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封面图说:麋鹿群在过河——麋鹿属于鹿科,是中国的特有动物。历史上麋鹿曾经广布于东亚地区,到 19 世纪时,只剩下在北京南海子皇家猎苑内一群。1900 年,八国联军攻陷北京,麋鹿被抢劫一空。1901 年,英国的贝福特公爵用重金从法、德、荷、比四国收买了世界上仅有的 18 头麋鹿,以半野生的方式集中放养在乌邦寺庄园内,麋鹿这才免于绝灭。在世界动物保护组织的协调下,1985 年起麋鹿从英国分批回归家乡,放养到北京大兴南海子、江苏省大丰等地。这是在江苏省大丰麋鹿国家级自然保护区放养的麋鹿群正在过河。

彩图提供:陈建伟教授 北京林业大学 E-mail: cites.chenjw@163.com

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中国石龙子母体孕期调温诱导幼体表型: 母体操纵假说的实验检测

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摘要:卵胎生是由卵生繁殖模式通过逐渐增加卵滞留和胚胎在母体子宫内发育的时间进化而来的繁殖模式。有鳞类爬行动物(蜥蜴和蛇)有着较高的繁殖模式多样性,因而是研究卵胎生繁殖模式进化及其适应意义的理想动物模型。至今对于卵胎生进化的选择压力尚无定论,目前有 3 种关于卵胎生进化的假说受到学者的关注,其中母体操纵假说最受关注但尚未得到充分的检测。研究继 1995 年母体操纵假说提出之后,以栖息于温带气候环境下的卵生中国石龙子(*Eumeces chinensis*)为模型动物检测该假说。37 条中国石龙子怀卵母体采自浙江丽水市郊。将怀卵母体分置于 3 个热处理中,其中 12 条母体提供每日 14 h 光照时间,13 条母体提供 10 h 光照,其余 12 条母体没有任何调温机会(体温随室内环境温度而改变)。结果显示:怀卵母体选择体温向下漂移。3 种处理下的雌体繁殖特征没有显著差异。长、短调温组下母体产卵时间要早于非调温组母体,但新生卵的胚胎历期没有显著差异。用 5 种热处理孵化卵,孵化温度分别为:1=室内波动温度孵化;2=27 °C;3=24—30 °C;4=22—32 °C(3 和 4 孵化处理中,孵化箱内的温度每隔 1d 改变 1 次,即卵分别在 22 和 24 °C 孵化 24 h,随后在 32 和 30 °C 孵化 24 h,每 2d 循环 1 次直至孵出);5=在实验室后院内模拟石龙子野外巢址孵化。结果显示:孵出幼体的体长、腹长和头部大小(头长和头宽)在 3 个母体热处理间存在显著差异,其他形态学特征不存在母体热处理间的显著差异;孵化温度以及孵化温度和母体热处理的交互作用对所有的幼体形态学特征均无显著影响。孵化温度以及孵化温度和母体热处理的交互作用对幼体疾跑速和最大持续运动距离无显著影响;但不同的母体热处理显著影响幼体疾跑速和最大持续运动距离。研究结果不仅为“热变异对在一定孵化温度范围内表型无显著变化的物种的幼体表型没有重要的修饰作用”这一假说提供了有力证据,并且支持母体操纵假说的两个主要预测:雌体在孕期通过体温漂变行为提供体内胚胎发育的最适热环境,而由母体调温行为诱导的后代表型的变异将增强后代的适合度。

关键词:中国石龙子;母体孕期体温;卵胎生进化;母体操纵假说;表型

Maternal thermoregulation during gestation affects the phenotype of hatchling Chinese skinks (*Eumeces chinensis*): testing the maternal manipulation hypothesis

