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封面图说:冬天低空飞翔的丹顶鹤——丹顶鹤是鹤类中的一种,因头顶有“红肉冠”而得名。是东亚地区特有的鸟种,因体态优雅、颜色分明,在这一地区的文化中具有吉祥、忠贞、长寿的象征,是传说中的仙鹤,国家一级保护动物。丹顶鹤具备鹤类的特征,即三长——嘴长、颈长、腿长。成鸟除颈部和飞羽后端为黑色外,全身洁白,头顶皮肤裸露,呈鲜红色。丹顶鹤每年要在繁殖地和越冬地之间进行迁徙,只有在日本北海道等地是留鸟,不进行迁徙,这可能与冬季当地人有组织地投喂食物,食物来源充足有关。

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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孵化温度对赤链蛇胚胎代谢和幼体行为的影响

孙文佳, 俞霄, 曹梦洁, 林隆慧 *

(杭州师范大学生命科学学院杭州市动物适应与进化重点实验室, 杭州 310036)

摘要: 研究了赤链蛇(*Dinodon rufozonatum*)在孵化过程中卵的生长、孵化期、胚胎代谢和孵出幼体行为表现的热依赖性。结果显示:孵化温度对孵化期、卵增重、孵化过程中消耗的总能量和孵出幼体的运动表现有显著影响,但不影响胚胎代谢率、孵化成功率和幼体吐信频次。孵化期随着孵化温度的升高而缩短,孵化过程中,24℃终末卵重和胚胎代谢率显著大于30℃,而27℃与其他两个温度没有差异;27℃孵出幼体游速较24℃快,30℃孵出幼体与其他两个温度孵出幼体的游速无显著差异。上述结果显示:24—30℃是赤链蛇适合的孵化温度范围,与赤链蛇所处的生境温度相近。

关键词: 游蛇科; 赤链蛇; 孵化期; 代谢; 游速

The effects of incubation temperature on embryonic metabolism and hatchling behavior in the Red-banded Snake, *Dinodon rufozonatum*

SUN Wenjia, YU Xiao, CAO Mengjie, LIN Longhui *

Hangzhou Key Laboratory for Animal Adaptation and Evolution, School of Life Sciences, Hangzhou Normal University, Hangzhou 310036, China

Abstract: We collected adult females of *Dinodon rufozonatum* (Colubridae) from a population in Zhejiang, Southeast China, to study the effects of incubation temperature on embryonic metabolism and hatchling behavior. We incubated eggs at three constant temperatures ranging from 24 °C to 30 °C, and weighed containers and eggs at 5-day intervals. The duration of incubation, measured as the number of days to pipping, was recorded for each egg. Eggs were measured for changes in size and embryonic metabolism at 5-day intervals. The response to chemical cues, respiration metabolism and sexual phenotype were determined for each hatchling. Because physiological and behavioral performances are highly sensitive to variation in body temperature in reptiles, we conducted all trials at the body temperature of 28 °C. This was achieved by placing hatchlings in an incubator at the test temperature for approximately 1 h prior to testing. We presented a cotton-tipped applicator soaked with cologne water to the lip of hatchlings and recorded tongue flicks for 1 min. Tongue flicking was measured because many reptiles flick their tongues frequently to detect both predators and prey and to gather information about other members of their own species. The behavioral character is therefore a potentially important indicator of fitness.

Incubation temperature affected incubation length, mass gain and energy consumption of eggs during incubation and locomotor performance of hatchlings, but not the rate of embryonic metabolism, hatchling success and tongue flicking. Incubation length decreased exponentially as incubation temperature increased. All eggs gained mass during incubation due to absorption of water. Incubation temperature affected water exchanges between eggs and their surroundings, thereby affecting the hydric conditions inside the egg. Eggs incubated at 24 °C gained more mass and consumed more energy to

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* 通讯作者 Corresponding author. E-mail: linlh@yahoo.cn

hatch than did eggs at 30 °C, but eggs incubated at these two temperatures did not differ from eggs incubated at 27 °C in mass gain and energy consumption during incubation. Swimming speed was greatest in hatchlings incubated at 27 °C and lowest in hatchling incubated at 24 °C, with hatchlings incubated at 30 °C in between. Hatchlings incubated at the three temperatures did not differ from each other in tongue flicking.

