

A Comparison of Embryonic Metabolic Rates in Two Lizards

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Abstract. -The metabolic rates of eggs in both the wall lizard *Gekko japonicus* and the grass lizard *Takydromus septentrionalis* were measured through incubation at 32°C. The ontogeny of embryonic metabolism in both species of lizards exhibits an exponential pattern, similar to that recorded for some squamates that develop in parchment-shelled eggs, but different from some crocodylians and chelonians that develop in parchment-shelled and brittle-shelled eggs.

Both the embryos and hatchlings of *T. septentrionalis* have higher metabolic rates than those of *G. japonicus*. An embryo of *T. septentrionalis* consumes more oxygen than that of *G. japonicus*, although the latter species has a much longer incubation period at 32°C.

Key words: Sauria, *Takydromus septentrionalis*, *Gekko japonicus*, Hatchling, Embryonic Metabolic Rate, Exponential Pattern, Incubation, Egg, Oxygen, Consumption.

Introduction

Embryonic metabolic characteristics of incubating eggs have been reported for at least 23 species of living reptiles, including seven species of snakes (Clark, 1953; Dim'el, 1970; Black et al., 1984), eleven species of chelonians (Lynn and Von Brand, 1945; Ackerman, 1981; Gettinger et al., 1984; Webb et al., 1986; Thompson 1989; Wang et al., 1990), one species of lizard (Wang et al., (1989), three species crocodylians (Thompson, 1989; Whitehead and Seymour, 1990), and one species of tuatara (Thompson, 1989). Three patterns of the ontogeny of embryonic metabolism in reptiles have been recognized in incubating reptilian eggs: peaked, sigmoid, and exponential (Thompson, 1989; Whitehead and Seymour, 1990; Wang et al., 1990). These patterns are very similar to those observed in birds (Vleck et al., 1980; Wang et al., 1991). However, it is still unclear whether patterns of metabolic ontogeny are species-specific, and whether patterns in lizards (especially in geckos) are different from those of other reptiles.

The two lizard species (*Gekko japonicus* and *Takydromus septentrionalis*) studied show distinct differences in activity patterns, foraging behavior, and microhabitats (Liu and Hu, 1940; Wang, 1964, 1966). The wall lizard (*G. japonicus*) is a nocturnal, sit-and-wait predator found on the walls of old houses and temples. It remains immobile for more than half of its nocturnal period. One to three clutches two eggs each, are oviposited annually (Liu and Wu, 1940; Ji et

al., 1991). In contrast, the grass lizard (*T. septentrionalis*) is a diurnal and active forager in high grasses (Wang, 1964). One or two, rarely three, clutches of two to five parchment-shelled eggs each, are laid annually in humid soil where they swell and become increasingly turgid during incubation (Wang, 1966). In this paper we compare the characteristics of the ontogeny of metabolism of the eggs of these species during incubation.

Materials and Methods

Gravid *Gekko japonicus* and *Takydromus septentrionalis* were collected on buildings in Shanghai and in fields on the Zhoushan Islands, respectively. The captured animals were taken to the laboratory, maintained in aquaria, and fed with mealworms (larvae of *Tenebrio molitor*). Eggs were laid at room temperatures of 24-28°C. Each freshly laid egg was numbered, the length and width were measured (nearest 0.1 mm), and the wet mass recorded (nearest 0.1 mg). Egg volume was calculated by using the ellipsoid equation $V = \frac{3}{4} \pi a^2 b$, where V = volume, $a = \frac{1}{2}$ of width and $b = \frac{1}{2}$ of length. The surface area of each eggshell was obtained by measuring the width and length axes of $2a$ and $2b$, respectively, and substituting them in the equation for the area of ellipsoid,

$$2 \left(b^2 + \frac{a^2 b}{\sqrt{b^2 - a^2}} \ln \sqrt{\frac{b^2 - a^2 + b}{a}} \right)$$

Table 1. Egg and hatchling dimensions of *Gekko japonicus* and *Takydromus septentrionalis* during incubation at 32°C.

