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升温对北草蜥雌体繁殖、卵孵化及幼体特征的影响

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摘要:在围栏条件下,比较升温和对照处理北草蜥(*Takydromus septentrionalis*)繁殖、卵孵化及幼体特征的差异,以揭示升温对其繁殖生活史特征的作用。升温处理对北草蜥母体体温有显著影响,但并不影响其繁殖输出。升温显著影响卵孵化期和幼体的运动能力,但不影响幼体大小等形态特征。升温条件下孵出的幼体运动能力较弱。结果表明,北草蜥母体能耐受短期的环境增温,维持相对恒定的繁殖输出;升温能影响幼体的功能表现,进而可能改变后代适合度。

关键词:北草蜥;气候变暖;繁殖输出;后代表型

The effects of warming on female reproduction, egg incubation and hatchling traits in the northern grass lizard, *Takydromus septentrionalis*

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Abstract: The potential influence of climate warming on organisms has long been acknowledged, but experimental tests of climate on life history traits of vertebrates are rare. Here we carried out an experiment to test the effects of increased ambient temperature on reproductive life history and hatchling traits of the northern grass lizard (*Takydromus septentrionalis*, Lacertidae). Adult northern grass lizards (60 females and 28 males) were captured from Wenzhou County of Eastern China in early April, the beginning of reproductive season. After the lizards were measured (snout-vent length and body mass), they were randomly assigned and maintained in warming or control outdoor enclosures (1.5m diameter). We provided two additional 100w infrared lamps in each warming enclosure to increase the ambient temperature. Ambient temperatures in the enclosures were recorded using temperature data-loggers (ibuttons, MAXIM Integrated Products Ltd, USA). Body temperatures of the females were monitored once a week using an electronic contact thermometer. Clutches of eggs laid by the females were collected to determine female reproductive traits including clutch frequency, clutch size, clutch mass, and egg mass. Eggs from the females were incubated at warming or control treatments in a split-clutch design. Young lizards were weighed and measured (snout-vent length, tail length and head width) within 24 h of hatching and their locomotor performance was then measured at 30℃. Repeated measures ANOVA was used to compare the between-treatment difference in body temperatures. ANOVA or ANCOVA was applied to examine the influence of the warming treatment on reproductive traits (with a covariate of female snout-vent length) and hatchling traits (with a covariate of initial egg mass). The mean ambient temperature in warming enclosures was 2℃ higher than that in control enclosures during the experimental period. Similarly, the mean temperature of egg incubation in the warming treatment was 2.5℃ higher than that of the control. Body temperatures were significantly affected by the warming treatment, and were 1.1℃ higher for females in the warming enclosures than in the control enclosures. All female reproductive traits measured in the current study were unaffected by the warming treatment. Hatchlings from eggs incubated in the warming treatment hatched sooner, but had decreased

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locomotor performance than their siblings from the control treatment. However, hatching success and hatchling body size did not differ between the treatments. These results indicate that (1) female *T. septentrionalis* can regulate body temperature to alleviate the impact of warming, given that the difference of body temperature between the treatments was smaller than that of ambient temperature, (2) females can maintain a relatively constant reproductive output relatively constant when facing short-term temperature increases; (3) temperature increases may decrease the functional performance of hatchlings, and potentially impose negative effects on offspring fitness.

Key Words: *Takydromus septentrionalis*; climate warming; reproductive output; offspring phenotype

气候变暖是全球变化的重要组分[1]。全球气候变暖可改变物种生态与遗传特征,群落结构及生物多样性,甚至导致物种的绝灭[2-7]。气候变暖作用于生物的过程必然涉及改变物种生活史特征,进而影响其种群生存力[8-9]。然而,迄今有关气候变暖对自然种群生活史特征影响的研究尚非常有限,气温上升影响生活史特征的实验研究则更不多见。

作为外温动物,爬行动物的生活史特征显著受环境温度的影响。已有研究表明环境温度能显著影响动物的繁殖、胚胎发育、后代大小、胚后生长乃至后代性别[10-16]。大多卵生蜥蜴生活史周期短,胚胎在母体体外发育,且缺乏亲代抚育行为,胚胎和个体发育均受制于环境温度[17]。因此,卵生蜥蜴是气候变暖影响爬行动物生活史实验研究的适宜模型。