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Abstract: Viviparity (live-bearing) is a reproductive mode that evolves from oviparity through gradual increases in the length of egg retention and thus intrauterine development. Squamate reptiles (lizards, snakes and amphisbaenians) provide a very useful model system for studying the evolutionary transition from oviparity to viviparity and the adaptive significance of this transition, because they exhibit a wide reproductive diversity. Approximately 20% of squamate reptiles are viviparous, and this reproductive mode has evolved far more often in this group of animals than in all other non-mammalian vertebrates combined. The selective forces responsible for evolution of viviparity remain unclear. To date, there are three main hypothesis of evolution of viviparity, cold-climate hypothesis, predictability hypothesis, and maternal manipulation hypothesis. Of these three main hypotheses, the maternal manipulation hypothesis is most widely accepted in scientific community, although empirical studies testing this hypothesis are still limited. Here, we used the Chinese skink *Eumeces chinensis*, a temperate-climate oviparous scincid lizard, as the model system to test the maternal manipulation hypothesis. Thirty-seven gravid females collected from a population in Lishui, Zhejiang province (eastern China) were maintained in the laboratory under three different thermal conditions until oviposition. Twenty-five females were provided with the basking opportunity, with 12 allowed to bask for 14-h daily (LT treatment), and 13 for 10-h daily (ST treatment). The remaining 12 females were not provided with the basking opportunity (NTR treatment), and their body temperatures simply tracked changes in ambient environment. Females of different treatments did not differ morphologically. Body temperatures selected by females were measured using a UT325 digital thermometer. We measured each female three times, once on each of three consecutive days, beginning at 15:00 and ended within 2 h on each day. Females selected lower body temperatures and thermoregulated more precisely when gravid, and gravid females selected lower body temperatures than did non-gravid females and males. LT and ST females laid eggs earlier than did NTR females. Females maintained under the three thermal regimes did not differ from each other in any reproductive trait examined, including embryonic stage at oviposition. Six eggs randomly selected from each clutch were assigned to one of the following five treatments: in a room where temperatures varied naturally; in a constant-temperature room at 27 °C; in two incubators where temperatures varied from 24—30 °C and 22—32 °C, respectively; in the backyard of the laboratory mimicking natural nests. Incubation temperature (IT) affected incubation length, but maternal thermoregulation (MT) and the IT × MT interaction did not. MT affected the phenotype hatchlings, but IT and the IT × MT interaction did not. Hatchlings from eggs produced by LT females were longer in SVL, abdomen length and head length, and ran faster than those produced by ST females; hatchlings from eggs produced by NTR females had the shortest SVLs, abdomen lengths and head lengths, and performed worst in the racetrack. Other hatchling morphological traits examined did not differ among treatments. Our data support the two main predictions from the maternal manipulation hypothesis: (1) gravid females shift their body temperature to provide the optimal thermal conditions for embryos; and (2) offspring phenotypes induced by maternal thermoregulation will enhance offspring fitness.

Key Words: Chinese skink (*Eumeces chinensis*); maternal body temperature; evolution of viviparity; maternal manipulation hypothesis; phenotype

脊椎动物生活史特征与环境因子之间最一致的经验性关联,就是爬行动物的繁殖模式与热体系之间的联系。从进化驱动力的角度探讨爬行动物繁殖模式进化的假说有很多,其中冷气候假说^[1-3],预见性假说^[4]和母体操纵假说^[5]最受关注。这3种假说均认为母体调温行为(孕期母体所处热体系)在有鳞类卵胎生繁殖模式进化过程中起重要作用。一些学者以卵胎生物种为对象研究母体调温与卵胎生进化之间的关系^[6-10],然而多数爬行动物具卵生繁殖模式。分类学和胚胎学的证据表明爬行动物的祖先营卵生繁殖模式,因此在现生许多爬行动物中同时存在卵生和卵胎生两种繁殖模式,表明历史上卵胎生繁殖模式经历了多次进化^[11]。因此,研究替代古生卵生种类的现生卵生爬行动物对了解驱使繁殖模式转变的选择压力非常重要。根据当前受关注最多的母体操纵假说的两个主要预测,孕期母体发生体温漂变,以提供体内胚胎发育的最适热环境,从而增

强后代的适合度^[5, 8]。孕期母体修饰调温行为,即母体在孕期会改变选择体温这一现象,在许多爬行动物中已有记载^[8]。一些学者认为母体这种修饰行为是对卵胎生繁殖模式进化的适应^[8]:在繁殖模式进化选择压力和孕期母体的调温行为之间存在因果联系,因为这种被母体特化的热体系十分利于胚胎发育。之前的研究多集中于卵胎生物种,比较而言,卵生物种在产卵前同样能提供体内胚胎发育的最适热环境,至少是在部分胚胎发育阶段。因为在卵生种类中,胚胎发育的前四分之一是在输卵管内完成的^[12],而且热体系在胚胎发育早期对孵出幼体形态的影响要大于后期^[13-14]。因此,在胚胎发育早期,处于孕期的卵生种类可以通过行为调温来调节体内胚胎发育的热体系。综上所述,卵生爬行动物比卵胎生物种更适合用于检测卵胎生进化假说。