	Pre-incubation egg		Changes in egg dimension (pre-pipping)			Incubation days	Hatchlings		
	Species	N	mass mg(SD)	vol. mm ³ (SD)	area mm ²		mass %	area %	SVL mm (SD)
<i>Gekko japonicus</i>	69	700.2 (84.1)	7510	-14	0	42.9 (2.9)	25.9 (1.5)	468.3 (43.4)	68.7
<i>Takydromus septentrionalis</i>	75	246.1 (35.0)	2510	280.9	298.9	26.3 (1.2)	24.0 (1.6)	309.2 (43.0)	111.6

The eggs were half buried in moistened sand substrates and placed at a nearly constant temperature of 32°C (SD=0.5°C). Relative ambient humidities were 80-85% for *G. japonicus* eggs and 99-100% for *T. septentrionalis* as indicated by an FC-1 Hydro Thermometer. Volume and wet mass of incubating eggs were recorded at five day intervals.

At five day intervals, oxygen consumption of incubating eggs was measured by using a small closed system respirometer (details of the apparatus are given in Wang, 1986). Oxygen consumption of hatchlings was measured in the same apparatus. All experiments were conducted at 32°C (SD=0.5°C) from 0830-1030 hr. Each experiment was completed within one hour and data were recorded every fifteen minutes. Carbon dioxide (CO₂) exhaled by animals was absorbed by 30% sodium hydroxide (NaOH) solution. All rates of oxygen consumption were corrected to STPD, and expressed as volume of O₂ per unit egg mass in grams or as volume O₂ per egg at the time of collection (ml O₂/g * h or ml O₂/egg * h).

The total O₂ consumption of each egg from initial incubation to hatching was derived by a stepwise regression of log₁₀ transformed data. A t-test was performed to test for statistically significant differences between means.

Results

Incubation Time

The mean duration of incubation to hatching of *Gekko japonicus* eggs was 42.9 days at 32°C, compared with 26.3 days in *Takydromus septentrionalis* eggs at 32°C (Table 1), so the latter is shorter 16.3 days than the former.

Changes in Eggs During Incubation

The surface area, volume, and wet mass to *T. septentrionalis* eggs during incubation increased to 283%, 280.9% and 298.9%, respectively, of initial values (Table 1). At hatching, the mean wet mass of *T. septentrionalis* was 309.2 mg or 111.6% of the initial egg mass (Table 1). In contrast, there were no changes in egg volume and surface area during incubation of *G. japonicus*, but egg wet mass at pre-pipping declined to 14% of the initial egg mass (Table 1), and the wet mass of hatchlings was only 68.7% of pre-incubation egg mass (Table 1).

Oxygen Consumption During Incubation. The rates of oxygen consumption of eggs in *G. japonicus* and *T. septentrionalis* are shown as a function of incu-