The carbon dioxide breathed out by eggs decreased as incubation temperature increased. The amount of energy consumed by embryos developing at 24, 27 and 30 °C during incubation was 6.63, 4.42 and 3.42 J, respectively. This result better explains why hatchlings incubated at lower temperatures are larger in snout-vent length and heavier than those incubated at higher temperatures. Though the rate of embryonic metabolism did not differ among three temperature treatments, incubation length was longer at lower than at higher temperatures so that embryos at lower temperatures needed more energy to complete development. This explains why hatchlings from eggs incubated at lower temperatures had more residual yolks than did those from higher incubation temperature.

Our results reveal that incubating eggs at temperatures ranging from 24—30 °C does not have important effects on embryonic metabolism and hatchlings behavior in *D. rufozonatum*. This temperature range seems like temperature at habitat of *D. rufozonatum*.

Key Words: colubridae; *Dinodon rufozonatum*; duration of incubation; metabolism; swimming speed

温度对爬行动物生活史、生态和生理的各项特征都有重要影响^[1],如生长速率、繁殖、季节性活动方式和生境利用、运动和地理分布等^[2-4]。而胚胎发育期间所经历温湿环境的变化甚至会持久而深远地影响到爬行动物后期的生理和行为。大量的研究结果证实孵化温度会影响爬行动物后代的运动、嗅觉、生长和幼体存活率等^[5-7]。但孵化温度对胚胎发育过程中能量投入的影响研究甚少,仅局限在少数几个物种^[8-10],如鳄目(*Crocodylus johnstoni*)在孵化温度29 °C时的代谢率和后代大小大于31 °C,东方强棱蜥(*Sceloporus undulatus*)在28 °C下幼体孵化总的代谢支出大于30—34 °C的能量支出。然而,在普遍存在着孵化温度和后代大小存在负相关的蛇类物种中,孵化温度对胚胎代谢率的影响仍然知之甚少。

赤链蛇(*Dinodon rufozonatum*)隶属于游蛇科(Colubridae)链蛇属(*Dinodon*),主要分布于我国的华北、华中、东北和朝鲜、日本等地^[11]。有关赤链蛇的研究主要涉及孵化温湿度对赤链蛇后代表型的影响^[12-13]。而孵化温度对胚胎能量代谢影响的研究具有至关重要的作用,它是解释孵化温度对后代大小影响机理的主要途径。本文主要检测孵化温度对赤链蛇胚胎发育过程中能量代谢和孵出幼体行为表现的影响,希望通过上述数据的收集,解释孵化温度对胚胎能量代谢和后代行为表现的影响以及它的生态学意义。

1. 材料和方法

1.1 动物的收集和饲养

于2010年6月从浙江杭州和睦水乡和西溪湿地采集14条赤链游蛇(体长71.5—91.5 cm)母体。随后动物被运到杭州师范大学两栖爬行动物中心实验室,饲养在室内60 cm×45 cm×50 cm(长×宽×高)的铁丝笼内,室内温度控制在(28±2) °C。期间提供充足的食物[中国石龙子(*Eumeces chinensis*)和泽蛙(*Rana limnocharis*)与富含维生素和矿物质的水]。

1.2 卵的收集和孵化

实验室内赤链蛇的产卵时间为7月16至7月31日。从产第一窝卵开始每天至少检查两次蛇笼以便及时收集和测量新生卵。母体产卵后测量其体长、尾长和体重以计算母体的生育力,并及时测量卵的大小(精确至0.01 mm)和重量(精确至1 mg)。14条母体共产卵114枚,本项研究用的赤链蛇每窝产卵5—13枚。我们取其中的28枚(同窝卵只取其中1枚,且尽量选取不同产地来源的卵)进行本项研究,这些卵被随机分配到3个孵化温度进行孵化。28枚赤链蛇的卵被随机分成3组分别置于加盖的250 mL塑料孵化盒中,盒内以蛭石和水(质量比为1:1)做孵化基质^[14]。卵长径的1/3埋在孵化基质中。为保证孵化盒湿度一致,孵化盒每

