Utilization of Energy and Material in Eggs and Post-hatching Yolk in an Oviparous Snake, *Elaphe taeniura*

XIANG JI[1], PING-YUE SUN[1], SHUI-YU FU[2], AND HUA-SONG ZHANG[2]

[1]*Department of Biology, Hangzhou Normal College, Hangzhou 310036, Zhejiang, China; Email (XJ): xji@public.hz.zj.cn;* [2]*Department of Chemistry, Hangzhou Normal College, Hangzhou 310036, Zhejiang, China*

Abstract.-The duration of incubation of *Elaphe taeniura* eggs at 30±0.3°C averaged 54.9 days. During incubation, pliable-shelled eggs of *E. taeniura* increased in wet mass. Dried shells of the freshly laid egg averaged 17.6% of the entire egg dry mass. Freshly laid eggs had significantly heavier shells than did hatched eggs with the same wet mass at oviposition. Dry mass conversion from egg contents of the freshly laid egg to hatchling averaged 84.5%. During incubation, approximately 74.6% of non-polar lipids and 80.8% of energy in egg contents of the freshly laid egg were transferred to the hatchling, with 25.4% of non-polar lipids and 19.2% of energy used for embryogenesis. Shells from freshly laid eggs had higher levels of calcium and magnesium than did shells from hatched eggs. Fully developed embryos could obtain almost all magnesium from the yolk but withdraw approximately 35.6% of their total calcium requirements from the eggshell. A few days after hatching, a decrease in post-hatching yolk mass was accompanied by an increase in carcass mass, indicating that post-hatching yolk could be used to support early growth of hatchlings.

Key words.-Reptilia; Squamata; *Elaphe taeniura*; Incubation; Egg; Post-hatching yolk; Hatchling

Introduction

As for reproductive investments in eggs and embryonic development, there are two patterns that seem to be common in oviparous reptiles. One pattern is that total energy and material stored in eggs generally exceed the needs for producing a complete hatchling. Hence, a portion of yolk, namely post-hatching yolk or residual yolk, may remain unutilized at the time of hatching. Post-hatching yolk represents a supply of energy and material for early activities of hatchlings (Kraemer and Bennett, 1981; Troyer, 1983, 1987; Wilhoft, 1986; Congdon and Gibbons, 1989); however, the exact function of this portion of resources allocated by the mother in eggs is not very clear. There is a growing evidence showing that resources in the post-hatching yolk can be transferred to the carcass (=total hatchling-yolk sac-fat bodies). The consequence of this transference is that carcass increases in mass during the first post-hatching days of hatchlings (Ji et al., 1997a). The other pattern is that embryos must mobilize minerals (e.g., calcium) from the eggshell to complete development (e.g., Bustard et al., 1969; Jenkins, 1975; Packard and Packard, 1984, 1989; Packard et al., 1984a, b; Shadrix et al., 1994; Ji et al., 1996, 1997a, b). As the consequence of this mobilization, eggshell decreases in mass and ash contents during incubation, particularly at the late stage of incubation (Ji et al., 1996, 1997a, b; Zhao et al., 1997). In this paper, we present data on a colubrid snake, *Elaphe taeniura*. We address the following topics: (1) conversion of energy and material from egg to hatchling during incubation, (2) sources of calcium and magnesium during embryogenesis, and (3) post-hatching yolk and its contribution to early growth of newly emerged hatchlings.

Material and Methods

Elaphe taeniura is one of the most common snakes in our study areas in the Zhoushan Islands (29° 32'-31° 04' N, 121° 30'-123° 25' E), Zhejiang, eastern China. The distributional range of *E. taeniura* covers most provinces of China (including Taiwan and Hainan), India (Darjeeling and Assam), Indochina, and the northern half of Malay Peninsula (Zhao and Adler, 1993). For this species, many aspects of biology species have been previously examined, but little information on incubation and reproduction is available other than incidental notes (see Huang and Jin, 1990).

