

温湿度对山地麻蜥孵化卵、孵化成功率及 孵出幼体特征的影响

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摘要: 用6种温湿度条件孵化安徽宿州乾山山地麻蜥 (*Eremias brenchleyi*) 卵, 观测孵化卵质量变化、胚胎利用卵内物质和能量以及孵出幼体特征。卵在产出后1 h内收集, 共设置3×2种温湿度处理(温度分别为27、30和33℃; 湿度分别为-220、0 kPa)。每隔5 d称卵重, 直至幼体孵出。幼体经测量、称重后, 解剖、分离为躯干、剩余卵黄和脂肪体三组分, 用于成分测试。卵从环境中吸水导致质量增加, 孵化温、湿度及其相互作用显著影响孵化卵的质量变化: 同一温度下, 高湿度(0 kPa)孵化卵的终末质量大于低湿度(-220 kPa)孵化卵; 同一湿度下, 低温(27和30℃)孵化卵的终末质量大于高温(33℃)孵化卵。温度显著影响孵化期, 随温度的升高孵化期缩短; 湿度及其与温度的相互作用对孵化期无显著影响。孵化温湿度对孵化成功率无显著影响。温度显著影响胚胎对卵内物质的动用、幼体大小、质量以及剩余卵黄质量; 除剩余卵黄外, 湿度及其与温度的相互作用不影响山地麻蜥孵出幼体几乎所有的被检测特征。33℃孵出幼体的大小和质量均显著小于27和30℃, 并特征性地具有较大的剩余卵黄。因此, 33℃不适宜孵化山地麻蜥卵。27℃和30℃中孵出幼体躯干发育良好, 各项被测定的特征指标极其相似。

关键词: 山地麻蜥; 卵; 孵化; 温度; 湿度

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Influence of Thermal and Hydric Environments on Egg Incubation, Hatching Success, and Hatchling Traits in a Lacertid Lizard, *Eremias brenchleyi*

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Abstract: Influence of thermal and hydric environments on incubation eggs, embryonic use of energy and hatchling traits were studied in the lacertid lizards, *Eremias brenchleyi*, which were collected in Qianshan, Suzhou, Anhui, Eastern China. The eggs were incubated at temperatures of 27, 30, and 33 °C on substrates with water potentials of 0 and -220 kPa using a 3 × 2 factorial design. Laid eggs were collected in one hour. Eggs were weighed at five-days intervals till hatchlings from eggs incubated. Each hatchling was thawed and separated into carcass, residual yolks, and fat bodies after measured and weighed. The components were preserved frozen for later determination of composition. All viable eggs increased in mass throughout the course of incubation due to absorption of water, and both thermal and hydric environments affected water exchanges between eggs and their surroundings. Final eggs incubated in wetter substrates (0 kPa) gained more mass than did eggs in drier substrates (-220 kPa) but at the same temperature; final eggs incubated at 27 and 30 °C gained more mass than did eggs at 33 °C but at the same substrate water potential. Incubation temperature significantly affected duration of incubation, and which decreased as incubation temperature increased, but substrate moisture and its interaction with temperature did not. Both incubation and substrate moisture did not affected hatching success. Substrate moisture and its interaction with temperature were unaffected almost all hatchling traits examined except residual yolk. However, Incubation temperature profoundly affected embryonic use of nutrients and size, mass, and residual yolk mass of hatchlings. 33 °C was not a suitable incubation temperature for *E. brenchleyi* eggs, because eggs in-

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cubated at 33 °C produced smaller hatchlings that contained larger residual yolks than did eggs incubated at 27 °C and 30 °C. Given that eggs incubated at 27 °C and 30 °C both produced well-developed hatchlings of which all measured variables were nearly the same, we conclude that 30 °C is better than 27 °C for incubation of *E. brenchleyi* eggs because of the shortened duration of incubation at 30 °C.