北草蜥(*Takydromus septentrionalis*)为一种小型昼行性卵生蜥蜴,广泛分布于中国中部和南方各省[18]。该物种自然种群生活史特征存在种群间和年间变异[19-22]。环境温度为其繁殖输出、胚胎发育和幼体大小等特征的重要影响因子之一[23-24]。本研究在上述前期工作的基础上,进一步开展围栏种群人工增温实验,比较增温条件下北草蜥繁殖、卵孵化和幼体特征与对照个体的差异,旨在揭示环境升温对北草蜥繁殖生活史特征的作用。

1　材料与方法

1.1　北草蜥采集与测量

研究用北草蜥于 2007 年的 4 月上旬捕自温州洞头岛(27.85N, 121.13E)。捕获的北草蜥成体带回杭州师范大学实验室后测定体重(±0.01g)(AB135-S Mettler 电子天平,瑞士)、体长和尾长(±0.01mm)(Mitutoyo 数显游标卡尺,日本),并逐一剪趾标号。应用随机数字表将编号后的动物分为加温和常温两个组。

1.2　实验设计、动物饲养及体温测定

实验在 4 个置于自然光照条件下的镀锌钢板圆形围栏(直径 1.5m)中进行,围栏分为升温和对照两种处理:加热围栏上方悬挂 2 盏 100W 的陶瓷加热器,对照围栏则无附加热源。

北草蜥随机分组(升温组:30♀14♂;对照组:30♀14♂)饲养于不同处理围栏中,围栏内覆盖泥土和草皮以模拟动物野外生境,每个围栏内饲养 15 条雌体,7 条雄体,提供足量的食物[黄粉虫幼虫(*Tenebrio molitor*)和蟋蟀(*Gryllus chi-nensis*)]和水(混有钙粉和维生素)。

在各围栏内随机放置 7 个 iButton 温度记录器(DS1921, 5.9 mm × 17.4 mm, 3.12 g, MAXIM 集成电路产品公司,Dallas, USA),设置每隔 0.5h 自动记录 1 次围栏环境温度。用 DM6801A 电子点温计(深圳胜利仪表有限公司)测定北草蜥 08:00,11:00,14:00 和 17:00 的泄殖腔体温。

1.3　母体产卵和孵化

每周检查雌体的怀卵状况,将怀后期卵的北草蜥雌体置于 200mm × 200mm × 400 mm(长 × 宽 × 高)的产卵缸中单独饲养,每天观测 3—4 次,及时收集新生卵。产后母体测量体重(±0.01g)和体长(±0.01mm)后放回围栏中饲养。

同窝新生卵称重后平均分配孵入升温和对照处理中。卵置于 170mm × 110mm × 50mm 孵化盒中,内装 -220kPa潮湿基质(干蛭石和水 1:1 混合)。孵化盒覆盖保鲜膜,减少水分散失以保持基质湿度。所有孵化盒

置于模拟自然巢穴的室外地面凹槽内,其中升温处理孵化盒上悬挂 60W 陶瓷加热器。在孵化盒中放置 iButton 温度记录器自动记录孵化温度。

1.4 测定孵化期,幼体形态特征及运动表现

孵化期为卵产出至幼体孵出的天数。孵出后,测定幼体重(±0.001g)及体长、尾长和头宽(±0.01mm)(左右颌关节间距)。通过观察幼体有无半阴茎来确定其性别。随后,将幼体置于 30℃恒温培养箱中适应 30 min,在木制跑道(2000mm 长 × 150mm 宽)上测试其运动能力,用摄像机(NV-GS38 松下数码摄像机)记录北草蜥幼体运动视频,导入电脑中分析计算 250mm 距离内的最大速度和 2m 内的平均速度。

1.5 数据处理

用 Kolmogorov-Smirnov 和 Bartlett 检验分别检验数据正态性和方差同质性,所有数据均符合参数统计条件。相对窝卵重为窝卵重与产后母体体重的比值[25]。产多窝卵母体的繁殖特征无显著窝间差异,故数据合并。应用重复测量 ANOVA 比较成体体温的处理间差异,应用 ANOVA 及 ANCOVA 比较母体繁殖输出处理间差异,应用双因子 ANOVA 检测幼体特征的组间差异。文中描述性统计值用平均值 ± 标准误表示,检验的显著水平设置为 $\alpha = 0.05$。

