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Metabolism, temperature relations, maternal behavior, and reproductive energetics in the ball python (*Python regius*)

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Summary. Thermogenic incubation has been documented in two large species of pythons, but the phenomenon has not been studied in small species with concomitantly large heat transfer coefficients. We describe behavior, metabolic rates, mass changes, and temperature relations for adult ball pythons (*Python regius*), the smallest member of the genus, during the reproductive cycle. Egg and hatchling metabolism and hatchling growth rates were also examined.

Rates of oxygen consumption ($\dot{V}_{O_2}$) of both gravid and non-gravid snakes showed typical ectothermic responses to changing ambient temperature (T_a). The Q_{10} for T_a's of 20–35 °C was 2.2–2.3. The $\dot{V}_{O_2}$ of gravid females was significantly greater than that of non-gravid snakes at all T_a. Maximum oxygen consumption ($\dot{V}_{O_2}$max) during forced exercise was about 12 times resting $\dot{V}_{O_2}$ at $T_a = 30$ °C.

Eggs (5–6 per female) were laid in April. Total clutch mass was approximately 32% of the females' pre-oviposition mass. After oviposition, mother snakes coiled tightly around their clutches and remained in close attendance until the eggs hatched in June. Sudden decreases in T_a elicited abrupt but transient 2- to 4-fold increases in the $\dot{V}_{O_2}$ of incubating females. Similar responses were not observed in non-incubating snakes. The steady-state $\dot{V}_{O_2}$ of incubating females was independent of T_a. In no case was body temperature (T_b) elevated more than a few tenths of a degree above T_a in steady-state conditions.

The $\dot{V}_{O_2}$ of developing eggs increased sigmoidally through the 58–70 day incubation period. Total oxygen consumption during incubation at $T_a =$ 29.2 °C was about 3.6 l per egg. Young snakes quadrupled their mass during their first year of growth.

Compared to larger python species which are endothermic during incubation, ball pythons have similar aerobic scopes and higher mass-specific $\dot{V}_{O_2}$max. However, effective endothermy in ball pythons is precluded by high thermal conductance and limited energy stores.

Introduction

Pythons inhabit the tropical and subtropical regions of Africa, Asia, and Australia. All are oviparous and are among the few reptiles showing extensive parental care. Females coil about their eggs shortly after oviposition and attend them until hatching, a period that may exceed two months. At least two species, the Indian python *Python molurus* and the diamond python *Morelia spilotes*, are able to keep clutch temperature substantially warmer than ambient temperature (T_a) by means of physiological thermogenesis. Heat production is apparently accomplished by spasmodic muscular contractions ('shivering'), and is adjusted so as to keep body and egg temperature between 30 and 34 °C at T_a of 23–33 °C. At low T_a, rates of oxygen consumption of incubating females may be 10–20 times greater than those of similar-sized non-incubating individuals (Hutchison et al. 1966; Vinegar et al. 1970; Van Mierop and Barnard 1978; Harlow and Grigg 1984).

The occurrence, function, and evolution of thermogenic incubation in the python family are poorly understood. Endothermy is thought to be favored by large body size, with concomitant small surface to volume ratios that favor the retention

of body heat (derived metabolically or gained by solar basking). This concept is applicable to *P. molurus*, a robust species which begins to breed at a mass of 15–20 kg and attains masses in excess of 60 kg. However, *M. spilotes* is considerably smaller (3–6 kg). Other reports of shivering during incubation have concerned both large and small species: the blood python *P. curtis* (Vinegar et al. 1970), Timor python *P. timorensis* (Murphy et al. 1978), green tree python *Chondropython viridis* (Kratzer 1962; Van Mierop et al. 1983), and three Australian forms, *Aspidites melanocephalus, Liasus fuscus,* and *L. amethystinus* (Boos 1979). None of these papers contain data on metabolic rates during incubation, so the degree of heat production is uncertain. Somewhat paradoxically, two very large species, the African python (*P. sebae*) and the reticulated python (*P. reticulatus*), have not been reported to regulate clutch temperature by endothermic means, although they do coil around their eggs (Vinegar et al. 1970; Sclater 1862; Wall 1926).

A second hypothesis explaining the evolution of endothermy was proposed by Vinegar et al. (1970), who suggested that endothermic brooding allows pythons to extend their geographic range into regions where T_a's are too low to support embryonic development. At least some species of pythons have eggs that require warm temperatures during incubation; for example, the eggs of *P. molurus* and *M. spilotes* fail to develop at temperatures below 27.5 °C (Vinegar 1973; Harlow and Grigg 1984). This model may explain the occurrence of endothermy in *P. molurus* and *M. spilotes*, both of which inhabit cool subtropical as well as tropical regions, and its apparent absence in *P. reticulatus* and *P. sebae*, which are restricted to warm habitats.

