

水热环境对中国石龙子孵化卵、孵化成功率及 孵出幼体特征的影响*

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摘要 用8种水热条件孵化中国石龙子 (*Eumeces chinensis*) 卵, 观测孵化卵质量变化、胚胎利用卵内物质和能量及孵出幼体特征。孵化卵因净吸水增重, 卵增重与入孵卵质量、孵化温度和基质湿度有关。孵出幼体湿重的处理间差异主要是因为幼体水分含量不同。温度显著影响孵化期、孵化卵吸水量、胚胎利用卵内物质和能量几乎所有被检的幼体特征; 温度甚至影响胚胎动用卵壳无机物。然而, 在24~32 范围内, 温度对卵孵化成功率无显著的影响。32 孵出幼体比较低于此温度的孵出幼体发育差, 表现为躯干小、未利用的卵黄多。此外, 32 孵出幼体的运动表现比低温孵出幼体差, 表现为特定体长 (snout-vent length, SVL) 的疾跑速小于低温孵出幼体, 表明高温孵化卵对孵出幼体的运动能力有不利的影响。潮湿基质中孵出幼体的体长和尾长大于干燥基质中孵出的幼体, 并特征性地具有较小的剩余卵黄。24 胚胎发育能耗较大, 胚胎从卵壳动用的无机物较少。温度影响孵出幼体的体形和头部大小, 30 孵出幼体的尾长最大, 32 孵出幼体的头部最小。基质湿度对孵出幼体的体形和头部大小无显著的影响。温度对孵出幼体特征的影响与湿度的影响无关。孵化水热环境诱导的幼体大小、质量和形态差异可能对幼体的生存和适应性具有重要的影响。26~30 为孵化中国石龙子卵的适宜温度范围。

关键词 中国石龙子 卵 孵化 幼体特征 运动表现

爬行动物卵具有相对较宽的存活孵化温度范围 (Deeming *et al.*, 1991), 极端温度对孵出幼体表型特征有不利的影响或能导致爬行动物胚胎畸形或死亡 (Vinegar, 1974)。存活孵化温度的上限和下限可以用孵化成功率和胚胎畸形率等指标来判定。然而, 即便在存活孵化温度范围内, 温度亦可能对胚胎一些热可塑性特征作细微、永久性的修饰, 这些修饰可能会长期影响动物的适应性。种类不同的爬行动物或产刚性卵 (rigid-shelled egg) 或产柔性卵 (pliable-shelled egg), 绝大多数卵生有鳞类爬行动物产柔性卵。柔性卵孵化时会因吸水或失水发生质量和体积的变化, 使胚胎在变化幅度较大的水环境中发育。小型柔性卵与孵化环境之间的水交换相对更为活跃, 孵化早期失水通常对胚胎具有致死效应 (林植华等, 1998; Vleck, 1991; Overall, 1994; Ji, 1992; Ji *et al.*, 1996, 1997a, 1997b, 1999a; Braña *et al.*, 2000)。然而, 人们对孵化水环境是否能精细地影响有鳞类爬行动物柔性卵孵

化一直存在不同的看法: 部分人认为孵化水环境显著影响孵化成功率, 孵化期和孵出幼体的体重、线性测量数据和剩余卵黄大小等一些重要特征 (Lutz *et al.*, 1984; Packard *et al.*, 1984, 1986, 1988; Gutzke *et al.*, 1987; Packard, 1991), 另一部分人则认为孵化水环境在一定范围内变化对爬行动物卵孵化无重要的影响 (林植华等, 1998; Tracy, 1980; Hotaling *et al.*, 1985; Plummer *et al.*, 1988; Ratterman *et al.*, 1989; Ji *et al.*, 1999a; 1999b)。这种观点上的分歧可能与不同同行的实验设计和所用卵的类型不同有关。

中国石龙子年产单窝小型柔性卵, 卵壳极薄, 雌体具有护卵行为, 孵化卵能从环境中吸水导致卵重的显著变化 (王培潮, 1966; De Fraipont *et al.*, 1996; Ji *et al.*, 1996)。这些特点使得该种卵非常适合用来检测水热环境对 (1) 孵化过程中卵质量的变化; (2) 孵化成功率; (3) 孵出幼体特征 (大小、形态、成分和运动表现等) 的影响。

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1 材料和方法

中国石龙子雌体于 1998 年 5 月上旬捕自浙江丽水三岩寺。捕回的石龙子带回杭州,经测量和称重后被关养在专用培养缸(900 mm × 650 mm × 500 mm)内,各缸内石龙子总数不超过 8 条。缸内模拟该种的野外生境,提供产卵巢址、足量面包虫(larvae of *Tenebrio molitor*)和饮水[含德国产爬行动物专用复合微量元素(Nektom-Rep)和儿童钙粉]。缸一端悬挂一只 300 W 灯泡作为石龙子体温调节的辅助热源,气温低于 24 ℃ 时灯泡自动开启,保证石龙子能将体温调整到喜好温度(计翔等, 1995)。饲养雌体于 5 月 31 日~6 月 28 日产卵。