Four gravid *E. taeniura* [snout-vent length: 110.0-155.0 cm; body mass (excluding the clutch): 233.4-778.7 g] were obtained from a private collector in Baiquan, Dinghai, the Zhoushan Islands, in mid-June 1994. The snakes were individually maintained in our laboratory in 80 × 80 × 80 cm wire cages until oviposition (mean=16.3 days). We removed eggs from the

cages, measured and weighed them within 6 h of oviposition, and then randomly selected two eggs from each of the first three clutches and one egg from the last clutch to determine egg composition. Egg contents (embryo plus yolk) of the dissected freshly laid eggs were removed, placed in pre-weighed small glass dishes, and weighed to the nearest 0.1 mg. Shells from the freshly laid eggs were rinsed briefly, weighed to the nearest o.1 mg, and then were saved for later analysis. All dissected freshly laid eggs contained a small embryo, which was too small and fragile to be sampled separately, and therefore was included with yolk.

Eighteen eggs, 1/3-buried in moistened substratum, were incubated in a constant temperature chamber at 30±0.3°C. The incubation medium consisted of sand to water in a ratio of 4:1, and water was added periodically to keep the initial water content. We measured and weighed the incubating eggs at weekly intervals before day 42, and daily intervals thereafter. Four eggs failed to hatch following incubation. Hatchlings were measured and weighed immediately after they left the eggs. Shells from hatched eggs were rinsed briefly, weighed to the nearest 0.1 mg, and then were frozen for later analysis. Nine hatchlings (2-3 from each clutch; hereafter 0-day hatchling) were frozen immediately after hatching. The remaining 5 hatchlings (1-2 from each clutch; hereafter 7-day hatchling) were fasted at room temperatures (26-38°C) for 7 days, and then frozen. The preserved hatchlings were later thawed, dissected, and separated into the carcass, yolk sac, and fat bodies.

All samples for determinations of non-polar lipids, ash, calories, calcium, and magnesium were oven dried to constant mass at 65 °C, weighed, and then ground in a mortar and pestle. Non-polar lipids were extracted from all samples of egg contents, carcass, post-hatching yolk, and fat bodies for a minimum of 5.5 h using absolute ether in a Soxhlet apparatus. The mass of non-polar lipids in each sample was calculated as the difference in sample dry mass before and after extraction.

Ash and calories of samples of egg contents, carcass, post-hatching yolk, and fat bodies were determined using a GR-2800 adiabatic bomb calorimeter (Changsha Instruments). Titrations were performed of the residue after calorimetry to correct for nitrogenous wastes. Samples of eggshells were burned in a muffle furnace at 550 °C for 24 h to determine ash mass.

Samples for calcium and magnesium determinations were weighed out into glass tubes and digested completely in hot concentrated nitric acid. Digestates were brought to volume in volumetric glassware and stored in a refrigerator until analysis for calcium and magnesium. Concentrations of the two elements in the digestates were determined using a WFX-1B model atomic absorption spectrophotometer (The 2nd Beijing Optical Instruments). To check if there were any differences in calcium and magnesium contents between shells from freshly laid eggs and hatched eggs, we took equal amount of sample from each shell, pooled separately the samples from the freshly laid eggs and hatched eggs, and treated them as two different samples.

All variables were tested for normality using Kolmogorov-Smirnov test and for homogeneity of variance using Bartlett's test prior to further statistical analysis, and arc-sine transformation was performed for percentage data. We used analyses of variance (ANOVA), analysis of covariance (ANCOVA), regression statistics, and partial correlation analysis to analyze our data. Significance level was set at α=0.05. Prior to testing for differences in adjusted means, the homogeneity of slopes was checked. Throughout this paper, values are presented as mean±1 standard error.

Results

Elaphe taeniura laid pliable-shelled eggs. Clutch size in our sample averaged 8.8±0.9 (range=8-11, N=4). Freshly laid eggs averaged 26.8±0.6 g (range=20.8-32.3, N=35) wet mass, 54.1±0.9 mm (range=45.7-63.2, N=35) length, and 28.8±0.4 mm (range=25.0-33.1, N=35) width. During incubation, eggs increased in wet mass and, one day prior to hatching, weighed 110.0±3.5% (range=98.6-135.9, N=14) of egg wet mass at oviposition. The incubation time averaged 54.9±0.2 days (range=54.1-55.7, N=14). Newly emerged young averaged 17.1±0.7 g (range=13.2-21.8, N=14) wet mass, 381.4±3.5 mm (range=357.0-405.0, N=14) SVL, and 88.5±1.9 mm (range=77.0-103.0, N=14) tail length.