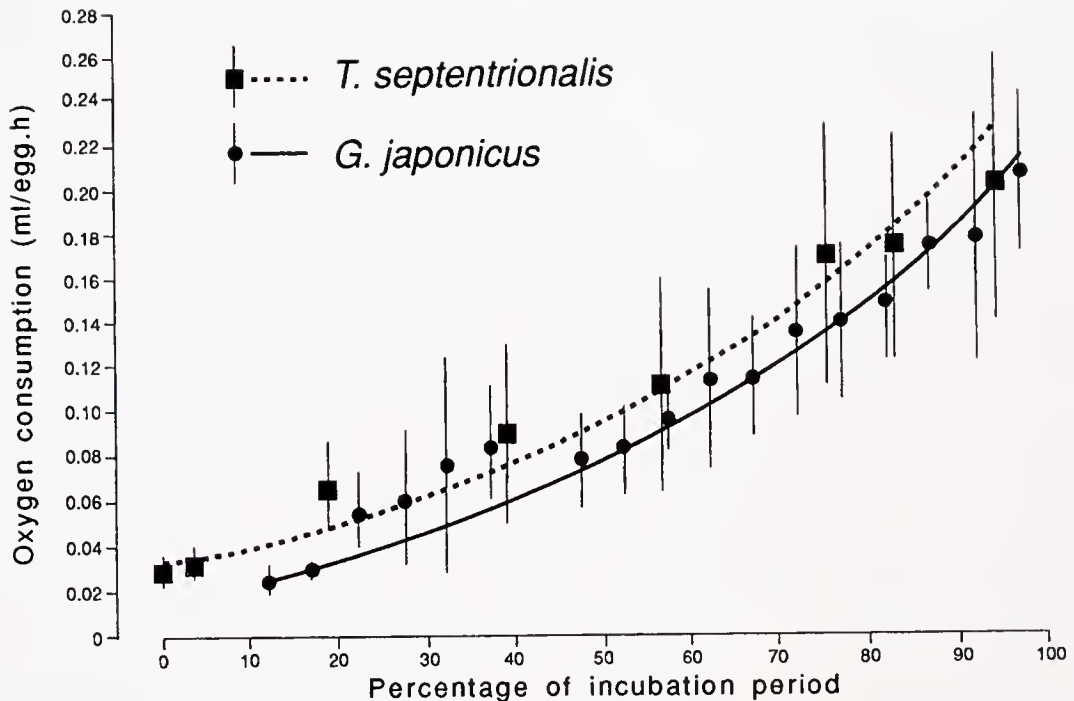


Figure 1. Relationship between oxygen consumption of eggs in two species of lizards (*Takydromus septentrionalis* and *Gekko japonicus*) and the percentage of incubation period at 32°C. Squares (*T. septentrionalis*) and circles (*Gekko japonicus*) represent mean values of oxygen consumption of eggs. Vertical lines indicate two standard deviations about the mean. The dashed lines indicate normalization curves of oxygen consumption per egg at different stages of incubation.

bation time in Fig. 1. The following semi-logarithmic regression equations are best fitted by those data. These equations are of the general form: $\log V = a + bT \pm c$, where V is oxygen consumption in $\text{ml O}_2/\text{eggs} \cdot \text{h}$, and T is time in days.

For *G. japonicus*:

$$\log V = -1.5017 + 0.0087T \pm 0.0768 \quad (r=0.98, P<0.01).$$

For *T. septentrionalis*:

$$\log V = -1.4340 + 0.0086T \pm 0.0740 \quad (r=0.95, P<0.01).$$

The slopes (b) of the regression equations of the two species lizards are nearly the same ($b=0.0086$ and $b=0.0087$). The two species had the same general patterns of exponential embryonic metabolic ontogeny as that usually observed in other squamate reptiles (Dim'el, 1970; Black, 1984) and in altricial birds (Vleck et al., 1979).

Embryonic metabolic rates of *T. septentrionalis* on the first and second days of incubation averaged $0.1179 \text{ ml O}_2/\text{g} \cdot \text{h}$ and $0.1196 \text{ ml O}_2/\text{g} \cdot \text{h}$ for per gram mass egg respectively. Oxygen consumption of eggs

of *G. japonicus* could not be detected until about the fourth day of incubation (12% of the incubation period). The average total oxygen consumed during embryonic ontogeny was $73.48 \text{ ml O}_2/\text{egg}$ or $274.79 \text{ ml O}_2/\text{g}$ per gram mass of initial egg mass, or $0.0293 \text{ ml O}_2/\text{mm}^2$ per square millimeter of initial egg surface area in *T. septentrionalis*, and only $104.42 \text{ ml O}_2/\text{egg}$ or $153.15 \text{ ml O}_2/\text{g}$, or $0.0204 \text{ ml O}_2/\text{mm}^2$ in *G. japonicus*, although the latter species had a much longer duration of incubation that averaged 42.9 days at hatching (Table 1).

Metabolic Rates of Hatchlings. The resting metabolic rate per gram mass of hatchlings averaged 0.6547 ($\text{SD}=0.0870$, $N=16$) $\text{ml O}_2/\text{g} \cdot \text{h}$ for *T. septentrionalis* and 0.4603 ($\text{SD}=0.0476$, $N=16$) $\text{ml O}_2/\text{g} \cdot \text{h}$ for *G. japonicus*. So that the resting metabolic rate of *T. septentrionalis* is $0.1944 \text{ ml O}_2/\text{g} \cdot \text{h}$, or 42% higher than that of *G. japonicus*. For *G. japonicus*, oxygen consumption of hatchlings and eggs just before pipping were 0.2144 ($\text{SE}=0.0186$, $N=19$) $\text{ml O}_2/\text{lizard} \cdot \text{h}$ and 0.2139 ($\text{SD}=0.0148$, $N=19$) $\text{ml O}_2/\text{egg} \cdot \text{h}$, respec-

tively. For *T. septentrionalis*, oxygen consumption of new hatchlings and eggs just before hatching were 0.2024 (SD=0.0069, N=16) ml O₂/lizard * h and 0.2072 (SD=0.0300, N=16) ml O₂/egg * h, respectively.