卵在产后 1 hr 内被收集。卵经测量和称重后被移入直径为 120 mm、内含不同水势(湿度)孵化基质的圆罐内。孵化卵的 1/3 被埋在基质中,同窝卵尽可能均匀分配在不同的温湿度处理中。圆罐上覆穿孔的塑料薄膜,放置在广东医疗仪器厂 LRH-250A 型生化培养箱中,每日调整圆罐在箱内的位置以减少相互间的温差。本研究采用 2(湿度) × 4(温度)实验设计。湿度设置为 0 kPa 和 -220 kPa,分别由干蛭石(vermiculite)水 = 1:3 和 1:1 配合而成;温度设置为 24、26、30 和 32 ℃。每日向圆罐内加适量的水,保持原有湿度;每隔 5 日称卵重,直至幼体孵出。

幼体出壳 1 hr 内被收集、测量和称重,随后测定疾跑速。测定前将幼体体温恒定为 30 ℃,该体温在成体跑速的适宜体温范围内(计翔等, 1995)。用 Panasonic NV-DS77 数码摄像机记录被强烈驱赶的幼体在 2 000 mm × 100 mm × 150 mm 跑道中的运动表现,每条幼体重复测定两次,疾跑速用两次测定中幼体跑过 250 mm 的最大速度表示。部分幼体在跑道上表现不佳(如中途折返等),对应数据不用于进一步的统计处理。测定完毕,所有幼体被冰冻处死。

冰冻幼体以后被解冻,分离成躯干和剩余卵黄,65 ℃ 烘箱中干燥至恒重。躯干和剩余卵黄的非极性脂肪(non-polar lipids)用索氏脂肪抽提仪在 55 ℃ 条件下至少抽提 5.5 hr,分析纯无水乙醚作抽提溶剂。躯干和剩余卵黄的能量用 GR-3500 弹式氧弹仪(长沙仪器厂)测定。卵壳和幼体灰分含量用马福炉在 700 ℃ 焚烧 12 hr 测定。

所有数据在作进一步统计检验前,用 Kol-

mogorov-Smirnov 和 Bartlett (STATISTICA 统计软件包)分别检验其正态性和方差同质性。部分数据需经 ln(自然对数)转化才符合参数统计的条件。用 G 检验、单向(one-way)和双向(two-way)方差分析(ANOVA)、线性回归、单向和双向协方差分析(ANCOVA)及 Post-hoc 比较(Tukey's 检验)等处理和比较相应的数据。全文中的描述性统计值用平均值 ± 标准误表示,比较矫正平均值前,检验斜率的均一性,显著性水平设置为 $\alpha = 0.05$ 。

2 结果

2.1 孵化过程中卵质量的变化

各时期孵化卵的质量变化与入孵卵质量呈正相关(all $P < 0.01$)。温度、湿度和温湿度相互作用影响孵化各时期卵质量的变化(two-way ANCOVA, all $P < 0.05$);同一温度潮湿基质中孵化卵的终末质量显著大于干燥基质中的孵化卵(one-way ANCOVA, all $P < 0.0001$) (图 1A~D)。双向 ANCOVA 显示温度($F_{3,420} = 90.37$, $P < 0.0001$)、湿度($F_{1,420} = 374.85$, $P < 0.0001$)和温湿度相互作用影响孵化末期的卵质量(all $P < 0.05$): 26 ℃ / -220 kPa 和 30 ℃ / (220 kPa 孵化卵的终末质量无显著差异(Tukey's test, $P > 0.05$), 24 ℃ / 0 kPa 和 30 ℃ / 0 kPa 孵化卵的终末质量无显著差异(Tukey's test, $P > 0.05$), 同一湿度低温孵化卵的终末质量大于高温孵化卵(Tukey's test, all $P < 0.0001$)。

2.2 孵化期和孵化成功率

双向 ANOVA 显示温度显著影响孵化期(ln 转化)($F_{3,436} = 9209.69$, $P < 0.0001$),湿度($F_{1,436} = 1.47$, $P = 0.225$)和温湿度相互作用对孵化期无显著的影响($F_{3,436} = 1.59$, $P = 0.191$)。孵化期随温度升高而缩短。24~26 ℃, 孵化期平均缩短 10.0 d; 26~30 ℃, 孵化期平均缩短 11.1 d; 30~32 ℃, 孵化期平均缩短 1.4 d(表 1)。在本研究设计的温湿度范围内,温度和湿度对孵化成功率无显著的影响(G-test, $P > 0.05$)。

2.3 孵化温、湿度对孵出幼体大小、质量和形态的影响

温度和湿度显著影响孵出幼体体重、体长和尾长(三者均经 ln 转化),温、湿度相互作用对幼体的体重、体长和尾长无显著影响(表 2)。潮湿基质中孵出幼体的体重、体长和尾长显著大于干燥基质