The data on components of the freshly laid eggs and 0-day hatchlings are given in Table1. Egg contents averaged 74.0% water by mass; egg contents averaged 92.4% organic material, 7.6% ash, 31.5% non-polar lipid, 1.36% calcium, and 0.39% magnesium by dry mass (Table 1). Shells from the freshly laid eggs averaged 17.6% of total egg dry mass, and 81.7% organic material and 18.3% ash by shell dry mass (Table 1). Shells from freshly laid eggs had higher levels of calcium (8.21%) and magnesium (0.75%) than did shells from hatched eggs (calcium: 6.31%; magnesium: 0.61%).

0-day hatchlings averaged 70.6% water by mass. These hatchlings averaged 89.1% organic material,

Table 1. Components and F values of the ANCOVA for 7 *Elaphe taeniura* freshly laid eggs and nine 0-day hatchlings. Data are expressed as adjusted meam±1SE with total egg wet mass at oviposition as the covariate. Symbols immediately after F values represent significant levels: NS P>0.05, * P<0.05, ** P<0.01, and *** P<0.001.

	Freshly laid egg	Hatched egg	F
	Egg contents	Total hatchling	
Wet mass (g)	25.4±0.1	18.8±0.3	306.58***
Dry mass (g)	6.64±0.14	5.61±0.14	19.68***
Water (g)	18.8±0.2	13.3±0.2	402.18***
Organic mass (g)	6.14±0.13	5.00±0.13	28.25***
Ash mass (mg)	502.4±24.2	604.7±15.7	10.31**
Non-polar lipid(g)	2.09±0.07	1.56±0.05	30.99***
Calcium(mg)	90.1±4.2	139.9±5.4	31.96***
Magnesium(mg)	26.0±1.2	27.1±1.0	0.84NS
Energy(Kcal)	39.6±0.8	32.0+0.8	33.41***
	Eggshell	Eggshell	
Dry mass(g)	1.42±0.04	1.21±0.05	7.82*
Organic mass(mg)	1.16±0.03	1.03±0.04	4.13NS
Ash mass (mg)	259.8±10.5	180.8±8.2	22.86***

10.8% ash, 27.8% non-polar lipids, 2.49% calcium, and 0.48% magnesium by dry mass (Table 1). Shells from hatched eggs averaged 85.1% organic material and 14.9% ash by dry mass (Table 1).

0-day hatchlings contained significantly lower quantities of total dry mass, organic mass, non-polar lipids, and energy, but significantly higher quantities of calcium and ash mass than did egg contents (Table 1). There was no significant difference in the quantity of magnesium between egg contents and 0-day hatchlings (Table 1). Shells from hatched eggs contained lower quantities of total dry mass and ash mass than did shells from the freshly laid eggs. No significant difference in organic mass was found between shells from the freshly laid eggs and hatched eggs (Table 1).

During incubation, approximately 84.5% of dry mass, 74.6% of non-polar lipids, and 80.8% of energy in egg contents of the freshly laid egg were transferred to the hatchling, with 15.5% of dry mass, 25.4% of non-polar lipids, and 19.2% of energy used for embryogenesis (Table 1). Fully developed embryos could obtain almost all magnesium from the yolk, but should withdraw 35.6% of their total calcium requirements from sources other than yolk (Table 1).

Egg contents (1.36±0.07%, range=1.14-1.62%, N=7) of the freshly laid egg had a higher level of calcium than did post-hatching yolk (0.99±0.10%, range=0.64-1.45%, N=9) (ANOVA: $F_{1,14}$=8.38, P<0.05). There was no significant difference in the level of magnesium between egg contents (0.39±0.03%, range=0.32-0.45%, N=7) and post-hatching yolk (0.42±0.05%, range=0.27-0.62%, N=9) (ANOVA: $F_{1,14}$=0.54, P>0.05).