5 d 称重 1 次并补充因卵吸收和空气蒸发而损失的水分。

将孵化盒置于 3 个不同温度的恒温室进行孵化, 室内温度分别设置为 24、27 和 30 ℃。为减少恒温室不同的热梯度所造成的影响, 孵化盒在恒温室中的位置按照事先设置好的程序按时移动。

1.3 卵代谢和后代行为

从产卵到幼体孵出的时间作为孵化期, 并记录每个卵的孵化期。每 10 d 称 1 次卵的重量随后测量其呼吸代谢。作者测定卵的呼吸代谢时均在每个卵所处的温度下测定, 测定代谢率先将卵取出孵化盒并称重。每个卵均置于无菌纸上, 放入 Qubit 公司生产的呼吸仪(RP1LP-FCM Low Range Respiration Package)内进行代谢率的测定。操作方法完全按照产品使用说明书要求的步骤进行, 实验数据由计算机软件 Logger Pro 3.7 采集并加以分析。代谢率的测定以卵在呼吸过程中平均每分钟所产生的二氧化碳毫升数为标准进行计算。

幼体孵出后立即被收集, 测量体长、尾长和体重等数据, 并通过挤压泄殖腔的方式辨别性别, 有半阴茎的为雄性。所有个体在测完形态数据后 12 h 内进行行为表现的测定, 由于生理和行为表现在爬行动物中的热敏感性, 作者在测定幼体行为前 1 h 将幼体置于 28 ℃ 恒温室进行驯化。通过测量后代吐信频次和游泳速度来评估其运动表现。由于许多爬行动物都是通过吐信的方式收集周围环境中的信息吐信行为可能是适合度的重要标志, 而且它会随着爬行动物体温的变化而变化^[15-16]。因此测量幼体的吐信频次用于检测孵化温度对幼体行为的影响, 测量方法是用蘸有花露水的棉签置于幼体吻端前 1 cm 处记录 1 min 内幼体的吐信次数。

游速在 1.5 m × 0.15 m × 0.45 m (长 × 宽 × 高) 的跑道里进行, 跑道内放入高 25 cm 的水, 一人用毛笔强烈驱赶小蛇(笔头频繁碰触蛇尾, 并避免笔杆碰触蛇尾), 另一人利用数码相机(松下 NV-DS77)由上而下进行拍摄。实验期间用 WMZ-3 点温计测量跑道内水温, 并把水温控制在 (28 ± 0.5) ℃。用 MGI ViedoWave 软件(MGI Software, Canada)分析拍摄的小蛇游泳的录像, 确定在 25 cm 内不间断的最快游泳速度为最快速度。

1.4 统计分析

用 Statistica 8 软件包进行统计分析, 由于性别对数据结果没有影响, 因此合并两种不同性别的数据。数据作参数统计分析前, 分别检验其正态性(Kolmogorov-Smirnov test)和方差同质性(F-max test)。用 G 检验检测 3 个温度下的孵化成功率和性比差异。重复测量方差分析(repeated measures ANOVA)分析孵化温度对卵重的影响。由于卵重对呼吸代谢的结果有影响^[17], 因此用重复测量协方差分析(repeated measures ANCOVA)分析孵化温度对胚胎呼吸代谢的影响, 双因子方差分析(two-way ANOVA)检验温度和性别对吐信频次和运动表型的影响, 用 Tukey 多重比较检验多样本各处理彼此间的差异。文中所有描述性统计值均用平均值 ± 标准误表示, 显著性水平设置为 $\alpha=0.05$ 。

2 结果

2.1 孵化温度对孵化成功率的影响

14 条赤链蛇母体窝卵数范围为 5—13 枚(平均 8.6 ± 0.7), 窝平均卵重范围为 5.40—7.61 g(平均 6.32 ± 0.2)。窝卵数和窝平均卵重与体长无明显相关性($P > 0.22$)。3 个孵化温度下的初始卵重没有差异(one-way ANOVA; $F_{2, 24} = 0.09$, $P = 0.91$)、孵化成功率和性比均没有差异(G 检验, $P > 0.05$; 表 1)。线性回归显示孵化期与卵重无相关性($r^2 = 0.004$, $t = 0.24$, $df = 16$, $P = 0.82$)。不同温度下孵化期差异显著($F_{1, 15} = 119.4$, $P < 0.0001$), 高温孵化期最短, 低温最长(表 1)。