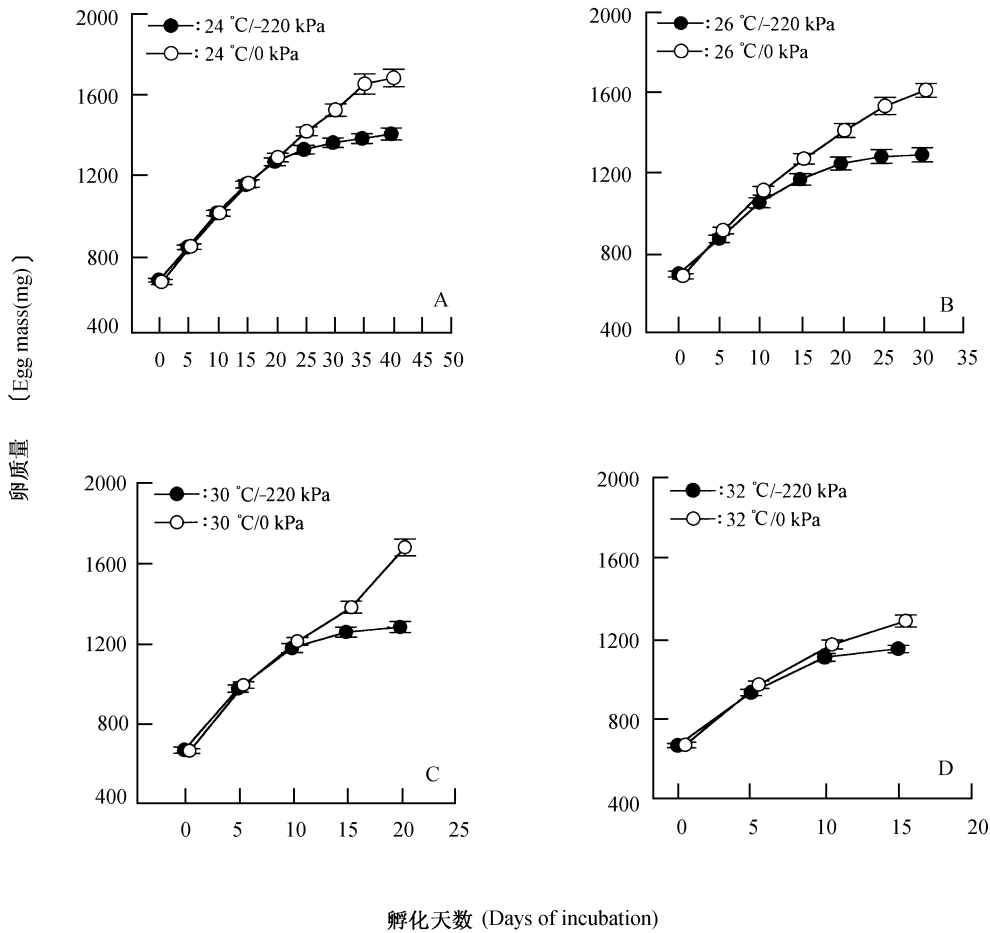


图 1 不同孵化水热环境中中国石龙子卵质量的变化

Fig. 1 Temporal changes in mass of *Eumeces chinensis* eggs incubated in different thermal and hyric environments

数据用平均值 ±标准误差表示，图中显示样本含量 (Data are expressed as mean ±SE. Sample sizes are indicated in the figures)

表 1 水热环境对中国石龙子孵化期和孵化成功率的影响

Table 1 Effects of thermal and hyric environments on duration of incubation and hatching success in *Eumeces chinensis*

温度/湿度 (/ kPa) Temperature/ Moisture	孵化卵数 Incubated eggs	孵化期 (d) Duration of incubation	孵化成功率 (%) Hatching success
24/ - 220	78	41.7 ±0.2 (35.5 ~ 45.8)	87.2 (68/ 78)
24/ 0	69	41.4 ±0.2 (35.9 ~ 45.0)	76.9 (53/ 69)
26/ - 220	51	32.0 ±0.2 (27.1 ~ 35.8)	88.9 (45/ 51)
26/ 0	75	31.4 ±0.2 (29.0 ~ 34.9)	88.0 (66/ 75)
30/ - 220	56	20.5 ±0.1 (17.8 ~ 22.7)	92.9 (52/ 56)
30/ 0	51	20.5 ±0.1 (18.0 ~ 22.5)	83.3 (47/ 51)
32/ - 220	72	19.0 ±0.1 (18.0 ~ 21.6)	80.6 (58/ 72)
32/ 0	62	19.2 ±0.1 (16.3 ~ 22.1)	88.7 (55/ 62)

中孵出的幼体；32 °C 中孵出幼体的体重和体长显著小于 24 °C、26 °C 和 30 °C 孵出幼体，后三个温度中孵出的幼体体重和 SVL 无显著差异；30 °C 中孵出幼体的尾长最大，26 °C 和 32 °C 孵出幼体的尾长大于 24 °C 孵出幼体 (表 2)。