2 结果

2.1 升温处理对北草蜥体温的影响

升温围栏的日平均温度(26.1 ± 0.5)℃显著高于对照围栏(24.1 ± 0.5)℃($F_{1,94} = 8.6$, $P = 0.004$)(图 1)。升温处理导致动物体温相应升高,升温组蜥蜴体温高于对照个体($F_{1,38} = 12.18$, $P = 0.001$);早晚动物体温较低($F_{3,196} = 55.71$, $P < 0.0001$)。实验期间升温组北草蜥个体平均体温较对照组个体高 1.1℃ [升温:(30.3 ± 0.2)℃;对照:(29.2 ± 0.2)℃](图 2)。

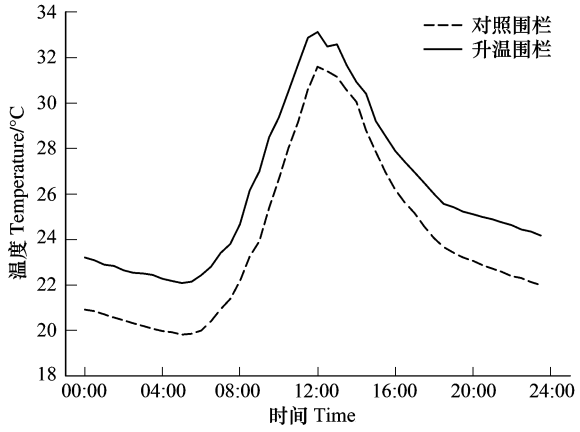

图 1 升温和对照围栏的平均温度日变异

Fig. 1 The daily variation of mean ambient temperatures in the warming and control enclosures

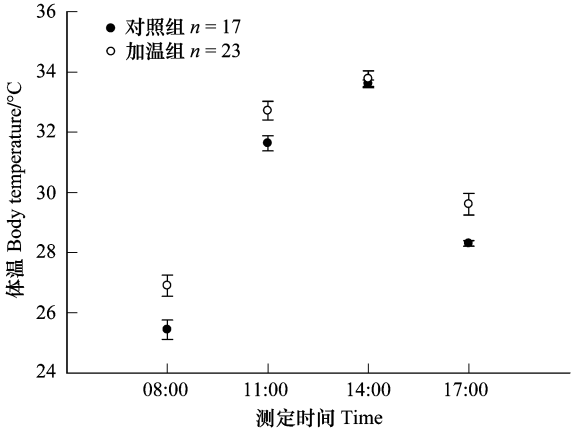

图 2 升温和对照围栏北草蜥雌体体温

Fig. 2 Body temperatures of female northern grass lizards (*Takydromus septentrionalis*) in the warming and control enclosures

2.2 升温处理对北草蜥母体繁殖特征的影响

实验期间,对照组 81.5%(22/27)的母体产卵,而升温组 76.9%(20/26)的母体产卵,两者无差异($X^2 = 2.311$, $df = 1$, $P = 0.129$)。升温处理对北草蜥母体的繁殖频率、总产卵量、总卵重和产卵间隔(第一窝卵与第二窝卵之间的时间间隔)无显著影响(表 1)。

处理间母体产前产后身体状态皆无差异(产前:$F_{1,40} = 0.588$, $P = 0.448$; 产后:$F_{1,40} = 0.515$, $P = 0.477$)。母体产后体长与窝卵重和窝卵数呈正相关(窝卵重:$F_{1,40} = 7.949$, $P = 0.007$; 窝卵数:$F_{1,40} = 4.335$, $P = 0.044$),与平均卵重则无关($F_{1,40} = 0.391$, $P = 0.535$)。升温处理对母体产后体重及单窝卵繁殖特征均

无显著影响(表 1)。

表 1　升温和对照处理下北草蜥的雌体繁殖输出

Table 1　Reproductive output of female northern grass lizard (*Takydromus septentrionalis*) maintained warming enclosures versus control enclosures