Key words: *Eremias brenchleyi*; Egg; Incubation; Temperature; Moisture

卵生爬行动物胚胎发育受孵化水热环境等诸多环境因子的影响。已有的研究证据显示孵化热环境能影响卵孵化成功率、胚胎代谢率、孵化期以及孵出幼体的形态、大小、行为、蜕皮和生长 (Packard & Packard, 1988; Packard, 1991; Congdon & Gibbons, 1990; Deeming & Ferguson, 1991; van Damme et al, 1992; Lin & Ji, 1998; Ji & Du, 2001; Ji & Zhang, 2001; Braña & Ji, 2000; Ji & Braña, 1999; Ji et al, 2001)。在环境决定性别的种类中, 孵化水热环境还决定孵出幼体的性别 (Bull, 1980, 1985; Deeming & Ferguson, 1988, 1991; Paukstis et al, 1984)。

爬行动物卵存活孵化温度范围内, 温度诱导产生的幼体特征变异会长期影响个体的适应性 (Ji & Du, 2001; Ji & Zhang, 2001; van Damme et al, 1992; Shine et al, 1997a, b; Braña & Ji, 2000)。绝大多数卵生有鳞类产柔性卵 (pliable-shelled egg)。柔性卵在孵化过程中会因吸水或失水而导致质量和体积改变, 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尤为明显, 孵化早期失水通常对胚胎有致死效应 (Ji & Braña, 1999; Ji et al, 2001; Lin & Ji, 1998; Ji & Du, 2001; Ji & Zhang, 2001)。然而, 水环境对有鳞类爬行动物柔性卵和孵出幼体的细微影响也有不同的看法, 部分研究结果显示孵化水环境显著影响孵化成功率、孵化期、孵出幼体的大小、形态以及剩余卵黄大小等 (Packard & Packard, 1986, 1988; Packard, 1991), 而另一部分研究结果则表明孵化水环境在一定范围内变化对孵化卵无重要影响 (Lin & Ji, 1998; Ji & Du, 2001; Ji & Zhang, 2001; Ji & Braña, 1999; Ji et al, 2001)。本研究用 6 种孵化处理条件, 进一步探讨水热环境对孵化过程中卵质量、孵化期和孵化成功率、孵出幼体特征的影响。

1 材料和方法

研究用 49 条山地麻蜥 (*Eremias brenchleyi*) 雌

体于 2004 年 4 月上旬捕自安徽宿州乾山。捕捉的蜥蜴被关养在蜥蜴专用玻璃缸 (长 × 宽 × 高 = 1 000 mm × 800 mm × 500 mm) 内。在缸内蜥蜴能自由取食面包虫 (larvae of *Tenebrio molitor*) 和饮水, 并接受自然光照。定期触摸判断雌体的怀卵状态, 将怀输卵管卵的雌体单个关养在有潮湿沙质基质的产卵缸 (长 × 宽 × 高 = 300 mm × 150 mm × 250 mm) 内。雌体于 2002 年 4 月 18 日至 5 月 14 日共产卵 158 枚。为避免卵失水, 所有卵均在产后 1 h 内被收集、测量、称重和编号。新生卵经鉴别可孵性后被移入直径 19 cm、内含不同孵化基质的塑料盆中, 放置在广东科力仪器厂产 PYX-250S-A 生化培养箱内孵化。卵的 1/3 埋在基质中, 胚点朝上, 孵化盆用穿孔的塑料薄膜覆盖。定期向孵化盆内加水, 以保持基质湿度的恒定。共设置 6 个孵化温湿度处理, 温度分别为 27、30 和 33 °C, 湿度设置为 -220 和 0 kPa [分别由干蛭石 (vermiculite): 水 = 1:1 和 1:3 组成]。每隔 5 d 称量被孵化卵的质量, 直至幼体孵出。幼体出壳 1 h 内被收集、测量体长 (snout-vent length, SVL) 和尾长 (tail length, TL), 称重后冰冻保存。冷冻幼体以后经解冻, 鉴定性别 (雄体有明显的半阴茎), 解剖分离成躯干、剩余卵黄和脂肪体, 分别在 65 °C 烘箱中干燥至恒重, 称出干质量。幼体非极性脂肪用索氏脂肪提取器在 55 °C 条件下抽提脂肪, 分析纯乙醚作抽提溶剂。能量用 HR-15 型弹式氧弹仪 (长沙高教仪器厂) 测定。幼体躯干、剩余卵黄和卵壳灰分用马福炉在 700 °C 条件下焚烧 12 h 测得。