孵出幼体总干质量、躯干和剩余卵黄干质量均与初始卵质量显著相关，故以初始卵质量为协变量的双向 ANCOVA 比较这些变量的处理间差异。孵出幼体的脂肪体干重的变化独立于初始卵质量的变化，故用双向 ANOVA 比较脂肪体干质量的处理间差异。温度、湿度和温、湿度相互作用对孵出幼体总干质量无显著影响 (表 2)。温度显著影响孵出幼体躯干干质量，湿度和温、湿度相互作用对躯干干质量无显著影响；32 °C 中孵出幼体的躯干干质量显著小于 24 °C、26 °C 和 30 °C 孵出幼体，后三个温度中孵出幼体的躯干干质量无显著差异 (表 2)。温

度和湿度显著影响孵出幼体剩余卵黄干质量, 温、湿度相互作用对孵出幼体剩余卵黄无显著影响; 潮湿基质中孵出幼体的剩余卵黄小于干燥基质中孵出的幼体, 剩余卵黄随孵化温度升高而增加 (表 2)。

温度影响孵出幼体的体形和头部大小。ANCOVA 设置体长恒定后仍然发现 30 孵出幼体的尾长显著大于其余温度的孵出幼体, 32 孵出幼体的头部最小 (表 3)。湿度及温、湿度相互作用对孵出幼体的体形和头部大小无显著的影响 (表 3)。

2.4 孵化温度对卵内物质和能量利用的影响

24~32 范围内, 温度影响幼体干质量以外的所有其它测定指标 (表 4)。温度显著影响中国石龙子胚胎对卵内物质和能量的利用, 24 的能量转化率最低, 24 和 32 的非极性脂肪转化率最低, 26 和 30 的脂肪和能量转化率较高 (表 4)。温度影响胚胎动用卵壳无机物, 24 孵出卵卵壳最重、灰分含量最高 (表 4)。

表 2 不同水热环境中孵出的中国石龙子幼体的体重、体长和尾长

Table 2 Body mass, snout-vent length, tail length of *Eumeces chinensis* hatchlings from the eggs incubated in different thermal and hydric environments

温度/湿度 (/ kPa) Temperature/ Moisture	样本 含量 (n)	体 重 (mg) Body mass		体 长 (mm) Snout-vent length	尾 长 (mm) Tail length	躯干干重 (mg) Carcass dry mass	剩余卵黄干重 (mg) Yolk sac dry mass	脂肪体干重 (mg) Fat body dry mass
		湿 重 (Wet mass)	干 重 (Dry mass)					
24/ - 220	68	680.6 ±8.8 (541.3 ~ 938.4)	147.4 ±2.5 (91.9 ~ 200.8)	29.7 ±0.3 (23.0 ~ 32.3)	35.8 ±0.3 (25.8 ~ 42.2)	131.3 ±2.1 (80.4 ~ 178.1)	15.7 ±1.9 (3.6 ~ 43.0)	0.36 ±0.04 (0.1 ~ 1.6)
24/0	53	676.1 ±10.0 (562.0 ~ 887.7)	143.7 ±2.6 (113.2 ~ 197.2)	30.0 ±0.2 (26.3 ~ 32.4)	35.7 ±0.4 (29.2 ~ 42.1)	128.3 ±2.3 (88.4 ~ 168.3)	15.1 ±1.2 (1.2 ~ 48.3)	0.29 ±0.03 (0.1 ~ 1.1)
26/ - 220	45	683.4 ±13.2 (536.7 ~ 936.3)	153.6 ±3.8 (109.6 ~ 217.0)	29.8 ±0.3 (24.7 ~ 33.3)	35.8 ±0.5 (27.6 ~ 41.3)	130.2 ±3.1 (82.3 ~ 179.5)	23.0 ±2.6 (2.9 ~ 90.4)	0.37 ±0.05 (0.1 ~ 1.1)
26/0	66	689.8 ±11.5 (486.8 ~ 943.2)	148.6 ±2.8 (105.7 ~ 204.5)	30.2 ±0.2 (25.0 ~ 33.0)	37.1 ±0.3 (30.0 ~ 43.6)	130.8 ±2.2 (90.7 ~ 183.1)	17.4 ±1.2 (4.1 ~ 57.4)	0.36 ±0.03 (0.1 ~ 1.1)
30/ - 220	52	670.9 ±13.3 (479.1 ~ 918.2)	148.6 ±3.3 (89.5 ~ 214.6)	29.8 ±0.2 (25.4 ~ 32.8)	37.2 ±0.5 (26.6 ~ 45.3)	127.5 ±2.7 (69.2 ~ 170.7)	20.8 ±1.9 (2.7 ~ 75.0)	0.34 ±0.04 (0.1 ~ 1.3)
30/0	47	673.9 ±9.9 (576.3 ~ 859.9)	147.9 ±2.9 (92.2 ~ 193.8)	30.3 ±0.2 (25.1 ~ 33.0)	38.2 ±0.4 (31.9 ~ 49.6)	129.1 ±2.4 (80.8 ~ 166.7)	18.4 ±1.3 (7.0 ~ 41.4)	0.34 ±0.04 (0.1 ~ 1.3)
32/ - 220	58	646.8 ±9.6 (498.7 ~ 837.9)	147.5 ±2.5 (109.7 ~ 201.6)	29.2 ±0.2 (25.5 ~ 31.7)	35.6 ±0.4 (26.7 ~ 41.5)	118.1 ±2.2 (70.0 ~ 150.5)	29.1 ±1.9 (5.8 ~ 64.4)	0.34 ±0.04 (0.1 ~ 1.4)
32/0	55	656.0 ±10.8 (507.8 ~ 851.4)	142.9 ±3.0 (63.9 ~ 194.0)	29.4 ±0.2 (24.6 ~ 31.7)	36.2 ±0.4 (28.6 ~ 41.4)	117.6 ±2.4 (61.1 ~ 158.5)	25.1 ±1.6 (2.7 ~ 62.5)	0.28 ±0.03 (0.1 ~ 0.9)
湿度 (Moisture)	$F_{1,435}$	5.05 * WS > DS	2.58 ns	9.62 ** WS > DS	8.25 ** WS > DS	0.23 ns	5.07 * WS < DS	0.76 ns
温度 (Temperature)	$F_{3,435}$	7.34 *** 24 ^a , 26 ^a , 30 ^a , 32 ^b	1.78 ns	6.50 *** 24 ^a , 26 ^a , 30 ^a , 32 ^b	12.43 *** 24 ^c , 26 ^b , 30 ^a , 32 ^b	14.57 *** 24 ^a , 26 ^a , 30 ^a , 32 ^b	26.01 *** 24 ^c , 26 ^b ^c , 30 ^b , 32 ^a	1.43 ns
相互作用 (Interaction)	$F_{3,435}$	0.35 ns	0.34 ns	0.23 ns	1.31 ns	0.51 ns	0.23 ns	0.39 ns