以卵生物种为模型动物开展研究支持母体操纵假说的经验性数据非常有限^[5],因为在该假说提出之后,后续的研究多集中于卵胎生种类。本研究提供中国石龙子(*Eumeces chinensis*)怀卵母体不同的调温机会(详细实验设计见材料和方法),所得数据用于检测母体操纵假说的两个主要预测。中国石龙子是中等体型、日行性的卵生石龙子,广泛分布于中国的中部和南部省份^[15]。

1 材料和方法

1.1 动物采集和孕期母体热处理

2011年4月上旬至5月上旬于浙江丽水(41°45'N, 107°01'E; 海拔约300 m)采用徒手捕捉或索套法采集37条成年雌体中国石龙子(体长SVL>101 mm),同时捕获15条雄体,一并带回南京师范大学两栖爬行动物实验室饲养。动物置于2.5 m×1.2 m×0.6 m(长×宽×高)的玻璃缸内,缸底铺以200 mm厚的细沙和泥土的混合物,夹杂少许小碎石和绿草皮,最大程度的模拟其自然栖息环境。缸的一端悬挂200瓦灯泡以提供调温热源,调温时长为12 L:12 D。夜间提供热源的灯泡关闭后,室内温度降至室温(24±1)℃。饲养期间提供充足的食物[面包虫(黄粉蝶(*Tenebrio molitor*)幼虫,蟋蟀(*Achetus domesticus*)和野生蝗虫],同时提供充足的饮水,并定期在饮水中添加维生素和钙粉,以确保实验个体获得充足营养。

动物在实验室环境下驯化1周左右,指触判定母体是否怀卵,随后怀卵母体被随机分至3个实验处理组:其中12条提供每天14 h光照(LT实验组),另13条提供每天10 h光照(ST实验组),余下12条置于不能自主调温的饲养缸内(NTR实验组)。

在第1条母体产卵后,每日间隔4 h检查箱内母体产卵情况,及时收集新生卵并称重。每窝卵随机取6枚用于孵化实验(剩余的卵用于其他实验——孵化期内胚胎生长以及物质能量功用)。孵化温度分别为:1=室内波动温度孵化;2=27℃;3=24—30℃;4=22—32℃(3和4孵化处理中,孵化箱内的温度每隔1 d改变1次,即卵分别在22℃和24℃孵化24 h,随后在32℃和30℃孵化24 h,每2 d循环1次直至孵出);5=在实验室后院内模拟石龙子野外巢址孵化。该孵化处理下,胚胎经历的温度具有日变化和月变化(图1),每天的最大热变异,最高平均温度、最低低温和最高高温分别为6.3、29.8、28.5、33.2℃。室内波动孵化温度的范围介于模拟巢址温度范围之内(图1中的两条水平线分别表示室内波动温度的最高和最低值)。每隔1 d称量孵化盒,添加必要的水分以补充蒸发的水分和孵化期间卵吸收的水分。将数据记录块(Tinytalk TK-0014, Gemini Pty, Australia)的探头置于孵化盒内的空气中,间隔1 h记录每个自然巢址中的温度变化情况,以追踪卵在胚胎发育期间所经历的孵化温度。

母体产卵后,测定其产后体重、体长和尾长。3种处理下37条雌体中共有28条母体产发育良好的卵,其余9条产未受精的卵,因此这些雌体未纳入统计分析。用窝卵重除以产后母体体重表示相对窝卵重,用窝卵数和母体体长的自然对数的回归剩余值表示相对生育力^[16]。

1.2 怀卵对雌体选择体温的影响

2007年4月中旬采集浙江丽水中国石龙子(11条怀卵母体、10条非怀卵母体和6条雄性成体(SVL>105 mm)),用于检测孕期内怀卵母体是否有体温漂移现象。该实验所用玻璃缸的条件同前,缸一端悬挂200瓦灯泡在箱内形成范围为18—55℃的热梯度,灯泡开启时长为每天14 h。从样本组中随机挑选10条石龙子,每天7:00灯泡开启时从低温端移入动物,用UT325数显点温计(上海医药器材公司)测量动物体温。为去除

选择体温的昼夜差异,每天15:00开始测量,每次测量在1h内结束。每条个体在连续3d被测量3次后就不再重复测量该个体。重复测量方差分析(repeated measures ANOVA)显示各组3次体温测量没有显著差异(所有 $P>0.05$),3次测量的体温的平均值作为石龙子的选择体温。