项目 Item	处理组(N=20) Warming	对照组(N=22) Control	差异显著性 Significance
繁殖频率 Clutch frequency	1.850 ±0.150	2.136 ±0.119	$F_{1,40}$=2.270, P=0.140
总产卵量 Eggs produced	5.250 ±0.566	6.272 ±0.480	$F_{1,40}$=1.922, P=0.173
总卵重 Total mass of eggs/g	1.367 ±0.150	1.618 ±0.121	$F_{1,40}$=1.724, P=0.200
产卵间隔 Clutch interval/d	14.275 ±2.752	19.068 ±1.916	$F_{1,40}$=2.103, P=0.155
母体产后体重 Post-oviposition body mass/g	4.684 ±0.197	4.428 ±0.134	$F_{1,40}$=1.193, P=0.281
窝卵数 Clutch size	2.942 ±0.194	2.917 ±0.153	$F_{2,39}$=0.086, P=0.771
窝卵重 Clutch mass/g	0.754 ±0.044	0.752 ±0.040	$F_{2,39}$=0.259, P=0.615
平均卵重 mean egg mass/g	0.262 ±0.007	0.262 ±0.007	$F_{1,40}$=0.001, P=0.976
相对窝卵重 Relative clutch mass	0.163 ±0.009	0.172 ±0.009	$F_{1,40}$=0.590, P=0.447

2.3　北草蜥卵孵化期,孵化成功率和幼体特征

升温组与对照组平均孵化温度相差 2.5℃ [升温组:26.3℃(20.0 — 37.8℃);对照组:23.8℃(18.8 — 34.3℃)](图 3)。升温显著缩短卵孵化期(表 2),但不影响孵化成功率(升温组:88.89%;对照组: 86.05%; X^2=0.05, df=1, P=0.83)。

尽管升温处理对幼体形态特征的影响并不显著,但升温条件下孵出的新生幼体的运动能力显著低于对照幼体(表 2,图 4)。升温和对照组幼体的体长均存在显著的两性差异,但其他形态指标和运动能力并无两性差异(表 2,图 4)。

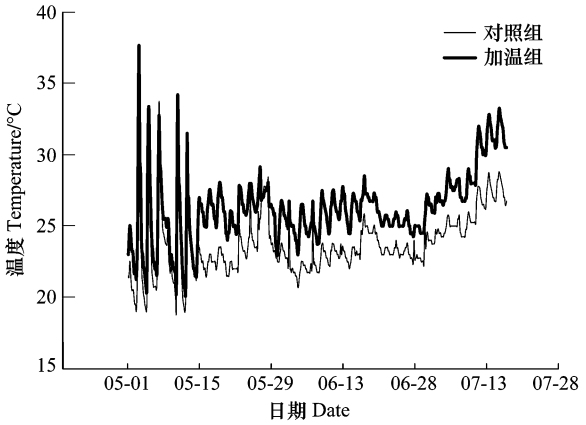

图 3　升温和对照处理中卵的孵化温度

Fig. 3　The profiles of incubation temperatures experienced by *Takydromus septentrionalis* eggs in warming and control treatments

3　讨论

环境温度是影响蜥蜴生活史特征的一个重要因子[26]。然而,本研究显示环境温度升高仅影响北草蜥的体温,并未导致其母体繁殖生活史特征的改变。究其原因,第一,北草蜥首窝卵所需的能量主要来源于繁殖季

表 2　升温和对照处理下北草蜥卵孵化和孵出幼体特征的比较

Table 2　Comparisons on the traits of eggs incubation and hatchlings in the northern grass lizard (*Takydromus septentrionalis*) kept at warming and control environments

项目 Item	处理 Treatment	性别 Sex	交互作用 Interaction
孵化期 Incubation duration	$F_{1,120}$=89.904, P < 0.0001	$F_{1,120}$=0.088, P=0.767	$F_{1,120}$=0.303, P=0.583
体重 Body mass	$F_{1,118}$=1.318, P=0.324	$F_{1,118}$=0.280, P=0.598	$F_{1,118}$=0.086, P=0.770
体长 Snout-vent length	$F_{1,118}$=1.318, P=0.253	$F_{1,118}$=7.068, P=0.009	$F_{1,118}$=1.137, P=0.288
尾长 Tail length	$F_{1,118}$=5.161, P=0.025	$F_{1,118}$=0.010, P=0.753	$F_{1,118}$=5.832, P=0.017
头宽 Head width	$F_{1,118}$=3.564, P=0.061	$F_{1,118}$=0.158, P=0.692	$F_{1,118}$=3.381, P=0.068
最大跑速 Sprint speed	$F_{1,81}$=7.420, P=0.008	$F_{1,81}$=0.904, P=0.344	$F_{1,81}$=0.240, P=0.625
平均跑速 Average speed	$F_{1,81}$=9.381, P=0.003	$F_{1,81}$=0.834, P=0.364	$F_{1,81}$=1.148, P=0.287

