喜好体温 (Preferred body temperature) 是其兼顾各项行为和生理功能最适温度的结果, 受激素水平、年龄、繁殖状态、热驯化、光照周期等多种内外因素的影响 (Patterson and Davies, 1978; Andrews, 1998; Rock et al., 2000; Lutterschmidt et al., 2002; Llewelyn et al., 2005; Lin et al., 2008)。野外爬行动物试图通过体温调节达到的喜好体温可通过测定实

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实验室梯度热环境下调温个体的选择体温 (Tsel, selected body temperature) 来估算 (Hutchison, 1976)。

爬行动物的喜好体温受摄食和摄入食物类型影响。例如, 澳洲沙漠鬣蜥 (*Amphibolurus nuchalis*) 摄入富含饱和脂肪酸食物后选择相对较高的体温 (Geiser and Learmonth, 1994), 澳洲短尾石龙子 (*Tiliqua rugosa*) 摄入含不饱和脂肪酸食物后选择相对较低的体温 (Geiser et al., 1992), 叩壁蜥 (*Sauromalus obesus*) 体温摄入纤维类食物后选择体温无显著变化 (Nussear et al., 1998)。蜥蜴在饥饿状态下选择较低的体温具有普遍性, 该现象在经常性处于空腹状态的动物中表现得尤其显著 (Huey et al., 2001)。例如, 安乐蜥 (*Anolis carolinensis*) 饥饿 5 天后体温调定点明显降低 (Brown and Griffin, 2005), 青海沙蜥 (*Phrynocephalus vlangalii*) 短时间禁食后会选择较低的体温 (丁国骅等, 2007)。然而, 目前尚缺乏爬行动物在禁食更长时间情况下如何漂移其喜好体温的报道。

北草蜥 (*Takydromus septentrionalis*) 是中国特有的卵生蜥蜴科动物, 亦是国内多项爬行动物生理生态学研究的模型动物, 其中热生物学方面的研究主要涉及运动表现和食物同化的热依赖性 (Ji et al., 1993, 1996)、Tsel 及其时空变异的原因分析 (杜卫国等, 2000; Du, 2006; Yang et al., 2008)、热环境对孵化卵和孵出幼体表型特征的影响 (林植华、计翔, 1998; Du and Ji, 2006) 等。本文中, 我们研究北草蜥禁食较长时间后喜好体温的变化模式。

1 材料与方 法

1.1 动物采集与饲养

研究用蜥蜴于 2006 年 4 月捕自浙江舟山嵊泗岛, 雌体在实验室完成当年产卵。当年 10 月挑选部分状态良好的成体, 将其移入直径 1 m、高 0.6 m 的室外围栏内, 围栏底部铺设 30 cm 厚的潮湿沙土, 其上覆盖草皮和碎瓦以模拟蜥蜴野外生存环境。提供足量黄粉虫 (*Tenebrio molitor*) 幼虫和添加维生素和钙粉的饮水, 以满足蜥蜴的营养需求。围栏内温度自然波动, 蜥蜴在围栏内越冬, 越冬前可利用外热源进行体温调节。

1.2 选择体温测定

选 36 条 2007 年 3 月出眠后数天、体长 (Snout-vent length) 58 – 79 mm 的成体, 将其均分为实验 (禁食) 组 (7 ♀♀: 11 ♂♂) 和对照组 (7 ♀♀:

11 ♂♂)。分组后蜥蜴移至铺有杂草和瓦片的 0.6 m × 0.2 m × 0.5 m (长 × 高 × 宽) 玻璃缸内, 每缸 9 条。玻璃缸置于 15°C – 24°C 的饲养室内, 缸一端悬挂一只 100 W 加热灯泡, 光照周期为 12L:12D, 06:00 h 自动开启灯泡; 光照期间, 缸内形成从室温到 60°C 的连续温度梯度。蜥蜴在灯泡开启期间可自主调温、摄食和饮水。

饲养 10 d 后, 于 11:00、13:00 和 15:00 h 前后 15 min 时间段用数字温度计测定实验和对照组蜥蜴的体温 (泄殖腔温度), 随后称蜥蜴体重。完成体温和体重测定后移去实验组缸内所有食物, 仅提供饮水。禁食 1 – 10 d 内每日在上述相同的时间段测定禁食蜥蜴体温, 禁食第 15 d 和第 20 d 后再测定其体温。北草蜥 Tsel 缺乏日节律变化 (杜卫国等, 2000), 故用测定当日 3 次测定的体温平均值表示其 Tsel; 不同天测得的摄食北草蜥 Tsel 缺乏时间变异 (Yang et al., 2008), 故用禁食起始日 3 次测定的体温平均值表示对照蜥蜴的 Tsel。实验期间, 每隔 5 天称禁食蜥蜴体重。