2.2 孵化温度对卵代谢率和后代行为的影响

线性回归检验结果发现代谢率(每分钟呼吸产生 CO₂ 的微升数)与卵重和孵化时间呈正相关($P < 0.0001$)。孵化期间随着孵化时间的延长卵因吸水增重显著(图 1)。以初始卵重为协变量孵化温度为因子的协方差分析显示幼体孵出前的终末卵重差异显著($F_{2, 15} = 4.00$, $P = 0.04$), 24 ℃ 下的终末卵重(10.17 g)显著大于 30 ℃ 的终末卵重(8.68 g), 而 27 ℃ 的终末卵重(8.87 g)与这两个孵化温度无显著差异(图 1)。

孵化温度对胚胎代谢率没有影响(one-way ANCOVA, $P > 0.05$)(图 2)。胚胎发育所产生的 CO₂ 量在 24、27 ℃ 和 30 ℃ 下分别为 0.33、0.22 L 和 0.17 L, 经计算这 3 个孵化温度卵代谢所消耗的能量分别为 6.63、

4.42 J 和 3.42 J。

表 1 孵化温度对幼体孵化期和孵化成功率的影响

Table 1 Effects of incubation temperature on incubation length, hatching success and the sex ratio of hatchlings

孵化温度 /℃ Thermal treatment	孵化卵数量 Number of incubated eggs	孵化期/d Duration of incubation	孵化成功率/% Hatching success	性比 Sex ratio (♀♀/♂♂)
24	10	78.4 ± 2.3 67—82	70.0 (7/10)	2/5
27	8	54.9 ± 0.4 54—56	71.4 (6/8)	2/4
30	10	45.1 ± 0.4 44—46	60.0 (6/10)	3/3

孵化期的数据用平均值±标准误和范围表示

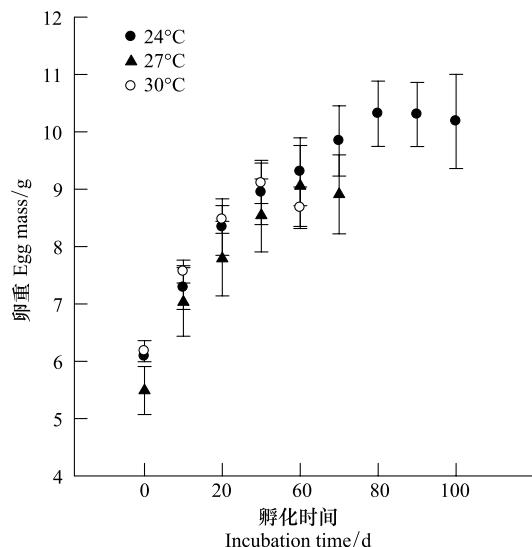


图 1 在 3 个不同的恒温条件下卵重的时间变异

Fig. 1 Temporal changes in egg masses incubated at three constant temperatures

数据用平均值±标准误表示, 卵重每 10 d 称量 1 次

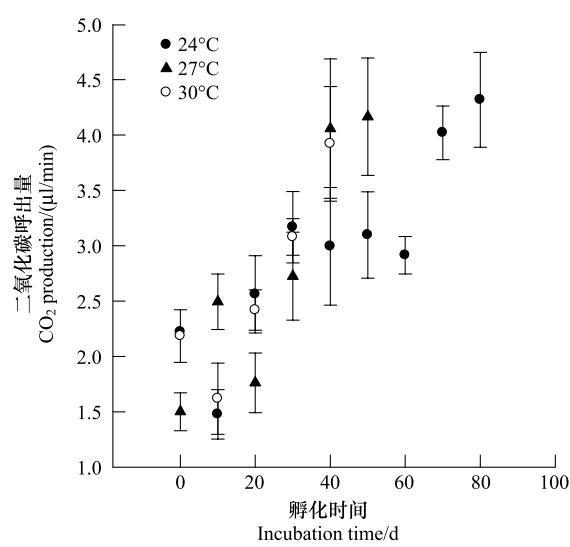


图 2 在 3 个不同的恒温条件下二氧化碳呼出量的时间变异

Fig. 2 Temporal changes in CO₂ production of eggs incubated at three constant temperatures