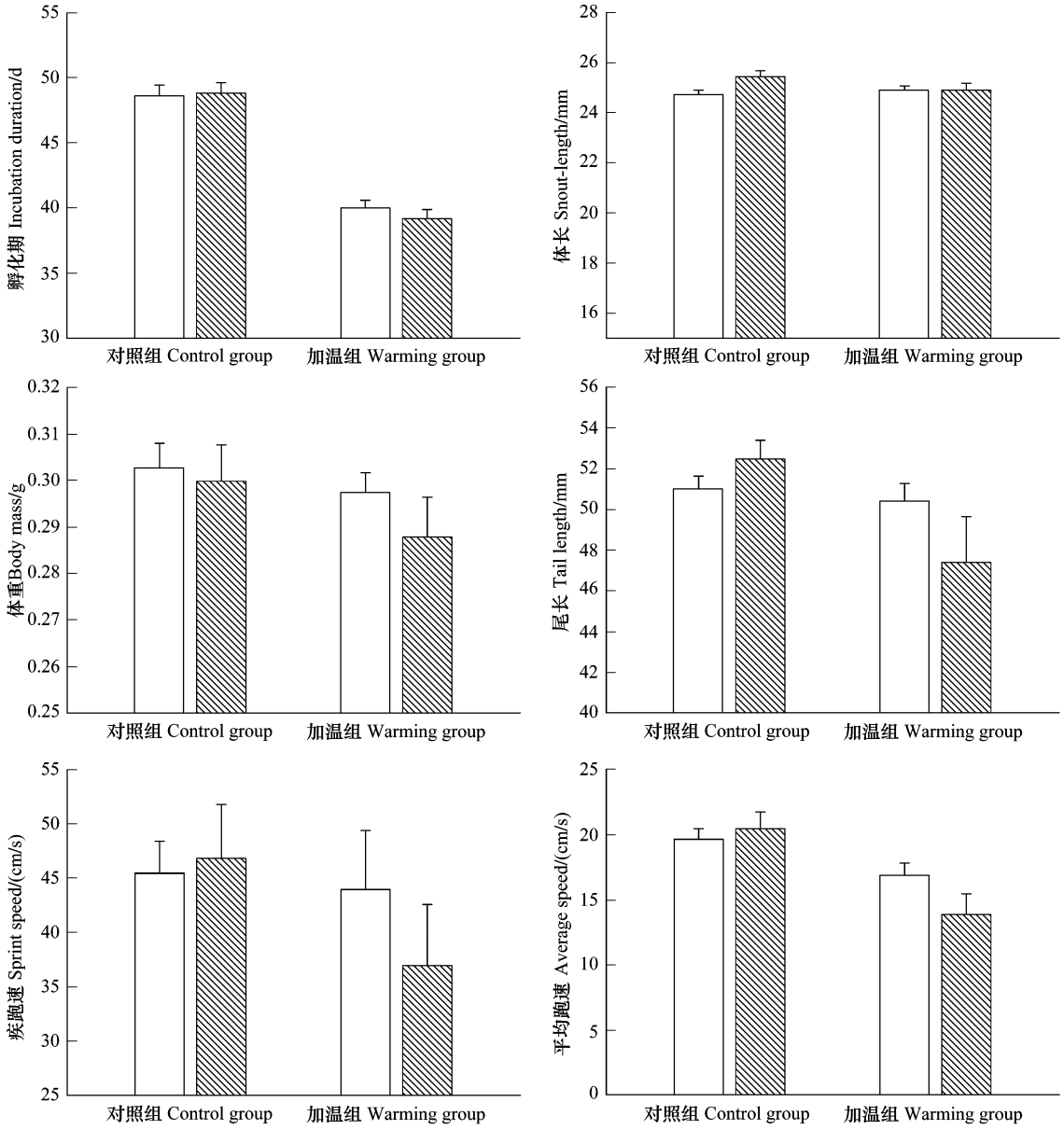

图 4 不同温度处理下的北草蜥卵孵化期和幼体体重、体长、尾长和运动表现

Fig. 4 Incubation duration, body mass, snout-vent length and tail length of hatchling lizards (*Takydromus septentrionalis*) from eggs incubated at different temperature treatments