所有数据在参数统计分析前, 分别检验其正态性 (Kolmogorov-Smirnov test) 和方差同质性 (F-max test)。经检验, 原始数据须经 ln 转化后才能用于参数统计分析。用 G-检验、线性回归、双因素方差分析 (two-way ANOVA)、双向协方差分析 (two-way ANCOVA) 和 Post-hoc 比较 (Tukey's 检验) 等处理和比较相应的数据。文中涉及的 ANCOVA 均以初始卵质量为协变量, 比较矫正平均值前, 检验斜率的一致性。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

2.1 孵化温湿度对卵质量的影响

山地麻蜥卵在孵化过程中从环境中净吸水导致质量增加 (图 1)。孵化温、湿度和温湿度相互作用显著影响山地麻蜥孵化卵的终末卵质量 (two-way ANCOVA, all $P < 0.01$)。同一温度下, 潮湿基质

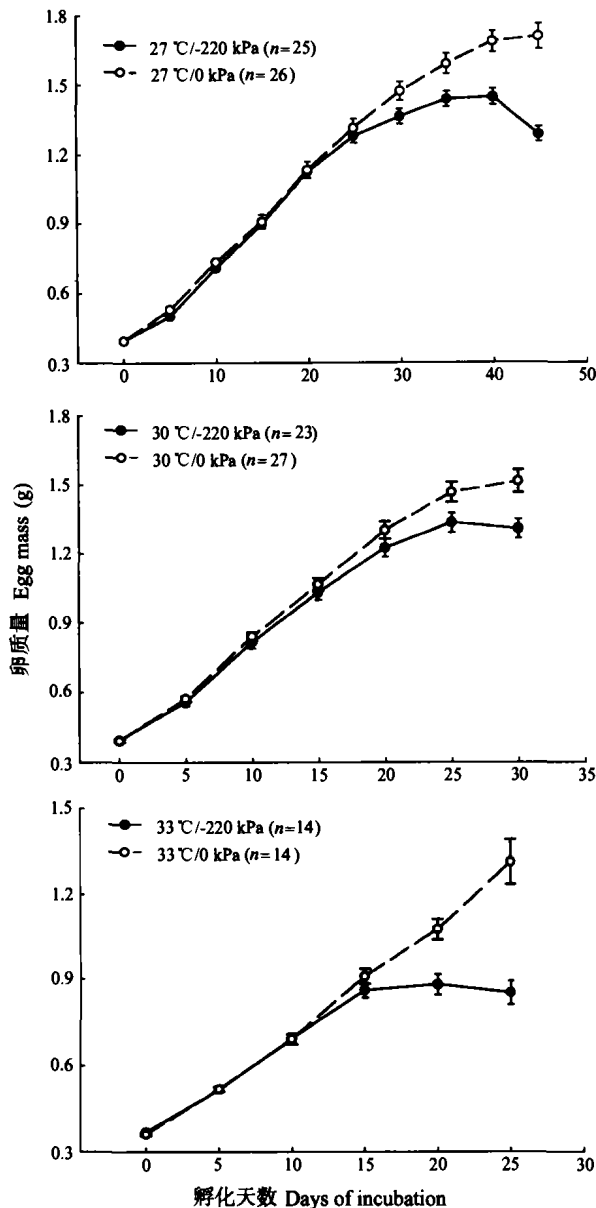


图 1 6 种温湿度条件下山地麻蜥卵孵化过程中质量变化

Fig. 1 Temporal changes in mass of *Eremias brenchleyi* eggs during incubation in six thermal and hydric environments

数据用平均值 \pm 标准误表示。

Data are expressed as mean \pm SE.

(0 kPa) 中终末卵质量显著高于干燥 (-220 kPa) 基质 (Tukey's test, $P < 0.0001$)。同一湿度下, 低温 (27 °C 和 30 °C) 孵化卵的终末质量大于高温孵化卵 (Tukey's test, $P < 0.0001$)。

2.2 孵化温湿度对孵化期和孵化成功率的影响

温度显著影响孵化期 (two-way ANCOVA, $F_{2,122} = 6753.50$, $P < 0.0001$), 湿度 ($F_{1,122} = 0.003$, $P = 0.95$) 和温湿度的相互作用 ($F_{2,122} = 0.93$, $P = 0.40$) 对孵化期无显著影响。孵化期随孵化温度的升高而缩短。27 ~ 33 °C, 温度每升高 3 °C, 孵化期分别缩短 13.5 和 4.9 d (表 1)。本研究的温湿度范围内, 温度和湿度对孵化成功率无显著影响 (G -test, all $P > 0.05$)。