1.3 孵出幼体表型的测定

第一枚卵破壳后,每日检查孵化盒数次,将破壳后的卵移至单独的100mL大小的玻璃罐中,以确保孵出幼体和卵一一对应。对每一孵出幼体称重并记录其孵出的时间,以此计算卵的孵化期。由于爬行动物的运动表现与体温水平密切相关,在检测幼体运动表现之前,先把幼体置于30℃的恒温箱内半小时以控制其体温在30℃左右。运动表现在长约1.6m的直行跑道上检测,用毛笔刷驱赶幼体,整个过程用松下数码摄像机NV-DS77录像,视频用MGI VideoWave III软件(MGI

Software Co., Canada)读取。幼体的疾跑速是用25cm间距里的最大运动速度表示,最大持续运动距离用幼体在没有停止动作情况下所经历的最长运动距离表示。每条幼体间隔30min休息后再重复检测运动表现,之后将幼体置于5℃培养箱内一段时间,然后测量形态学指标。形态学指标包括:体长、尾长、腹长、头长、头宽、前肢长、后肢长和腹鳞数。所有幼体在结束上述实验后择机放回其原栖息地。

1.4 统计分析

产未受精卵的雌体繁殖数据未被采用;表型测定实验中4条幼体拒绝跑动,因此相关数据未被采用。数据用统计软件包Statistica 5.0分析。在作进一步统计分析前,用Kolmogorov-Smirnov和Bartlet方法分别检验数据的正态性和方差均质性。用线性回归、双因子方差分析(对初始卵重的比较)和双因子协方差分析(以初始卵重为协变量,母体热处理和孵化温度为因子)分析相关数据。Tukey多重比较检验存在显著差异的不同热处理之间的幼体特征。本文所有统计值用平均值±标准误表示,显著性水平设置为 $\alpha=0.05$ 。

2 结果

2.1 雌性繁殖

雌体产卵时间为5月下旬至6月下旬,繁殖期内产单窝卵。28条母体一共产下360枚卵,平均窝卵数为12.9(表1)。新生卵胚胎周期为30—34期,3种母体热处理下所产新生卵的胚胎周期没有显著差异($F_{2,21}=0.09$, $P=0.915$)。不同孵化温度下的孵化期有显著差异($F_{4,129}=10.67$, $P=0.004$),但母体热处理间没有显著差异($F_{2,129}=0.66$, $P=0.520$),母体热处理和孵化温度的交互作用对孵化期也没有显著影响($F_{4,129}=1.35$, $P=0.225$)。3种母体热处理下的所有雌体繁殖特征均无显著差异(表1),这些雌体繁殖特征包括:体长、产后体重、窝卵数、窝卵重、平均卵重和相对窝卵重。当把3种母体热处理下的数据合并后,发现窝卵数($r^2=0.46$, $F_{1,26}=22.20$, $P<0.0001$)、窝卵重($r^2=0.37$, $F_{1,26}=15.08$, $P<0.007$)和母体体长成正相关,但平均卵重与母体体长无显著相关性($r^2=0.05$, $F_{1,26}=1.46$, $P=0.239$),平均卵重和相对生育力之间亦无显著相关性($r^2=0.05$, $F_{1,26}=1.51$, $P=0.230$)。

2.2 选择体温

怀卵雌体、非怀卵雌体以及雄性成体的选择体温具有显著差异($F_{2,24}=36.99$, $P<0.0001$;表2)。雄性成体和非怀卵雌体的选择体温高于怀卵雌体的选择体温,雄性成体和非怀卵雌体的选择体温没有显著差异。怀卵雌体、非怀卵雌体和雄性成体选择体温的热变异分别为0.2,0.3和0.6,三者在统计上没有显著差异(所

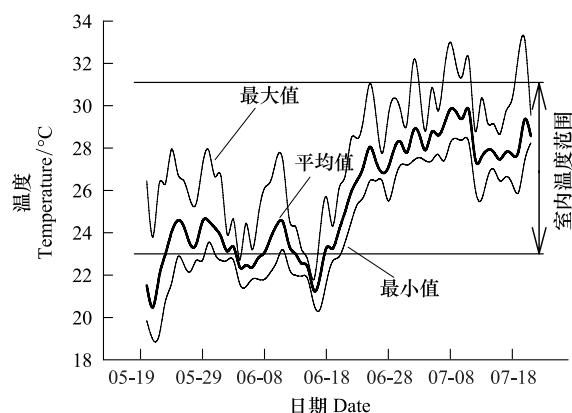


图1 实验室后院巢址中孵化的中国石龙子(*Eumeces chinensis*)卵经历的日最低温,日均温和日最高温的瞬时变化

Fig. 1 Temporal variation in daily minimal, mean and maximal temperatures experienced by *Eumeces chinensis* eggs incubated in the nests built in the backyard of the laboratory