In this paper we describe the behavior, metabolism, and overall energetics of reproduction in ball pythons, *P. regius*. This African species is the smallest member of the genus *Python*, attaining an adult length of about 1.5 m and a body mass of about 2 kg. Because of its small size, and because its range is apparently limited to warm tropical lowlands (Pitman 1974), *P. regius* would not be expected to show a significant endothermic brooding ability. Nevertheless, as in larger pythons, female ball pythons closely attend their clutches. We felt that a study of the metabolic and behavioral responses of *P. regius* might produce data which, in conjunction with published information on *P. molurus* and *M. spilotes*, could provide useful insights into the evolution of python incubation behavior.

Materials and methods

Animals. Adult *Python regius* (6 gravid females, 2 non-gravid females and 3 males) were purchased in November 1983, shortly after their importation from Africa. The animals were housed individually in cages (1.5 × 0.45 × 0.45 m) which were kept in a large environmental room maintained at 29.1 ± 0.2 °C and 70–80% R.H. with a 12 h photoperiod. Drinking water was always available. Mice (*Mus* and *Peromyscus*) were offered to all snakes weekly.

Gravid females laid eggs in their cages in late April or early May. After oviposition the female and a subset of the egg clutch (usually 4 of 6 eggs) were placed into a plastic dishpan (0.33 × 0.30 × 0.12 m) containing 400 g of sterile particulate mica hydrated with 400 ml of chlorinated tap water. Copper-constantan thermocouples were positioned in the substrate at least 0.15 m from the female and also in the air ca. 0.10 m above the substrate. The eggs removed from each clutch were weighed, measured and incubated separately. Some of them were placed individually into 2 l respirometers containing 300 g of a 1:1 mixture of sterile mica and water. Other eggs were implanted with 36-gauge thermocouple wire with the couple positioned approximately in the geometric center of the egg. The leads were secured to the egg shell with methyl methacrylate adhesive. Thermocouple-equipped eggs were either returned to the maternal female or placed separately into plastic boxes (0.31 × 0.17 × 0.08 m) containing 400 g of 1:1 mica and water. Thermocouple implants did not affect subsequent embryonic development. Additional thermocouples were also placed in the substrate and air immediately adjacent to the egg. Eggs, and later hatchlings, were kept in the same environmental room as the adults.

Metabolic measurements. Oxygen consumption ($\dot{V}_{O_2}$) and in some cases carbon dioxide production ($\dot{V}_{CO_2}$) from post-absorptive animals were determined in open-circuit respirometer systems. Pythons were weighed to ±0.1 g on a Mettler PC 4000 balance and placed into plastic metabolism chambers. Chamber volumes were 10.3, 17.6 and 0.8 l for adult snakes, incubating females with their eggs, and hatchlings, respectively. Metabolism chambers were placed into a large temperature-controlled (±0.2 °C) environmental cabinet. Dry air was metered through Applied Materials mass flow controllers (model AFC-550), humidified to 50–80% R.H., and routed into the metabolism chamber via 2 side ports. A portion (40 ml/min) of the excurrent air from ports at the top of the metabolism chamber was dried (Drierite) and analyzed for CO_2 (Beckman LB-2 or Applied Electrochemistry CD-3A), then passed through CO_2 absorbent (Ascarite), redried and analyzed for oxygen (Applied Electrochemistry S-3A). The CO_2 analyzer was standardized against calibration gases daily and both analyzers were referenced against air diverted from immediately upstream of the flow controllers ca. every 5 min during measurements. Air flow was adjusted during experiments so that $[O_2]$ was not less than 20.5% and $[CO_2]$ did not exceed 0.5%. This required flow rates between 0.50–1.20 l/min for adults and 0.06–0.20 l/min for eggs about to hatch and for young snakes.

During metabolic measurements on incubating females, temperature data were collected from several thermocouples placed in the air surrounding the animal, affixed to its scales, and inserted within the egg mass. Body temperatures (T_b) of incubating snakes were determined using temperature sensitive radio-telemeters (Mini-Mitter, model XM) which were force-fed to the females prior to oviposition.

Steady-state metabolic measurements were obtained at ambient temperatures (T_a) between 20 and 36 °C. We assumed that an animal was in steady-state if it was quiescent and T_a,