2.3 孵化温湿度对孵出幼体大小、质量和组分的影响

湿度以及温、湿度的相互作用对山地麻蜥孵出幼体的湿质量、SVL 和 TL 无显著影响, 温度显著影响孵出幼体的湿质量、SVL 和 TL (表 2)。33 °C 孵出幼体的质量、SVL 和 TL 均显著小于 27 和 30 °C 的孵出幼体。

孵出幼体的干质量、躯干和剩余卵黄干质量均与初始卵质量呈正相关, 故用初始卵质量为协变量的双向 ANCOVA 处理和比较这些变量的差异。孵出幼体脂肪体干质量独立于初始卵质量的变化, 故用双向 ANOVA 处理和比较各孵化条件下脂肪体干质量之间的差异。温度显著影响孵出幼体的干质量和躯干干质量, 湿度以及温、湿度的相互作用对幼体的干质量和躯干干质量无显著影响; 33 °C 孵出幼体的干质量和躯干干质量均显著小于 27 °C 和 30 °C 的孵出幼体 (表 2)。温度和湿度显著影响孵出幼体的剩余卵黄干质量, 温、湿度的相互作用对孵出幼体剩余卵黄干质量无显著影响; 干燥基质中孵出幼体的剩余卵黄干质量大于潮湿基质中的孵出幼体, 剩余卵黄干质量随温度升高而增大 (表 2)。

2.4 孵化温度对卵内物质和能量动用的影响

27 ~ 33 °C 范围内, 温度显著影响山地麻蜥孵出幼体的干质量和灰分 (表 3); 显著影响胚胎对卵内物质的利用, 33 °C 干物质的转化率最低。温度对能量和非极性脂肪的转化无显著影响, 但 33 °C 能量和非极性脂肪的转化率均较低。温度影响山地麻蜥胚胎动用卵壳内无机物, 33 °C 孵出卵壳最重、灰分含量最高 (表 3)。

表 1 6种温湿度条件下山地麻蜥的孵化期和孵化成功率

Tab. 1 Duration of incubation and hatching success in *Eremia brechleyi* in six thermal and hydric environments

处理 Treatment (°C/kPa)	孵化卵数 (枚) No. of incubation eggs	孵化期 Duration of incubation (d)	孵化成功率 Hatching success (%)
27/-220	30	48.6 ± 0.2 ^a (47.3 - 50.5)	83.3 (25/30)
27/0	28	48.8 ± 0.2 ^a (47.0 - 50.7)	92.9 (26/28)
30/-220	30	35.3 ± 0.2 ^b (34.1 - 37.8)	76.7 (23/30)
30/0	32	35.3 ± 0.1 ^b (34.1 - 37.0)	84.4 (27/32)
33/-220	19	30.4 ± 0.1 ^c (29.4 - 31.0)	73.7 (14/19)
33/0	19	30.2 ± 0.2 ^c (28.9 - 31.2)	73.7 (14/19)

孵化期数据用平均值 ± 标准误 (范围) 表示, 不同上标的平均值之间差异显著 (Tukey's 检验, α = 0.05)。
Data on duration of incubation are expressed as mean ± SE (range). Mean with different superscripts are statistically different (Tukey's test, α = 0.05)].

表 2 6种温湿度条件下山地麻蜥孵出幼体的大小、质量和组分

Tab. 2 Size, mass and composition of *Eremias brechleyi* hatchlings from eggs incubated in six thermal and hydric environments