注 (Notes): 双向 ANOVA (脂肪体干质量) 和双向 ANCOVA (入孵卵初始质量为协变量) 的 F 值 [F values correspond to single effects and factor interactions in two-way ANOVA (for fat body dry mass) and two-way ANCOVAs (with initial egg mass as the covariate)]

上标不同的平均值差异显著 (Tukey's test, $\alpha = 0.05$), $a > b > c$ [Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$), $a > b > c$]

WS: 潮湿基质 (0 kPa) [Wetter substrate (0 kPa)] DS: 干燥基质 (-220 kPa) [Drier substrate (-220 kPa)]

ns: $P > 0.05$ * $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

表 3 不同孵化环境中中国石龙子孵出幼体的体形和头部大小

Table 3 Body shape and head size of *Eumeces chinensis* hatchlings from the eggs incubated in different thermal and hydric environments

温度/湿度 (/ kPa)	样本含量 Sample size (<i>n</i>)	体重 (mg)	尾长 (mm)	头长 (mm)	头宽 (mm)
Temperature/ Moisture		Body mass	Tail length	Head length	Head width
24/ - 220	68	690.1 ±7.4	36.2 ±0.2	7.5 ±0.03	5.2 ±0.03
24/0	53	676.1 ±9.3	35.7 ±0.3	7.4 ±0.03	5.2 ±0.03
26/ - 220	45	689.8 ±8.9	36.1 ±0.3	7.5 ±0.03	5.1 ±0.03
26/0	66	683.9 ±7.5	36.8 ±0.2	7.5 ±0.02	5.1 ±0.02
30/ - 220	52	677.3 ±8.8	37.5 ±0.3	7.4 ±0.02	5.1 ±0.03
30/0	47	663.3 ±9.2	37.7 ±0.4	7.4 ±0.03	5.0 ±0.03
32/ - 220	58	675.3 ±6.9	36.9 ±0.2	7.4 ±0.02	5.0 ±0.02
32/0	55	676.9 ±8.0	37.1 ±0.3	7.4 ±0.02	4.9 ±0.03
湿度 (Moisture)	$F_{1,435}$	1.89 <i>ns</i>	0.52 <i>ns</i>	0.50 <i>ns</i>	0.55 <i>ns</i>
温度 (Temperature)	$F_{3,435}$	1.52 <i>ns</i>	15.40 ^{***} 24 ^b , 26 ^b , 30 ^a , 32 ^b	4.38 ^{**} 24 ^a , 26 ^a , 30 ^{ab} , 32 ^b	22.16 ^{***} 24 ^a , 26 ^b , 30 ^b , 32 ^c
相互作用 (Interaction)	$F_{3,435}$	0.42 <i>ns</i>	1.94 <i>ns</i>	0.17 <i>ns</i>	2.55 <i>ns</i>

注 (Notes): 双向 ANCOVA (幼体 SVL 为协变量) 的 F 值数据用校正平均值 ±标准误表示 [F values correspond to single effects and factor interactions in two-way ANCOVAs (with hatchling SVL as the covariate) Data are expressed as adjusted means ±SE]