节前的储备[27-28],而本实验处理开始于繁殖初期的 4 月份,不影响其繁殖期前的能量储备。第二,北草蜥后续窝卵所需的能量主要来源于繁殖季节的即时摄入[28],而本研究升温和对照组蜥蜴体温差异仅 1.1℃,不足以导致动物能量获取的差异[29]。因此,升温处理对雌体繁殖输出无显著影响。当然,自然条件下的温度作用可能比在食物充足的人工围栏条件下更为复杂。环境温度变化可导致食物种类或可利用性的差异,进而间接影响动物的生长速率、产卵频率、窝卵数和后代大小等生活史特征[30-31]。

卵生爬行动物胚胎发育及幼体的形态特征,运动表现和生长速度等显著受环境温度的影响[11],北草蜥亦不例外。前期恒温孵化研究表明:随着孵化温度的上升,孵化期呈非线性缩短。孵化温度能影响孵出幼体的形态和运动表现[19, 23]。本研究则显示,升温组卵的孵化期较对照组卵的孵化期平均缩短了 8.5d,符合前期研究有关北草蜥孵化温度与孵化期关系的结论[18, 23]。在本实验中,升温处理对后代特征的影响主要表现为幼体运动能力的差异。升温条件下孵出幼体的最大跑速和平均跑速均显著低于对照组幼体。在升温条件下,

卵孵化过程中经历了一段时间的 30℃以上高温环境(图 3)。高温孵化能导致北草蜥后代运动能力减弱[19, 23],因此,升温处理组幼体的运动能力较弱与前期研究结论吻合。幼体功能表现一直被认为与其适合度密切相关。虽然本研究未直接测定升温组幼体运动能力降低与其适合度的关系,但是,类似研究提示,此种运动能力下降可影响其后代适合度,进而影响种群生存力[28, 32]。

概括而言,模拟气候变暖的升温并不显著影响北草蜥的繁殖输出,但对胚胎发育速率和幼体的运动表现有显著影响。该结果提示:北草蜥母体能耐受短期的环境温度上升,维持相对恒定的繁殖输出。然而,环境升温能影响幼体的功能表现。若环境条件持续变化(如气候变暖),个体功能表现的改变可能对其适合度产生负面影响。因此,进一步的长期实验研究可深入揭示气温上升对个体生活史特征、适合度和种群生存力的影响。

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References:

[1] Easterling D R, Horton B, Jones P D, Peterson T C, Karl T R, Parker D E, James Salinger M, Razuvayev V, Plummer N, Jamason P, Folland C k. Maximum and minimum temperature trends for the globe. Science, 1997, 277: 364-367.

[2] Hughes L. Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution, 2000, 15: 56-61.

[3] Root T L, Price J T, Hall K R, Schneider S H, Rosenzweig C, Pounds J A. Fingerprints of global warming on wild animals and plants. Nature, 2003, 421: 57-60.

[4] Thomas C D, Cameron A, Green R E, Bakkenes M, Beaumont L J, Collingham Y C, Erasmus B F N, Siqueira M F, Grainger A, Lee Hannah L, Hughes L, Huntley B, van Jaarsveld A S, Midgley G F, Miles L, Ortega-Huerta M A, Townsend Peterson, Phillips O L, Williams S E. Extinction risk from climate change. Nature, 2004, 427: 145-148.

[5] Spicer R A, Chapman J L. Climate change and the evolution of high-latitude terrestrial vegetation and floras. Trends in Ecology and Evolution, 1990, 5: 279-284.

[6] Sanz J J, Potti J, Moreno J, Merino S, Frías O. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. Global Change Biology, 2003, 9: 461-472.

[7] Réale D, Mc Adam A G, Boutin S, Dominique B. Genetic and plastic responses of a northern mammal to climate change. Proceedings of the Royal Society of London-Series B, 2003, 270: 591-596.

[8] Bradshaw W E, Holzapfel C M. Genetic shift in photoperiodic response correlated with global warming. Proceedings of the National Academy of Sciences, USA, 2001, 98: 14509-14511.

[9] Walther G R, Post E, Convey P, Menzel A, Parmesan C, Beebee T J C, Fromentin J M, Guldberg O H, Bairlein F. Ecological responses to recent climate change. Nature, 2002, 416: 389-395.

[10] Huey R B. Temperature, physiology and the ecology of reptiles // Gans C, Pough F H eds, Biology of the Reptilia 12. New York: Academic Press, 1982: 25-91.