图中两条水平线显示室内波动温度的范围

有 $P > 0.05$)。

表 1 3 种热处理下中国石龙子的雌体繁殖特征

Table 1 Reproductive traits of females maintained under three thermal treatments

繁殖特征 Reproductive traits	母体热处理 Maternal thermal treatments			协方差分析结果 Results of ANCOVA
	LT	ST	NTR	
样本数 N	9	13	6	
体长/mm Snout-vent length	103.4 ± 1.7 $96.8 - 110.7$	102.8 ± 2.0 $88.7 - 117.7$	101.7 ± 1.0 $99.7 - 105.9$	$F_{2, 25} = 0.14, P = 0.869$
产后体重/g Postpartum body mass	20.8 ± 1.1 $16.6 - 27.1$	20.8 ± 0.8 $13.9 - 26.7$	19.4 ± 0.9 $17.1 - 23.1$	$F_{2, 24} = 0.53, P = 0.595$
窝卵数 Clutch size	13.6 ± 1.6 5—22	13.1 ± 1.4 7—25	12.0 ± 1.7 6—17	$F_{2, 24} = 0.06, P = 0.942$
窝卵重/g Clutch mass	9.35 ± 1.24 $3.95 - 16.06$	9.70 ± 0.85 $4.63 - 15.36$	7.47 ± 1.10 $4.41 - 10.53$	$F_{2, 24} = 1.04, P = 0.368$
平均卵重/g Egg mass	0.70 ± 0.03 0.56—0.80	0.77 ± 0.04 0.58—1.07	0.67 ± 0.04 0.52—0.76	$F_{2, 25} = 1.66, P = 0.210$
相对窝卵重 Relative clutch mass	0.44 ± 0.05 0.22—0.70	0.47 ± 0.03 0.21—0.66	0.39 ± 0.06 0.22—0.55	$F_{2, 24} = 0.58, P = 0.569$

数据用平均值±标准误和范围表示; 表中给出单因子方差分析(体长)或以雌体体长为协变量(窝卵数, 窝卵重和母体产后体重)以及产后体重为协变量(相对窝卵重)的协方差分析的 F 值; $P > 0.05$ 表示不显著

表 2 实验室热梯度下怀卵、非怀卵雌体及雄性成体选择体温的描述性统计值

Table 2 Descriptive statistics for body temperatures selected by gravid females, non-gravid females and adult males on the laboratory thermal gradient

类别 Category	样本数 N	平均值 Mean	标准误 SE	范围 Range
怀卵母体 Gravid females	11	28.1	0.2	26.9—29.3
非怀卵母体 Non-gravid females	10	30.9	0.3	29.9—32.2
雄性成体 Adult males	6	31.9	0.6	29.9—33.2

2.3 孵出幼体的表型特征和运动表现

所有被检测的形态学特征与初始卵重呈正相关, 所以用经初始卵重矫正后的相关形态学数据来比较孵出幼体的表型特征。以初始卵重为协变量, 母体热处理和孵化温度为因子的双因子协方差分析结果显示: 孵出幼体的体长、腹长和头部大小(头长和头宽)在 3 个母体热处理间存在显著差异(图 2), 其他形态学特征不存在母体热处理间的显著差异; 孵化温度以及孵化温度和母体热处理的交互作用对所有的幼体形态学特征均无显著影响(表 3)。疾跑速和最大持续运动距离与所有被检测的 7 个形态学特征均不存在相关性(所有 $P > 0.05$), 因此用两因子(母体热处理和孵化温度)方差分析进行统计。结果显示孵化温度($F_{4, 105} = 0.65, P = 0.631$)以及孵化温度和母体热处理的交互作用($F_{8, 105} = 1.17, P = 0.326$)对疾跑速无显著影响; 但不同的母体热处理显著影响幼体疾跑速($F_{4, 105} = 3.99, P = 0.021$)(图 2; 表 3)。最大持续运动距离的结果与疾跑速相似: 孵化温度($F_{4, 105} = 0.94, P = 0.447$)以及孵化温度和母体热处理的交互作用($F_{8, 105} = 1.06, P = 0.399$)对最大持续运动距离无显著影响; 但不同的母体热处理显著影响幼体最大持续运动距离($F_{2, 105} = 3.23, P = 0.044$)(图 3; 表 3)。