Dry masses of carcass (r^2=0.96, $F_{1,7}$=157.76, P<0.001) and fat bodies (r^2=0.88, $F_{1,7}$=55.29,

Table 2. A comparison between nine 0-day and five 7-day hatchlings of *Elaphe taeniura*. Data are expressed as mean±1 SE; all mass units are in grams.

	0-day hatchling	7-day hatchling
Hatchling wet mass at hatching	18.8±0.9	15.7±0.3
Hatchling wet mass 7 days after hatchling	——	15.0±0.2
Decrease in wet mass	——	0.70±0.22
Hatchling dry mass	5.28±0.31	4.00±0.06
Carcass	3.51±0.20	3.18±0.05
Yolk sac	0.66±0.05	0.09±0.01
Fat bodies	1.11±0.09	0.73±0.02
% water of hatchling	70.6±0.5	73.2±0.3

P<0.001) of the 0-day hatchlings were both correlated with total hatchling dry mass. In the 7-day hatchlings, we only found a positive correlation between carcass dry mass and total hatchling dry mass (r^2=0.88, $F_{1,3}$=22.34, P<0.05). 7-day hatchlings had significantly heavier carcasses than did 0-day hatchlings with the same wet mass at hatching (ANCOVA: $F_{1,11}$=16.38, P<0.01) (Table 2). There was a negative correlation between post-hatching yolk dry mass and carcass dry mass when holding total hatchling dry mass and fatbody dry mass constant (r=-0.90, t=6.53, df=10, P<0.001). There was no significant correlation between post-hatching yolk dry mass and fatbody dry mass when holding total hatchling dry mass and carcass dry mass constant (r=0.43, t=1.50, df=10, P>0.05). There was no significant correlation between carcass dry mass and fatbody dry mass when holding total hatchling dry mass and post-hatching yolk dry mass constant (r=-0.20, t=0.65, df=10, P>0.05). 7-day hatchlings (23.2±0.4%, range=22.1-24.1%, N=5) had significant lower levels of non-polar lipids than did 0-day hatchlings (27.4±0.6%, range=25.3-29.5%, N=9) ($F_{1,12}$=32.1, P<0.001).

Discussion

Similar to that reported for pliable-shelled eggs of other reptiles (e.g., Fitch, 1954; Fitch and Fitch, 1967; Andrews and Sexton, 1981; Vitt and Cooper, 1986; Vleck, 1991; Ji et al., 1996, 1997a, b), eggs of *E. taeniura* overall increased in wet mass and swelled during incubation due to a net gain of water absorbed from the substrate on which the eggs were incubated. However, water uptake seemed not to be obligate for *E. taeniura* eggs, because some eggs whose final mass was less than initial mass also hatched successfully.

Small *E. taeniura* embryos were present in all freshly laid eggs, but they, relative to the large egg size, were too small to be considered as an important part of the egg at oviposition. Therefore, the transference of energy and material from egg to hatchling during incubation was approximately equal to the transference overall. This makes it possible to compare our data with those for other oviparous reptiles whose freshly laid eggs also contain small embryos and embryonic stage is near the oviparous end in the oviparity-viviparity continuum (Shine, 1983). *Elaphe taeniura* exhibited high conversion efficiencies of energy and material from egg to hatchling. The values in Table 3 show that the conversion efficiencies of energy and material recorded in *E. taeniura* were higher than those reported for any other studied reptiles. The values in the Table also show that the conversion efficiencies vary considerably among species; however, the explanations to these differences are unknown at this time. It has been known that costs of embryonic development vary considerably among reptiles (Dmi' el, 1970; Black et al., 1984), parental investment in each offspring should be related to its survivorship (Congdon ad Gibbons, 1989; Fischer et al., 1991), and incubation environments may influence embryonic development (Gutzke and Pachard, 1987). So, further studies in a wider field covering parental reproductive investment, embryonic metabo-

Table 3. Comparison of conversion efficiencies of dry mass, non-polar lipids, and energy between *Elaphe taeniura* and other oviparous reptiles.