1.3 数据分析

用 Statistica Version 5.0 统计软件包分析所有数据。用 Kolmogorov-Smirnov 和 Bartlett 检验分别检验数据的正态性和均质性。Tsel 和体重数据均无须转化即符合参数检验的条件。用单因子方差分析、重复测量方差分析和 Tukey 多重比较等方法分析相应的数据。描述性统计值用平均值 ± 标准误表示, 显著性水平设置为 $\alpha = 0.05$ 。

2 结 果

实验组雌、雄蜥蜴禁食起始日的体重分别 7.6 ± 0.5 g (5.7 – 9.5 g) 和 $8.0 \text{ g} \pm 0.3$ g (6.4 – 9.6 g), 平均体重无显著两性差异 ($F_{1, 16} = 0.58$, $P = 0.458$)。以性别为处理间因子、禁食时间为处理内因子的重复测量方差分析显示实验期间体重变化无显著两性差异 ($F_{1, 16} = 0.55$, $P = 0.468$)、不同禁食时间体重差异显著 ($F_{4, 64} = 70.06$, $P < 0.0001$)、性别和禁食时间的交互作用对体重变化无显著影响 ($F_{4, 64} = 0.56$, $P = 0.689$)。合并两性数据后的重复测量方差分析显示实验期间体重变化显著 ($F_{4, 64} = 74.61$, $P < 0.0001$), 持续递减, 至禁食第 20 d 两性平均减重 $81.1\% \pm 1.7\%$ (68.3% – 93.1%)。

以性别为处理间因子、禁食时间为处理内因子的重复测量方差分析显示禁食蜥蜴 Tsel 变化无显著

两性差异 ($F_{1, 16} = 0.55$, $P = 0.468$)、不同禁食时间的 T_{sel} 差异显著 ($F_{12, 192} = 4.97$, $P < 0.0001$)、性别和禁食时间的交互作用对 T_{sel} 变化无显著影响 ($F_{12, 192} = 0.44$, $P = 0.945$)。合并两性数据后的重复测量方差分析显示实验期间禁食蜥蜴 T_{sel} 变化显著 ($F_{12, 204} = 5.20$, $P < 0.0001$)， T_{sel} 平均值从禁食起始日的 $32.4^{\circ}\text{C} \pm 1.3^{\circ}\text{C}$ ($30.4 - 34.2^{\circ}\text{C}$) 降至第 4 d 的最低值 $30.9^{\circ}\text{C} \pm 1.3^{\circ}\text{C}$ ($29.3 - 33.3^{\circ}\text{C}$)，

两者差异显著 (Tukey *post hoc* test, $P < 0.008$)；禁食第 5 d 后 T_{sel} 平均值逐渐增大 (图 1)；禁食第 9 d 及以后测得的 T_{sel} 与起禁食始日相近 ($F_{4, 68} = 0.77$, $P = 0.546$)，这些 T_{sel} 的总平均值 [$32.6^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$ ($31.6 - 34.0^{\circ}\text{C}$)] 与对照组 [$32.9^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ ($30.1 - 34.8^{\circ}\text{C}$)] 无显著差异 ($F_{1, 34} = 1.14$, $P = 0.293$)。