数据用平均值±标准误表示, 二氧化碳呼出量每 10 d 称量 1 次

孵化温度对后代吐信频次无显著影响 (one-way ANOVA, $F_{2,16} = 0.11$, $P = 0.89$), 但对泳速影响较显著 (one-way ANOVA, $F_{2,16} = 4.65$, $P = 0.03$) (图 3)。27 °C 下孵出的幼体游速较 24 °C 快, 30 °C 孵出幼体与其他两个温度没有差异 (图 3)。

3 讨论

在爬行动物中, 胚胎发育所经历的温度环境对其孵出后幼体的形态、生长和发育有着重要的影响, 甚至会直接影响幼体的适合度。例如极端高温不仅能降低孵化成功率还会增加胚胎的畸形率, 而低温则会减缓胚胎的发育速率, 但对孵化成功率和胚胎畸形率没有影响^[18]。赤链蛇在 24—30 °C 的孵化期随着温度的升高逐渐缩短, 但各孵化温度下的孵化成功率没有显著差异 (表 1)。

孵化温度对爬行动物胚胎发育有很大的影响, 常见

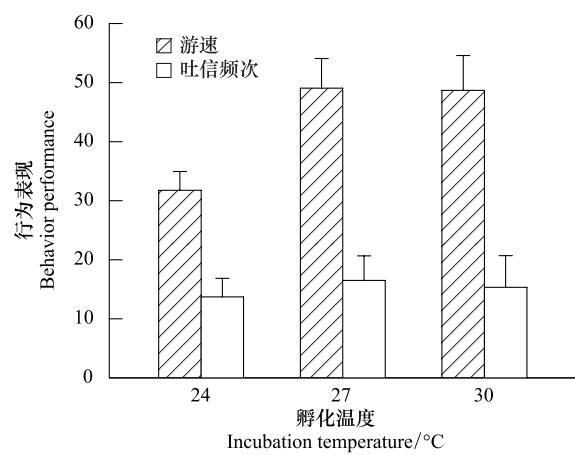


图 3 在 3 个不同的恒温条件下孵出的赤链蛇幼体的游速 (cm/s) 和吐信频次 (次/min)

Fig. 3 Swimming speed (cm/s) and tongue flicking (numbers/min) of *D. rufozonatum* hatchlings incubated at three constant temperatures

数据用平均值±标准误表示

于产柔性卵的有鳞类爬行动物^[14, 19-21], 卵在孵化过程中, 与周围的环境进行水分散换净吸水导致胚胎增重, 吸水的速率与周围热环境有明显的相关性, 随温度的上升吸水率逐渐下降。赤链蛇在胚胎孵化过程中, 也有相似的结果, 随温度的上升胚胎吸水率下降(图1)。

爬行动物的代谢与其体重、体温、年龄和个体状态有密切的关系^[22-23]。赤链蛇在整个孵化期间胚胎发育所产生的CO₂量和消耗的能量数随着孵化温度的上升而减少。这一点与张永普和计翔的研究结果相一致, 他们的研究结果显示30℃下孵出幼体的剩余卵黄大于低温孵出幼体的剩余卵黄。原因主要是由于高温下孵化的卵孵化期较短, 消耗能量少, 因此剩余卵黄较多。

一定的温度范围内, 爬行动物在低温和温和温度下孵出的幼体功能表现较好, 而高温孵出幼体功能表现较差^[18, 21, 24]。本研究说明赤链蛇对24—30℃孵化温度的影响不敏感, 孵化温度对赤链蛇孵出幼体的行为影响较小, 仅27℃孵化温度孵出的幼体游速好于24℃(图3)。比较赤链蛇的其他研究结果^[12-13]和2009—2010年野外赤链蛇活动区的温度发现, 24—30℃没有达到赤链蛇活动区温度的临界值, 这一温度范围适合其生存和繁育后代。

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E-mail: shengtaixuebao@rcees.ac.cn 网 址: www.ecologica.cn

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电话:(010)62941099
www.ecologica.cn
shengtaixuebao@rcees.ac.cn

主 编 冯宗炜
主 管 中国科学技术协会
主 办 中国生态学学会
中国科学院生态环境研究中心
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