Species	Conversion efficiency (%)			Data resources
	Dry mass	Non-polar lipids	Energy	
Lizards				
Podarcis muralis	75	46	61	Ji & Braña, submitted
Eumeces chinensis	66	44	62	Ji et al., 1996
Snakes				
Elaphe taeniura	85	75	81	This study
Elaphe carinata	81	64	72	Ji et al., 1997a
Dinodon rufozonatum	81	70	79	Ji et al., submitted
Ptyas korros	77	54	69	Ji et al., submitted
Xenochrophis pisctor	74	52	66	Ji et al., submitted
Rhabdophis tigrinus lateralis	70	37	61	Zhao et al., 1997
Zaocys dhumnades	76	63	70	Ji, unpubl. data
Naja naja atra	75	64	69	Ji et al., 1997b
Turtles				
Chelydra serpentina	—	60	60	Wilhoft, 1986
Deirochelys reticularia	72	—	—	Congdon et al., 1983
Chrysemys picta	72	—	—	Ewert, 1979
Alligator				
Alligator mississippiensis	79	74	—	Fischer et al., 1991

lism, and ecology of neonates will be very important for our giving reliable explanations.

As in other oviparous squamates (Packard et al., 1984a, 1985; 1988; Ji et al., 1996, 1997a, b), turtles (Packard et al., 1984b; Packard and Packard 1986), and the American alligator (Packard and Packard, 1989), *Elapeh taeniura* embryos use eggshell as a secondary source of calcium. The result that eggshells decreased in mass and calcium content during incubation supports this interpretation. The level (35.6%) of calcium withdrawn by *E. taeniura* embryos from the eggshell was much lower than the values reported for crocodilians and turtles (50-80%; Bustard et al., 1969; Jenkins, 1975; Packard and Packard, 1984, 1989). In squamates, the level was slightly lower than that reported for *Eumeces fasciatus* (39%; Shadrix et al., 1994) but higher than those reported for *Eumeces chinensis* (19%; Ji et al., 1996), *Coluber constrictor* (20%; Packard et al., 1984a), *Elaphe carinata* (31%; Ji et al., 1997a), and *Naja naja atra* (14%; Ji et al., 1997b). These differences presumably reflect the interspecific differences in eggshell structure and allocation of minerals between eggshell and yolk.

The level of calcium in *E. taeniura* post-hatching yolk was significantly lower than that in egg contents of the freshly laid egg. This suggests that *E. taeniura*

embryos deplete the yolk of almost of its calcium before hatching and none of the calcium withdrawn from the eggshell is deposited in the yolk. This pattern of mobilization and deposition of calcium is similar to that observed in other non-crocodilian reptiles (e.g., Packard et al., 1984b, 1985, 1987; Packard and Packard, 1986; Packard and Packard, 1988; Shadrix et al., 1994).

The estimated amount of magnesium in egg contents of the freshly laid egg (95.9% of total magnesium in the hatchling) was slightly less than that in the hatchling. We are presently not very certain that *E. taeniura* embryos use the eggshell as an additional source of magnesium, because any slightly biased estimation might account for the remaining 4.1% of magnesium. However, the fact that shells from hatched eggs were lighter in mass and lower in the level of magnesium seemed to imply that *E. taeniura* embryos should withdraw a small portion of magnesium from the eggshell. Since studies of embryonic magnesium metabolism have been unfortunately extremely limited, we cannot discuss this problem in detail. In the American alligator (Packard and Packard, 1989) and other species of snakes that have studied by us, embryos apparently obtain all magnesium necessary for development from the yolk.

One interesting finding In this study was that a decrease in post-hatching yolk mass was accompanied by an increase in carcass mass a few days after hatching. This finding quantitatively confirms that post-hatching yolk can be used to support early growth of hatchlings. Compared with post-hatching yolk, fat bodies were used mainly for hatchling maintenance. An obvious decrease in the level of non-polar lipids in the 7-day hatchlings supports this interpretation.

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