3 讨论

本研究以卵生爬行动物为模型, 检测 Shine^[5]提出的母体操纵假说。迄今支持该假说的经验性数据还相当匮乏, 尤其是来自卵生爬行动物的实验证据。该假说被认为是适用于任何情况下的任何物种: 母体在孕期能通过体温调节行为维持自身较为稳定或更可预见的体温, 以此提供体内胚胎发育的最适热环境从而达到增强后代适合度(也是母体自身适合度)的目的^[8]。因而该假说近年来广受关注。然而之后的所有相关研究均以卵胎生物种为模型来验证该假说^[8-10], 本研究首次采用卵生爬行动物为模型验证该假说。

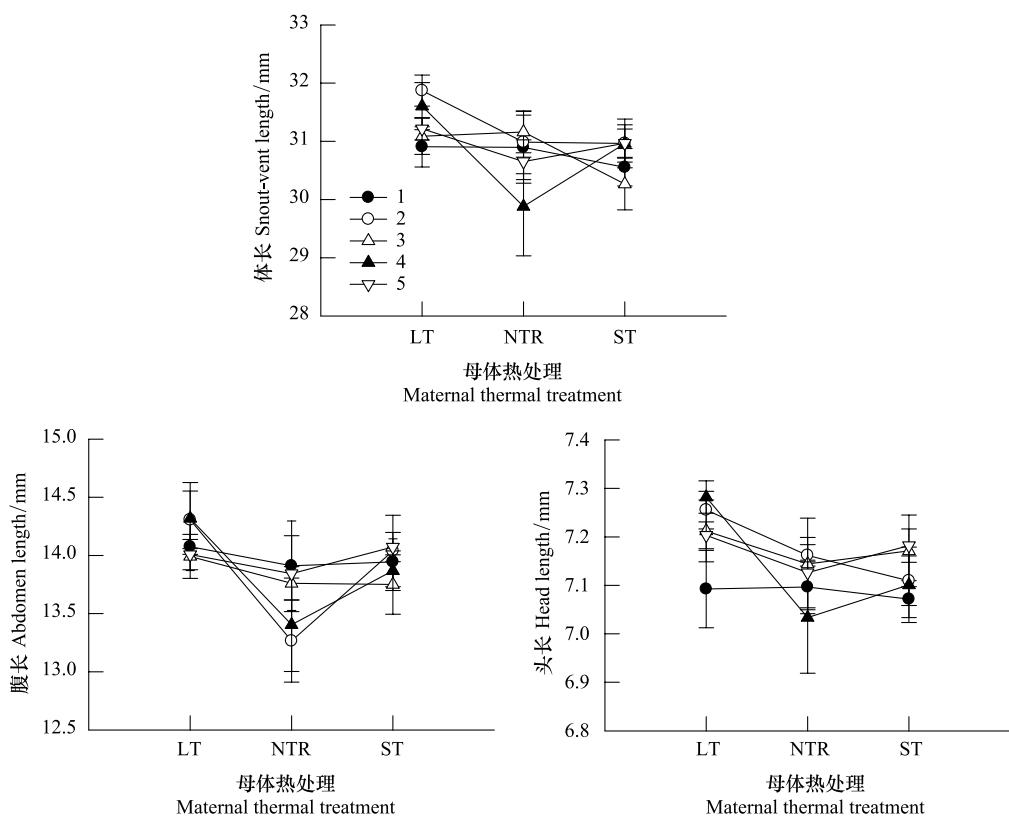


图2 3种母体热处理下所产卵在5个孵化温度下孵出的幼体体长、腹长和头长的平均值(±标准误)

Fig.2 Mean values (\pm SE) for SVL, head length and head width of hatchling derived from eggs laid by females maintained under three thermal treatments at five incubation temperature

孵化热环境设置如下:1=室内波动温度孵化;2=27℃;3=24—30℃;4=22—32℃(3和4孵化处理中,孵化箱内的温度每隔1d改变1次);5=在实验室后院内模拟石龙子野外巢址孵化

表3 以母体热处理和孵化温度为因子的方差或协方差(以初始卵重为协变量)分析比较孵出幼体的形态学特征和运动表现

Table 3 Two-way ANCOVA (using initial egg mass as the covariate) or ANOVA analysis compared the morphological traits and locomotor performance of hatching, with maternal treatment and incubation temperature as the factors