上标不同的平均值差异显著 (Tukey's test, $\alpha = 0.05$), $a > b > c$ [Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$), $a > b > c$]

ns: $P > 0.05$ ** $P < 0.01$ *** $P < 0.001$

表 4 孵化温度对中国石龙子孵出幼体含能量、脂肪含量和灰分含量及孵出卵壳干重的影响

Table Effects of incubation temperature on energy contents, lipid mass and ash mass of *Eumeces chinensis* hatchlings and dry mass and ash mass of hatched egg shells

温度 () Temp.	样本含量 Sample size (<i>n</i>)	孵出幼体 Hatchling				卵壳 Eggshell	
		干质量 (mg) (Dry mass)	能量 (KJ) (Energy)	非极性脂肪 (mg) (Non-polar lipids)	灰分 (mg) (Ash mass)	干质量 (mg) (Dry mass)	灰分 (mg) (Ash mass)
24	121	146.3 ±1.2	3.38 ±0.03	34.8 ±0.5	15.5 ±0.1	8.1 ±0.1	0.82 ±0.01
26	111	148.0 ±1.4	3.43 ±0.03	36.1 ±0.6	15.8 ±0.1	7.7 ±0.1	0.79 ±0.01
30	99	150.4 ±1.4	3.55 ±0.04	37.5 ±0.6	16.2 ±0.1	7.2 ±0.1	0.73 ±0.01
32	112	147.9 ±1.4	3.53 ±0.04	32.1 ±0.9	16.2 ±0.1	7.2 ±0.1	0.73 ±0.01
$F_{3,438}$		1.35 <i>ns</i>	5.30 ^{**} 24 ^b , 26 ^{ab} , 30 ^a , 32 ^a	16.10 ^{***} 24 ^b , 26 ^a , 30 ^a , 32 ^b	3.96 ^{**} 24 ^b , 26 ^{ab} , 30 ^a , 32 ^a	19.01 ^{***} 24 ^a , 26 ^a , 30 ^b , 32 ^b	19.82 ^{***} 24 ^a , 26 ^{ab} , 30 ^b , 32 ^b

注 (Notes): 数据用校正平均值 ±标准误表示, 初始卵质量 (设置为 680 mg) 为协变量 (Data are expressed as adjusted means ±SE, with initial egg mass (set at 680 mg) as the covariate), 上标不同的校正平均值差异显著 (Tukey's test, $\alpha = 0.05$, $a > b$) [Adjusted means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$), $a > b$]

F 值 (ANCOVA) 之后的符号代表显著性水平 (F values of ANCOVAs are indicated. Symbols immediately after F values represent significant levels)

ns: $P > 0.05$ ** $P < 0.01$ *** $P < 0.001$

2.5 孵化温度对孵出幼体运动能力的影响

幼体 SVL ($r = 0.21$, $F_{1,342} = 16.27$, $P < 0.0001$) 和尾长 ($r = 0.24$, $F_{1,342} = 20.03$, $P < 0.0001$) 与疾跑速呈正相关, 幼体状态 [用 \ln (体重) 和 \ln (体长) 的回归剩余值表示] 与疾跑速无关 ($r = 0.06$, $F_{1,342} = 1.49$, $P = 0.222$)。温度显著影响幼体疾跑速 (ANOVA, $F_{3,340} = 12.65$, $P < 0.0001$), 32 孵出幼体的疾跑速显著小于 24~30 孵出幼体; 用 ANCOVA 去除幼体个体大小 (体长) 差异的影响后, 得出同样的结论 (ANCOVA, $F_{3,339} = 10.28$, $P < 0.0001$) (表 5)。

表 5 孵化温度对中国石龙子孵出幼体 (体温 30) 疾跑速的影响

Table 5 Effects of incubation temperature on sprint speed of *Eumeces chinensis* hatchlings (the body temperature of 30)

孵化温度 () Temperature	样本含量 (n) Sample size	观测值 (m/s) Observed values		矫正值 (m/s) Adjusted values	
		平均值 (Mean)	标准误 (SE)	平均值 (Mean)	标准误 (SE)
24	95	0.49 ^a	0.02	0.49 ^a	0.02
26	84	0.53 ^a	0.02	0.52 ^a	0.02
30	77	0.47 ^a	0.02	0.46 ^a	0.02
32	88	0.38 ^b	0.02	0.39 ^b	0.02

注 (Notes): 上标不同的平均值差异显著 (Means with different superscripts differ significantly)

3 讨 论

爬行动物卵与环境之间的水分交换能导致卵内容物水含量变化, 从而影响胚胎发育所处的卵内水环境。卵与环境之间的水分交换受生物 (胚胎发育速率、卵产出时胚胎发育的阶段和胚胎发育对水的需求)、化学 (卵内渗透活性物质含量和卵产出时的水含量) 和物理 (卵壳结构和表面积) 等因素的影响 (Ackerman *et al.*, 1985; Packard *et al.*, 1988; Vleck, 1991)。然而, 卵内水环境是否对爬行动物胚胎发育速率、胚胎存活率和孵出幼体特征有精细的影响迄今不明。