Discussion

To our knowledge, this is the first report on the embryonic metabolic ontogeny of lizards. Our results show that both these lizards have an exponential embryonic metabolic pattern. (Fig. 1). This pattern is similar to some snakes or lizards that develop in parchment-shelled eggs and those birds with altricial hatchlings, but differs from the peaked and sigmoid patterns observed in some crocodylians, sea turtles, and fresh water turtles (Vleck et al., 1979; Ackerman, 1981a, 1981B; Whitehead and Seymour, 1990).

Whitehead and Seymour (1990) showed that six species of reptiles with brittle-shelled eggs exhibited the peaked pattern, and ten of thirteen reptilian species with parchment-shelled eggs exhibited a non-peaked metabolic pattern, i.e., seven species snake for an exponential pattern, and three species sea turtles of those for a sigmoid pattern, and other three species fresh turtles of those are only a peaked pattern. Why does *G. japonicus*, with a non-parchment-shelled egg, also exhibit an exponential pattern? Unfortunately, there are few data dealing with the reasons for the observed patterns of embryonic metabolic ontogeny in reptiles, especially in lizards. Some data suggest that the patterns of embryonic metabolic ontogeny in reptiles may be species specific, but do not necessarily depend upon the type of eggshell. For example, there are three patterns of embryonic metabolic ontogeny among reptiles with parchment-shelled eggs, i.e., peaked, sigmoid, and exponential pattern (Whitehead and Seymour, 1990). However, all of seven snakes examined exhibited an exponential pattern of embryonic metabolic ontogeny, three sea turtles showed a sigmoid pattern, and three crocodylians and seven freshwater turtles exhibited a peaked pattern. Metabolic rates of developing embryos reflect the energetic demands of both growth and maintenance (Wang et al., 1991). Peaked and sigmoid patterns of embryonic metabolic rates are likely to be associated with defining embryonic growth rates late in incubation, and exponential patterns of metabolic rate in reptilian embryos is likely due to continuous increase of the embryonic growth rate through incubation.

Although *G. japonicus* had a longer incubation period than did *T. septentrionalis*, the former species consumed less oxygen through incubation. The total

oxygen consumption during embryonic ontogeny at 32°C per gram or per square millimeter of initial incubation egg mass or surface area in *G. japonicus* was only 153.15 ml O₂/g or 0.0204 ml O₂/mm², compared to 274.79 ml O₂/g or 0.0293 ml/mm² for *T. septentrionalis* i.e., 179.4% or 143.6% higher, respectively. In addition, Fig. 1 shows that the regression curve of oxygen consumption for *G. japonicus* was clearly lower than that of *T. septentrionalis*. Also, the standard rates of evaporative water loss in some gekko eggs are lower than other reptiles (Dunson and Bramham, 1981; Dunson, 1982). The low level of metabolism may be a characteristic of gekko eggs.

Besides this phylogenetic difference, another possible reason for the difference in embryonic metabolism between the two species may be related to the structural characteristics of the eggshells. The eggs of *T. septentrionalis* are parchment-shelled and when placed in suitable substrates, tend to become larger during incubation because of water absorption. The enlarged eggs of *T. septentrionalis* have a surface area at hatching that reached 282.7% of initial eggshell area (Table 1). This possible increase in pore diameter and shell permeability (Packard, 1980) may promote increased embryonic metabolism.

Both the metabolic rates per hatchling and egg at pipping were nearly the same. The resting metabolic rate of new hatchlings can be used to estimate metabolic rates of their eggs just before pipping. The resting metabolic rate of hatchlings of *T. septentrionalis* was about 29.7% higher than that of *G. japonicus*. The difference in resting metabolic rates of new hatchlings between the two species may be due to phylogenetic characteristics, as geckos have a low metabolism (Feder and Feder, 1981; Dunson and Bramham, 1982). To eliminate the effect of body mass on metabolic rate, we used the formula $M/W^{0.73}$ to correct the results, where M is metabolic rate, W is body mass, and 0.73 is close to the average of the interspecies coefficient and has the advantage of correcting for difference in mass. The corrected resting metabolic rates of hatchlings are 0.4768 ml O₂/W^{0.73} * h for *T. septentrionalis* and 0.2942 ml O₂/W^{0.73} * h for *G. japonicus*; the former species is 31.1% higher than the latter.

We conclude that the difference in metabolic rates of hatchlings between the two species is not primarily caused by difference in body mass. Instead, there must be an interspecific difference in metabolic rates between the two lizard species.

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