变量 Variables	因子效应 Effects		
	母体热处理 Maternal treatment	孵化温度 Incubation temperature	交互作用 MT × IT Interaction
体长 Snout-vent length	$F_{2,108} = 3.80, P < 0.025$; LT ^a , ST ^b , NTR ^b	$F_{4,108} = 0.62, P = 0.649$	$F_{8,108} = 0.99, P = 0.445$
腹长 Abdomen length	$F_{2,108} = 4.06, P < 0.020$; LT ^a , ST ^{ab} , NTR ^b	$F_{4,108} = 0.22, P = 0.926$	$F_{8,108} = 0.70, P = 0.693$
尾长 Tail length	$F_{2,108} = 0.50, P = 0.613$	$F_{4,108} = 0.49, P = 0.742$	$F_{8,108} = 1.17, P = 0.326$
头长 Head length	$F_{2,108} = 3.41, P < 0.037$; LT ^a , ST ^b , NTR ^b	$F_{4,108} = 0.96, P = 0.435$	$F_{8,108} = 0.60, P = 0.776$
头宽 Head width	$F_{2,108} = 2.80, P < 0.065$	$F_{4,108} = 0.75, P = 0.563$	$F_{8,128} = 1.09, P = 0.379$
前肢长 Fore-limb length	$F_{2,128} = 2.03, P = 0.137$	$F_{4,108} = 1.15, P = 0.337$	$F_{8,108} = 1.01, P = 0.437$
后肢长 Hind-limb length	$F_{2,108} = 1.90, P = 0.154$	$F_{4,108} = 0.93, P = 0.448$	$F_{8,128} = 0.65, P = 0.736$
疾跑速 Sprint Speed	$F_{2,105} = 3.99, P = 0.021$; LT ^a , ST ^{ab} , NTR ^b	$F_{4,105} = 0.65, P = 0.631$	$F_{8,105} = 1.17, P = 0.326$
最大运动距离 Maximal length	$F_{2,105} = 3.23, P = 0.044$; LT ^{ab} , ST ^a , NTR ^b	$F_{4,105} = 0.94, P = 0.447$	$F_{8,105} = 1.06, P = 0.399$

因子效应显著时用经初始卵重(设定初始卵重为0.75g)矫正后的孵出幼体形态学特征进行Tukey's多重比较(a>b)

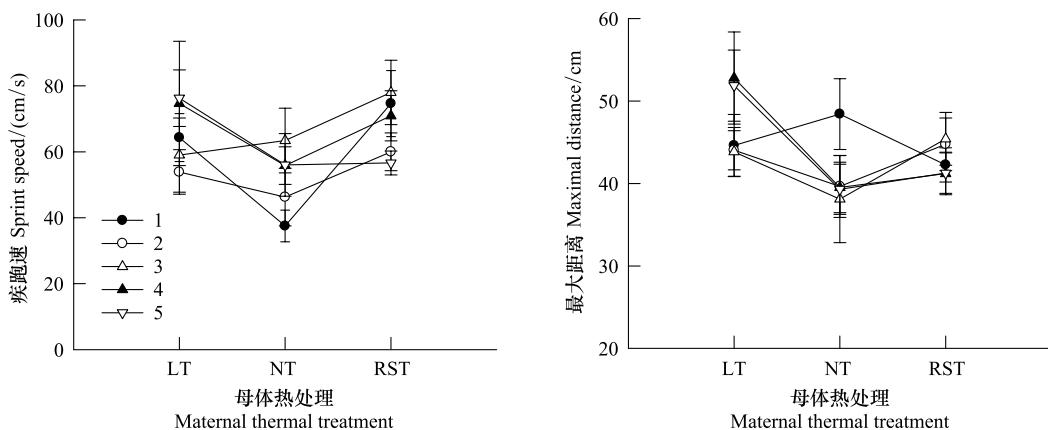


图3 3种母体热处理下所产卵在5种孵化温度下孵出的幼体疾跑速和最大运动距离的平均值(±标准误)

Fig.3 Mean values (\pm SE) for sprint speed and the maximal distance of hatching derived from eggs laid by females maintained under three thermal treatments at five incubation temperature