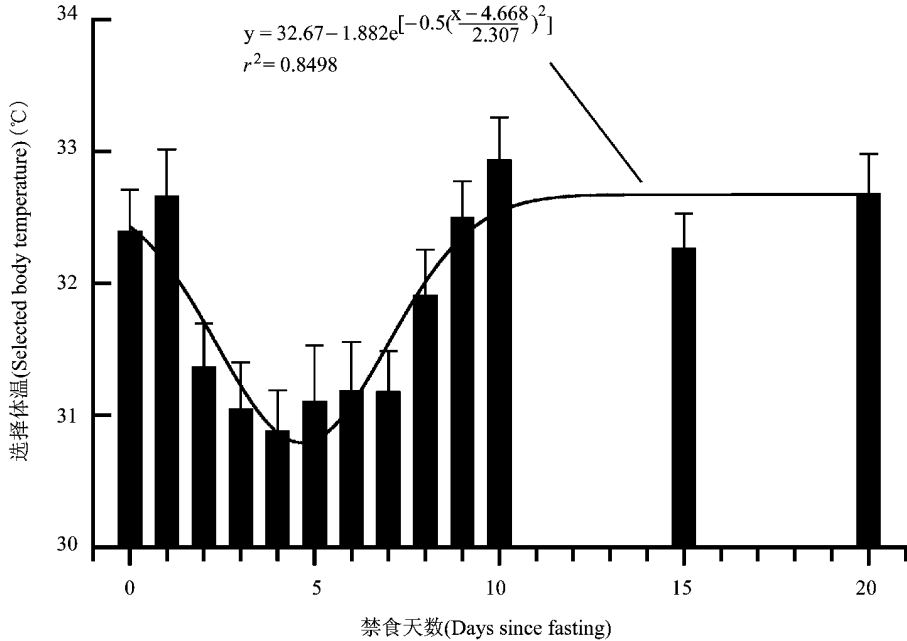


图 1 禁食北草蜥喜好体温的时间变化

数据用平均值 + 标准误差表示。用高斯峰曲线对两性选择体温合并的原始数据进行拟合，图中给出相关曲线的函数

Fig. 1 Temporal variation in thermal preferences in fasted northern grass lizards

Data are expressed as mean + SE. The curve is generated from a Gaussian peak curve on the original data of selected body temperatures pooled for both sexes, and the relevant function is given in the figure

3 讨论

北草蜥禁食期间体重持续下降是一个可预见的结果，因为维持需要消耗能量。舟山北草蜥的产卵期通常为 5–7 月 (Ji et al., 1998)，该种形成一窝卵所需要的时间一般不超出 30 d (Ji et al., 2007a)，据此判断实验期间雌体处于非繁殖期。同该种前期研究 (Ji et al., 1996; Yang et al., 2008) 以及印度蜓蜥 (*Sphenomorphus indicus*; Ji et al., 2006)、多线南蜥 (*Mabuya multifasciata*; Ji et al., 2007b; Lin et al., 2008) 等蜥蜴得到的结果一致，非繁殖期北草蜥的喜好体温不存在两性差异。本研究测得的选择体温普遍高于直接捕自舟山野外的

北草蜥 (平均 30.0°C ; Ji et al., 1996)，这可能与测定前蜥蜴的热驯化条件存在差异有关。例如，高温驯化导致喜好体温向上漂移，低温驯化则导致喜好体温向下漂移 (Yang et al., 2008)。

本项研究最令人瞩目的结果是北草蜥禁食期间喜好体温存在规律性的漂移。北草蜥禁食 4 d 期间内喜好体温持续下降，与安乐蜥 (Brown and Griffin, 2005) 和青海沙蜥 (丁国弊等, 2007) 在短期禁食条件下选择较低体温的结果基本一致，但后两种蜥蜴中缺乏禁食更长时间喜好体温变化的数据。本研究中，北草蜥平均喜好体温从禁食起始日的 32.4°C 降至禁食第 4 d 的 30.9°C (最低值)，减幅约 1.5°C 。这个温度差值与安乐蜥 (Brown and

Griffin, 2005) 和青海沙蜥 (丁国骅等, 2007) 在短期禁食条件下喜好体温的减幅相近。蜥蜴短期禁食后为什么选择相对较低的体温? 答案可能在于: (1) 蜥蜴同其它变温动物一样代谢率随体温升高而增加, 选择低体温有利于降低维持能耗; (2) 体温在一定范围内变化对蜥蜴消化或同化效率无显著的影响 (Xu and Ji, 2006), 短期禁食的蜥蜴通常并非处于排空摄入食物或吸收后状态, 体温稍向下漂移对其继续消化和吸收消化道内残留食物无任何重要影响。例如, 在 28°C – 36°C 范围内, 体温对北草蜥食物同化能力无显著影响 (Ji et al., 1996)。

北草蜥在禁食第 5 d 后逐渐提高喜好体温水平, 禁食第 9 d 后选择与禁食起始日和 (摄食) 对照个体几乎相同的体温且保持相对稳定 (图 1)。这种喜好体温在禁食期间先降后增的漂移模式从未见文献报道, 当前尚难以对此现象开展深入的讨论。禁食更长时间的北草蜥向上漂移喜好体温的利益何在? 本研究结果显示禁食 9 d 后喜好体温的总平均值 32.6°C, 这个体温与舟山北草蜥最大程度地表达运动潜力的体温 (~32°C; Ji et al., 1996) 十分吻合。向上漂移喜好体温固然会增加维持能耗, 但同时能强化逃避天敌、捕捉食饵所必须的运动能力 (Pough, 1989; Bauwens et al., 1995; Miles et al., 1995)。因此, 禁食较长时间的北草蜥将喜好体温漂移至接近 32°C 的水平极可能是其综合权衡利益 – 代价关系后的结果。由于缺乏来自更多物种的可比数据, 北草蜥禁食期间喜好体温的漂移模式是否具有普遍性尚待进一步研究。

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