中国石龙子卵质量变化与孵化水热环境之间的一般关系是: (1) 高湿环境中孵化卵增重的比例大于低湿环境中的孵化卵; (2) 孵化中后期以后, 高湿环境中孵化卵增重的速率大于低湿环境中的孵化卵; (3) 高温环境中孵化卵增重的速率一般大于低

温环境中的孵化卵。显然, 不同水热环境中发育的胚胎所处的卵内水环境是不同的。本研究中, 孵化水环境影响中国石龙子孵出幼体的湿重、体长、尾长和剩余卵黄干质量。潮湿基质中孵出的中国石龙子较大, 幼体内剩余卵黄较小, 表明高湿条件下发育的胚胎对卵黄的利用较为充分。这些结果表明孵化水环境对中国石龙子孵出幼体的影响是显著的, 并很容易使人将此与 *Eumeces* 属石龙子的母体护卵行为联系起来。 *Eumeces* 属母体的护卵行为被认为具有维持孵化水热环境稳定的作用 (王培潮, 1966; De Fraipont *et al.*, 1996), 偏离相对较为稳定的水热环境可能不利于胚胎发育。据已有的证据, 野外中国石龙子繁殖期的性比偏移十分显著, 雌性成体出现率极低 (计翔等, 1995; 林植华等, 2000; Ji *et al.*, 1996)。这种性比的偏移是季节性的, 主要与雌体因护卵而减少巢外活动有关。由于产卵后的摄食活动对雌体恢复能量储存、提高越冬和未来繁殖能力是十分重要的 (Rose, 1981; Andrews *et al.*, 1994), 中国石龙子母体减少产卵后活动的代价将是高昂的, 这种代价应当与维持孵化环境稳定、提高孵出幼体的适应性、最终强化雌体的繁殖利益有关。然而, 湿度对中国石龙子孵出幼体的体形和头部形态特征无显著的影响。

孵化水环境对中国石龙子孵化成功率、孵化期和孵出幼体特征无显著的影响, 这些结果在柔性卵中被认为是个别现象 (Tracy *et al.*, 1985; Gutzke *et al.*, 1987; Packard *et al.*, 1988; Phillips *et al.*, 1990; Packard *et al.*, 1993; Phillips *et al.*, 1994; Janzen *et al.*, 1995), 但确实有一些种类中曾被报道过 (林植华等, 1998; 计翔等, 2001; Packard *et al.*, 1987; Plummer *et al.*, 1988; Thompson, 1990; Overall, 1994; Castilla *et al.*, 1996; Ji *et al.*, 1999a; Braña *et al.*, 2000)。同一问题的不同结论表明: (1) 不同种类的有鳞类柔性卵并非以相同或相似的方式对孵化水环境的变化作出反应; (2) 孵化水环境缺乏对孵化成功率和孵出幼体特征的精细影响可能不是个别现象。

极端低温和高温均不利于爬行动物的胚胎发育, 但两者对胚胎发育的影响是有差别的。低温主要导致胚胎发育减缓或停滞, 持续将卵暴露在孵化临界低温中会导致胚胎死亡。高温虽能加速胚胎发育, 亦能导致胚胎死亡率和畸形率升高 (Deeming *et al.*, 1991; Van Damme *et al.*, 1992; Ji *et al.*, 1999a)。本研究中, 温度对中国石龙子卵孵

化的重要影响表现在三个方面：(1) 胚胎对卵内物质和能量的利用；(2) 孵出幼体的大小和形态；(3) 孵出幼体的运动能力。

高温 (32 °C) 孵出的中国石龙子幼体较小、有较多的未被动用卵黄，这是所有已被研究的有鳞类爬行动物的共同特点 (计翔等, 2001; Beuchat, 1988; Phillips *et al.*, 1990, 1994; Van Damme *et al.*, 1992; Ji *et al.*, 1999a)。温度对孵出幼体个体大小 (体长 + 尾长) 的影响主要与幼体躯干的发育状况有关, 32 °C 孵出的幼体个体较小显然与胚胎卵黄利用不充分、幼体躯干发育较差有关 (表 2)。24 °C 发育的胚胎对卵黄的利用最为充分, 剩余卵黄最小。由于有鳞类胚胎发育所需的无机物来自卵黄和卵壳 (计翔等, 1999c; Ji *et al.*, 1996; 1997a; 1997b; 1999a; 2000), 24 °C 发育的胚胎因从卵黄获得的无机物较多、从卵壳获得的无机物较少, 故该温度孵出的幼体灰分含量较低, 孵出卵的卵壳较重、灰分含量较高 (表 4)。此外, 24 °C 孵化期最长 (表 1), 胚胎发育的能耗最大 (表 4)。中国石龙子卵在较低和温和温度 (24 ~ 30 °C) 中孵出较大的幼体, 这一结果与多数卵生爬行动物相似 (Gutzke *et al.*, 1987; Beuchat, 1988; Packard *et al.*, 1988; Phillips *et al.*, 1990, 1994; Van Damme *et al.*, 1992; Ji *et al.*, 1999a)。