温度/湿度 Temperature/ Moisture (°C/kPa)	n	幼体质量 Body mass (mg)		体长 Snout-vent length (mm)	尾长 Tail length (mm)	躯干干质量 Carcass dry mass (mg)	剩余卵黄干质量 Yolk sac dry mass (mg)	脂肪体干质量 Fat body dry mass (mg)
		湿质量 Wet mass	干质量 Dry mass					
		27/-220	25	497.7 ± 5.7 439.0 - 555.6	91.7 ± 1.9 77.9 - 113.6	27.7 ± 0.2 ^a 26.0 - 29.4	39.0 ± 0.6 ^a 35.4 - 46.4	84.4 ± 1.6 ^a 72.0 - 105.1
27/0	26	503.1 ± 9.6 404.2 - 614.0	87.6 ± 2.2 72.4 - 121.3	27.6 ± 0.3 ^a 21.7 - 30.3	37.9 ± 0.5 ^{ab} 32.5 - 43.3	82.2 ± 2.0 ^a 68.2 - 111.1	4.2 ± 0.4 ^b 0.5 - 7.8	1.2 ± 0.2 0.3 - 3.0
30/-220	22	471.6 ± 6.4 415.8 - 530.2	91.2 ± 2.1 78.9 - 117.4	27.2 ± 0.2 ^{ab} 24.8 - 29.2	38.4 ± 0.5 ^{ab} 33.5 - 43.2	83.6 ± 1.8 ^a 72.2 - 105.9	5.7 ± 0.7 ^b 1.1 - 16.3	1.4 ± 0.2 0.2 - 4.2
30/0	27	472.8 ± 8.7 365.2 - 542.2	88.3 ± 2.3 52.1 - 111.6	27.3 ± 0.2 ^a 25.0 - 28.8	38.0 ± 0.4 ^{ab} 31.8 - 41.8	82.3 ± 2.2 ^a 50.1 - 107.5	4.5 ± 0.5 ^b 0.4 - 9.5	1.6 ± 0.1 0.6 - 3.3
33/-220	14	437.9 ± 9.3 377.2 - 484.2	82.7 ± 2.0 67.4 - 91.9	25.2 ± 0.3 ^c 23.2 - 26.8	35.0 ± 0.7 ^c 29.2 - 40.7	69.4 ± 2.4 ^c 55.4 - 82.5	10.2 ± 1.4 ^a 0.9 - 17.7	1.7 ± 0.2 0.3 - 3.1
33/0	14	456.3 ± 7.7 414.5 - 499.3	77.0 ± 2.6 59.4 - 89.2	25.8 ± 0.3 ^{bc} 24.0 - 27.2	35.8 ± 0.7 ^{bc} 31.3 - 41.4	69.6 ± 2.2 ^{bc} 54.7 - 78.3	6.2 ± 0.8 ^b 3.2 - 13.6	1.2 ± 0.1 0.2 - 2.1
湿度 Moisture	F _{1,122}	1.91 ^{ns}	3.36 ^{ns}	2.45 ^{ns}	0.10 ^{ns}	0.06 ^{ns}	16.75 ^{***} WS < DS	2.94 ^{ns}
温度 Temperature	F _{2,122}	17.53 ^{***} 27 ^a , 30 ^b , 33 ^c	3.81 [*] 27 ^a , 30 ^a , 33 ^b	22.90 ^{***} 27 ^a , 30 ^a , 33 ^b	10.02 ^{***} 27 ^a , 30 ^a , 33 ^b	15.59 ^{***} 27 ^a , 30 ^a , 33 ^b	18.34 ^{***} 27 ^b , 30 ^b , 33 ^a	3.01 ^{ns}
相互作用 Interaction	F _{2,122}	0.74 ^{ns}	0.32 ^{ns}	1.85 ^{ns}	1.65 ^{ns}	0.86 ^{ns}	2.62 ^{ns}	0.51 ^{ns}

数据用平均值 ± 标准误 (范围) 表示, 上标不同的平均值差异显著 (Tukey's 检验, α = 0.05), a > b > c。

Data on duration of incubation are expressed as mean ± SE (range). Means with different superscripts differ significantly (Tukey's test, α = 0.05), a > b > c.

^{ns} P > 0.05; ^{*} P < 0.05; ^{***} P < 0.0001。

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

表 3 3 种温度下山地麻蜥孵出幼体含能、脂肪、灰分含量以及孵出卵壳干质量

Tab. 3 Energy densities, lipid mass and ash mass of hatchlings and dry mass and ash mass of hatched egg shells in *Eremias brenchleyi* from three incubation temperatures