[11] Deeming D C. Reptilian Incubation: Environment, Evolution and Behaviour. Nottingham: Nottingham University Press, 2004.

[12] Shine R. Adaptive consequences of developmental plasticity // Deeming D C ed. Reptilian Incubation: Environment, Evolution and Behaviors. Nottingham: Nottingham University Press, 2004: 187-210.

[13] Bull J J. Sex determination in reptiles. Quarterly Review of Biology, 1980, 55: 4-21.

[14] Janzen F J, Paukstis G L. Environmental sex determination in reptiles: ecology, evolution, and experimental design. Quarterly Review of Biology, 1991, 66: 149-179.

[15] Valenzuela N, Lance V. Temperature Dependent Sex Determination in Vertebrates. Washington D C: Smithsonian Books, 2004.

[16] Janzen F J, Phillips P C. Exploring the evolution of environmental sex determination, especially in reptiles. Journal of Evolutionary Biology, 2006, 19:1775-1784.

[17] Vitt L J, Pianka E R, eds. Lizard Ecology: Historical and Experimental Perspectives. Princeton: Princeton University Press, 1994.

[18] Zhao E M, Adler K. Herpetology of China. Oxford, Ohio: Society of the study of amphibians and reptiles, 1993.

[19] Lin Z H, Ji X. The effects of thermal and hydric environments on incubating eggs and hatchlings of the grass lizard, *Takydromus septentrionalis*. Zoological Research, 1998, 19: 439-445.

[20] Du W G, Wang X L, Shen J Y, Shen X J, Shou L, Zhang J L. Field active body temperatures of the northern grass lizards (*Takydromus septentrionalis*) from different geographic localities. Herpetologica Sinica, 2005, 10: 117-126.

[21] Du W G. Phenotypic plasticity in reproductive traits induced by food availability in a lacertid lizard, *Takydromus septentrionalis*. Oikos, 2006, 112: 363-369.

[22] Ji X, Du W G, Lin Z H, Luo L G. Measuring temporal variation in reproductive output reveals optimal resource allocation to reproduction in the northern grass lizard, *Takydromus septentrionalis*. Biological Journal of the Linnean Society, 2007, 91:315-324.

[23] Du W G, Ji X. Effects of constant and fluctuating temperatures on egg survival and hatchling traits in the northern grass lizard (*Takydromus septentrionalis*). Journal of Experimental Zoology, 2006, 305A: 47-54.

[24] Du W G, Lu Y W, Shen J Y. The effects of maternal thermal environments on reproductive traits and hatchling traits in a Lacertid lizard, *Takydromus septentrionalis*. Journal of Thermal Biology, 2005, 30: 153-161.

[25] Shine R. Relative clutch mass and body shape in lizards and snakes: Is reproductive investment constrained or optimized?. Evolution, 1992, 46: 828-833.

[26] Adolph S C, Porter W P. Temperature, activity and lizard life histories. American Naturalist, 1993, 142: 273-295.

[27] Xu X F, Wu Y L, Ou Y Y. Water and energy content variation of the major energy reserves in adult grass lizards, *Takydromus septentrionalis*. Zoological Research, 2002, 23: 44-48.

[28] Du W G, Lu Y W, Ji X. Utilization of lipid in northern grass lizards *Takydromus septentrionalis* in Hangzhou in the breeding season. Zoological Research, 2003, 24: 392-394.

[29] Ji X, Du W G, Sun P Y. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, *Takydromus septentrionalis*. Journal of Thermal Biology, 1996, 21: 155-161.

[30] Ford N B, Seigel R A. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. Ecology, 1989, 70: 1768-1774.

[31] James C D, Whitford W G. An experimental study of phenotypic plasticity in the clutch size of a lizard. Oikos, 1994, 70: 49-56.

[32] Kingsolver J G, Watt W B. Thermoregulatory strategies in *Colias* butterflies: thermal stress and the limits to adaptation in temporally variable environments. American Naturalist, 1983, 121: 32-55.

参考文献:

[19] 林植华, 计翔. 孵化温湿度对北草蜥孵化卵和孵出幼体的影响. 动物学研究, 1998, 19: 439-445.

[20] 杜卫国, 王小雷, 沈建洋, 沈学军, 寿鹿, 张建龙. 不同北草蜥地理种群的野外活动体温. 两栖爬行动物研究, 2005, 10: 117-126.