卵在高温 (32 °C) 中孵出头部较小的幼体 (表 3)。头部大小与蜥蜴野外征服和获得食物的能力有关, 也与野外蜥蜴的食物利用谱有关, 较小的头部

能限制动物获得和利用食物的能力。据此可以推测, 高温中孵出的幼体在营养生态学意义上处于竞争的劣势, 不利于幼体未来的生长、生存和正常进入繁殖群体。30 °C 孵出幼体尾部最大, 但其决定机制和适应意义待进一步明确。

24 ~ 30 °C 孵出的幼体运动能力强, 特定 SVL 的疾跑速显著大于 32 °C 孵出的幼体。由于蜥蜴运动表现与个体大小和一些与运动直接有关的局部形态特征 (如四肢长度) 有关, 大个体一般运动表现较好 (Garland, 1985; Huey *et al.*, 1990; Bauwens *et al.*, 1995; Braña *et al.*, 2000)。因此, 24 ~ 30 °C 孵出的较大幼体运动表现好很容易被理解。然而, ANCOVA 去除个体大小 (体长) 差异的影响后仍然发现高温孵出的幼体运动表现较差, 这说明温度不仅在形态方面 (个体大小及与运动相关的局部特征, 如四肢长) 而且在生理方面影响孵出幼体的运动能力。由于较好的运动表现对野外生活的蜥蜴逃避天敌、获得食物和保护领域等均十分重要, 孵化温度对幼体运动能力的影响将对幼体的生存几率和生长速率产生实质性的影响。

本研究结果表明 26 ~ 30 °C 是中国石龙子适宜的卵孵化温度范围。32 °C 孵出发育程度较低、运动表现较差、头部较小的幼体。24 °C 孵出的幼体虽然较大、运动表现较好, 但孵化期长, 孵出幼体当年越冬前的生长期短, 胚胎发育能耗大。因此, 24 °C 和 32 °C 不是中国石龙子较为适宜的孵化温度。

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外 文 摘 要(Abstract)

EFFECTS OF THERMAL AND HYDRIC ENVIRONMENTS ON INCUBATING EGGS, HATCHING SUCCESS, AND HATCHLING TRAITS IN THE CHINESE SKINK (EUMECES CHINENSIS)

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Effects of thermal and hydric environments on incubating eggs, embryonic use of energy and nutrients, and hatchling traits were studied in the Chinese skink (*Eumeces chinensis*) from a population in Lishui, Zhejiang, eastern China. The eggs were incubated at temperatures of 24, 26, 30, and 32 °C on substrates with water potentials of 0 and -220 kPa using a 4 × 2 factorial design. All viable eggs increased in mass over the course of incubation due to absorption of water, and mass gain during incubation was dependent on initial egg mass, temperature, and substrate water potential. Variation in the wet mass of hatchlings among treatments stemmed mainly from variation in water content. Temperature profoundly affected duration of incubation, water uptake by eggs during the course of incubation, embryonic use of energy and nutrients, embryonic mobilization of inorganic material from the shell, and almost all hatchling traits examined. However, incubation temperature did not affect hatching success within the range from 24 °C to 32 °C. Hatchlings from eggs incubated at 32 °C were less developed, as indicated by smaller carcasses and more unutilized yolks, and hence were smaller than their siblings from lower incubation temperatures. Moreover, hatchlings from eggs incubated at 32 °C did not perform as well as their siblings from the temperatures lower than 32 °C in the racetrack, even when the hatchling size (snout-vent length) was kept constant. This indicates that high incubation temperatures have an impaired effect on locomotor performance of *E. chinensis* hatchlings. Eggs incubated in wetter substrates produced larger hatchlings that contained smaller residual yolks than did eggs incubated in drier substrates. At the time of hatching, shells from eggs incubated at 24 °C were heavier in dry mass and contained more ash than those from eggs incubated at

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lower temperatures, suggesting that less inorganic material be withdrawn from the shell by embryos developing at the temperature. Incubation temperature subtly affected body shape and head size of *E. chinensis* hatchlings: hatchlings from eggs incubated at 30 °C had the longest tails, and hatchlings from eggs incubated at 32 °C had the smallest heads. On the contrary, substrate water potential was not an important source of variation for body shape and head size of hatchlings. The effects of temperature on hatchling traits were independent of the effects of water potential. Variation in size and mass induced by incubation thermal and hydric environments would be important to post-hatching survival and fitness of hatchlings. Although temperature did not significantly influence hatching success within the range of 24 to 32 °C, 26 °C and 30 °C were more suitable for incubating *E. chinensis* eggs, as eggs incubated at temperatures within this range produced larger and well-performed hatchlings at a lower energy expenditure.

Key words Chinese skink (*Eumeces chinensis*), Egg, Incubation, Hatchling traits, Locomotor performance