温度 Temp. (°C)	n	孵出幼体 Hatchling				卵壳 Shell	
		干质量 Dry mass (mg)	能量 Energy (kJ)	脂肪 Lipid (mg)	灰分 Ash mass (mg)	干质量 Dry mass (g)	灰分 Ash mass (mg)
27	51	88.5 ± 1.2 ^a	2.03 ± 0.03	15.0 ± 0.3	9.9 ± 0.1 ^a	11.3 ± 0.2 ^{ab}	0.99 ± 0.07 ^b
30	49	88.7 ± 1.0 ^a	2.04 ± 0.03	15.5 ± 0.3	9.7 ± 0.1 ^a	10.7 ± 0.2 ^b	1.15 ± 0.05 ^{ab}
33	28	83.3 ± 1.5 ^b	1.97 ± 0.04	14.5 ± 0.5	8.6 ± 0.2 ^b	12.0 ± 0.3 ^a	1.33 ± 0.13 ^a
<i>F</i> _{2,124}		3.86 [*]	0.77 ^{ns}	1.49 ^{ns}	16.01 ^{***}	7.80 ^{***}	3.95 [*]

数据用矫正平均值 ± 标准误表示, 初始孵卵质量为协变量。上标不同的热环境间差异显著, a > b > c。

Data are expressed as mean ± SE. Using initial egg mass as the covariate. The thermal environments with different superscripts differ significantly, a > b > c.

^{ns} P > 0.05; ^{*} P < 0.05; ^{***} P < 0.0001.

3 讨论

山地麻蜥产柔性卵 (Xu & Wu, 2003)。入孵卵与孵化环境之间进行水分交换导致质量增加 (图 1)。卵吸水速率与孵化环境之间显著相关。孵化卵的终末质量由初始卵质量以及孵化基质湿度决定。胚胎发育后期, 潮湿基质中卵的质量显著高于干燥基质中卵。然而, 山地麻蜥卵孵化期、孵化成功率、孵出幼体大小、质量和组分在较大的湿度范围内保持相对恒定, 孵化基质湿度仅仅影响入孵卵后期的质量和孵出幼体的剩余卵黄, 而对胚胎发育并不产生更多细微的影响。因此, 孵化水环境在一定范围内变化对山地麻蜥卵孵化没有重要的影响。这一结果在柔性卵中认为是个别现象 (Packard et al, 1980; Packard & Packard, 1988), 但确实有一些种类中有过报道 (Packard & Packard, 1987; Lin & Ji, 1998; Ji & Braña, 1999; Plummer & Snell, 1988; Ji & Du, 2001; Ji & Zhang, 2001; Braña & Ji, 2000)。因此, 不同种类的爬行动物卵不必以相同的方式对基质湿度的变化作出反映 (Ji & Du, 2001; Ji & Zhang, 2001)。

27 ~ 33 °C 范围内, 孵化温度主要影响山地麻蜥卵的孵化期及孵出幼体的质量、SVL 和 TL; 孵化期随温度升高而缩短, 这一结果与所有被研究的卵

生有鳞类爬行动物一样; 山地麻蜥在 27 和 30 °C 孵出幼体的质量、SVL 和 TL 均大于 33 °C 孵出幼体, 与其他爬行动物中发现的较低或温和温度中孵出的幼体较大 (van Damme et al, 1992; Ji & Braña, 1999; Braña & Ji, 2000; Ji & Du, 2001; Ji & Zhang, 2001) 的结论一致。27 ~ 33 °C 范围内, 孵化温度影响胚胎对卵黄的利用。33 °C 下孵出幼体小、剩余卵黄多, 这是许多有鳞类爬行动物的共同特点 (van Damme et al, 1992; Ji & Braña, 1999; Braña & Ji, 2000; Ji & Du, 2001; Ji & Zhang, 2001)。33 °C 孵出幼体剩余卵黄利用灰分含量高与剩余卵黄较大有关 (表 2、3)。33 °C 孵出卵壳干质量较大表明高温下胚胎对卵壳无机物的利用程度低, 使得幼体躯干的灰分含量低于其他热环境的孵出幼体。综合 33 °C 下孵出幼体小、剩余卵黄多的特点, 我们判定 33 °C 不适宜山地麻蜥卵的孵化。

27 和 30 °C 孵出幼体对卵黄的利用较充分, 且孵出幼体各项测定指标极为相似。由于在适宜温度范围内较高的孵化温度能缩短孵化期, 使得幼体有相对较长的适宜活动时间, 并通过摄食生长和储存能量, 最终增强越冬能力、越冬后存活率更高 (Ji & Du, 2001)。因此, 30 °C 是本研究的最适孵化温度。

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