3.1 孕期雌体选择体温发生漂移

爬行动物的热喜好并不是固定不变的特征,因为该特征可以受到很多内在和外在因素的作用^[17]。在有鳞类爬行动物的许多物种中,孕期雌体发生热喜好漂移(向上或向下漂移)^[8, 10, 18-21]。孕期雌体对行为调温和热喜好的修饰作用的产生可能同雌体通过这些修饰能提供体内胚胎发育的最适热环境所带来的利益相关联,而这一点被认为是爬行动物发生卵胎生进化的非常合理的原因^[5, 7]。正如同域分布的但利用更为郁闭生境的印度蜓蜥(*Sphenomorphus indicu*)^[22],中国石龙子孕期雌体的选择体温(28.1℃)低于产后雌体(30.9℃)和雄性成体的选择体温(31.9℃)(表2)。这个结果验证了母体操纵假说的第一个预测:雌体在孕期发生了热喜好漂移现象。在爬行动物中,孵化温度或者孕期母体的体温能影响孵出(或产出)幼体的形态特征和功能表现^[23-25]。而在卵生种类中,孵化期随孵化温度的升高而缩短,但在母体产卵前,母体输卵管内胚胎的发育状况决定于母体的选择体温,且热体系在胚胎发育早期对孵出幼体形态的影响要大于胚胎发育后期^[13-14]。本实验室之前对印度蜓蜥(*S. indicu*)^[22]的研究表明,中国石龙子孕期内野外环境的日平均温度,日最高温度以及日最低温度分别为27.9、20.9、36.5℃,所以孕期内母体要选择相对较低的体温以防止高温对体内胚胎的不利影响。通过本实验室之前对中国石龙子的多项研究表明,26至30℃为孵化中国石龙子的适宜温度,24℃孵化温度下,中国石龙子胚胎发育能耗较大,胚胎从卵壳动用的无机物极少,而高温32℃下孵出的幼体头部最小;孵化温度从24到26℃,孵化期平均缩短10 d,从26到30℃,孵化期平均缩短11 d,而当孵化温度从30转到32℃时,孵化期仅仅缩短了1.4d^[26]。中国石龙子这种孵化期长度的热依赖模式表明:雌体在孕期通过调高体温以加速胚胎发育(或者说提前产卵所获得的利益)呈逐渐减小的趋势。因此孕期内母体通过选择体温向下漂移以提供体内胚胎发育的最适热环境,即选择相对较低的体温。

3.2 由母体调温行为诱导的后代表型特征变化

产卵前怀卵雌体的调温时长或是否有调温机会不仅影响中国石龙子雌体的产卵时间,而且影响孵出幼体的形态学特征和运动表现。通常卵滞留在母体输卵管内的时间在胚胎发育整个周期内占据重要的地位^[12],具有较多调温机会的母体可以通过频繁的调温行为以加速体内胚胎发育,促使母体产卵时间提前。本研究中处于长调温和短调温处理下的母体产卵时间要明显早于非调温组处理下的母体,尽管这3种母体热处理下新生卵的胚胎历期没有显著差异。一种可能的解释是:长短调温组下的母体因为比非调温组下母体具有更多的调温机会以提供体内胚胎发育最适的热环境,因此具有较多调温机会的母体产卵时间提前。早期胚胎发育主要涉及组织分化和器官形成,后期则主要涉及胚胎长度的增长和生理上的变化,因此热体系对早期胚胎发育的影响要显著大于胚胎发育后期^[13-14]。本研究中,相对于短调温组和非调温组,长调温组下的幼体不仅具有较大的体长、腹长和头长,而且具有更好的运动表现(疾跑速和最大持续运动距离)(表3, 图3)。这是

因为长调温组下的母体具有更多调温机会,从而在更长时间内可以维持自身体温处于最适宜体内胚胎发育的水平,以达到优化后代表型的目的。后代运动表现对于逃避天敌和增强摄食成功率都有重要影响^[27-29]。有文献显示较大的后代要比同物种中较小的个体具有更强的适应自然环境的能力(蛾类^[30];海生无脊椎类^[31-32];节肢动物类^[33];鱼类^[34];和爬行类^[8, 35])。中国石龙子产卵前的怀卵母体调温机会越多,它们产卵后孵化出的幼体表型越好,从而增强了后代的适合度,同时也增强了母体自身的适合度。因此,当前研究所得数据证实了母体操纵假说的另一预测:母体体温漂移所诱导的后代表型变异将增强后代的适合度。

4 结论

本研究以一种卵生爬行动物——中国石龙子为模型,尝试验证母体操纵假说的两个主要预测:雌体在孕期通过体温漂变行为提供体内胚胎发育的最适热环境,而由母体调温行为诱导的后代表型的变异将增强后代的适合度。

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