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Change of cardiac function, but not form, in postprandial pythons

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ABSTRACT

Pythons are renowned for a rapid and pronounced postprandial growth of the heart that coincides with a several-fold elevation of cardiac output that lasts for several days. Here we investigate whether ventricular morphology is affected by digestive state in two species of pythons (*Python regius* and *Python molurus*) and we determine the cardiac right-to-left shunt during the postprandial period in *P. regius*. Both species experienced several-fold increases in metabolism and mass of the digestive organs by 24 and 48 h after ingestion of meals equivalent to 25% of body mass. Surprisingly there were no changes in ventricular mass or dimensions as we used a meal size and husbandry conditions similar to studies finding rapid and significant growth. Based on these data and literature we therefore suggest that postprandial cardiac growth should be regarded as a facultative rather than obligatory component of the renowned postprandial response. The cardiac right-to-left shunt, calculated on the basis of oxygen concentrations in the left and right atria and the dorsal aorta, was negligible in fasting *P. regius*, but increased to 10–15% during digestion. Such shunt levels are very low compared to other reptiles and does not support a recent proposal that shunts may facilitate digestion in reptiles.

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1. Introduction

Pythons exhibit an extraordinary phenotypic flexibility of the visceral organs during digestion (e.g. Secor, 2008). In addition to a pronounced increase in the mass and functional performance of the gastrointestinal organs, the python heart may grow more than 40% within 48 h after ingestion of a meal (Secor and Diamond, 1995, 1997; Andersen et al., 2005). This response is likely to represent an important component in the ability of these snakes to augment stroke volume and cardiac output in response to the large rise in metabolism associated with digestion (Secor and Diamond, 1998; Secor et al., 2000; Overgaard and Wang, 2002; Secor, 2008).

As other snakes, pythons have a complex ventricular anatomy, allowing for some mixture of oxygen-rich and oxygen-poor blood within the ventricle (Webb et al., 1971; Holmes, 1975; Burggren, 1987; Wang and Hicks, 1996; Farrell et al., 1998; Hicks, 1998). The single ventricle has three communicating chambers, but a number of functional and anatomical studies show that ventricular blood flows are kept surprisingly separate throughout the cardiac cycle. Thus, mixing of blood streams are prevented during cardiac filing by the large atrioventricular valves, while the well developed muscular ridge separates the heart during cardiac contraction (Wang et al., 2002, 2003a; Jensen and Wang, 2009; Jensen et al. 2010a–b). According to this view, the small cardiac shunts should primarily be due to the amount of blood that resides in the cavum venosum at the end of diastole and systole. The cavum venosum receives oxygen-poor blood from the right atrium during cardiac filling, but also conveys the oxygen-rich blood from the cavum arteriosum into the two aortae during cardiac contraction, and this 'cross-over of blood flows' gives rise to 'wash-out shunts' in both directions. The cavum venosum, however, is very small in pythons (Jensen et al., 2010c), and a small right-to-left shunt (*i.e.* pulmonary bypass) is evident from high arterial oxygen levels in fasting and digesting pythons (Overgaard et al., 1999; Wang et al., 2001).

In contrast to the view that the python heart is functionally divided with a low capacity for cardiac shunts, Starck (2009) recently concluded that up to 50% of the blood entering the heart may be shunted during digestion. This large shunt is surprising because a right-to-left shunt lowers arterial oxygen concentration (e.g. Wang and Hicks, 2002), a response that could be maladaptive during the digestive period where aerobic metabolism is increased several-fold. Also, in spite of the detrimental effects on oxygen delivery, it has been suggested that reptilian right-to-left shunts aids gastric acid secretion during digestion by supplying proton-rich blood to the parietal cells (Jones and Shelton, 1993; Farmer et al., 2008; cf. Hicks and Wang, 1996). Given the pronounced anatomical separation of the python heart, the very large cardiac shunts suggested by Starck (2009) remain difficult to understand. Nevertheless, it is possible that the functional separation of blood streams within the python heart is disrupted by ventricular remodelling in connection with the cardiac growth during digestion.

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In the present study we seek to characterise the extent to which the heart grows and shunts during digestion in two species of pythons (*Python regius* and *Python molurus*). By comparing fasting and digesting snakes, we hypothesise that a substantial change in cardiac shunting should be related to a change in ventricular anatomy. We calculate the right-to-left cardiac shunt in fasting and postprandial ball pythons from atrial and arterial blood gases. Both the right-to-left shunt and the systemic bypass, also called the left-to-right shunt, inevitably occur in the python ventricle. The right-to-left shunt, however, is larger since it is the consequence of the end-diastolic volume of the cavum venosum and not the end-systolic volume as in the left-to-right shunt (Heisler et al., 1983; Hicks, 1998). While previous studies report postprandial changes in wet and dry mass of python ventricles (e.g. Secor and Diamond, 1995; Andersen et al., 2005; Ott and Secor, 2007; Jensen et al., 2010b), this is the first study to compare ventricular morphology of fasting and digesting snakes.

2. Materials and methods

2.1. Animals

Twenty-six ball pythons (*Python regius*, Shaw) and ten Burmese pythons (*Python molurus*, Linneaus) of both sexes were purchased from a commercial supplier and maintained at Aarhus University for several months prior to the experimental studies. All snakes were housed individually in 10 L boxes under a 13 h light:11 h dark photoperiod and a room temperature of 26–28 °C. All boxes contained a heating pad at the rear allowing for behavioural thermoregulation. Snakes were fed mice every week and always had access to water. Food was withheld for at least 21 days before experimentation. All experiments were conducted in accordance with the EC Directive 86/609/EEC for animal experiments and with permission from the Danish Inspectorate for Animal Experiments.

2.2. Measurements of specific dynamic action upon voluntary ingestion and force-feeding

The ball pythons that were instrumented with catheters for measurements of blood gases to calculate cardiac shunt patterns had to be force-fed. It was imperative, therefore, to investigate whether force-feeding elicited similar metabolic responses as voluntary ingestion of prey. Five snakes (87 ± 3 g) were force-fed with ground chicken breast and egg (2:1) and placed in 2.5 L respirometers at 30 °C to determine VO_2 by closed respirometry (Overgaard et al., 1999). 50 mL gas samples were removed from the chambers once every hour and gas composition was analysed using an O_2 analyzer (S-3A/I, Ametek, Pittsburgh USA, PA 15238). Oxygen uptake (VO_2) was calculated as

$$\dot{V}_{O_2} = \frac{\left(\frac{V_{chamber}\left(F_{StartO_2} - F_{EndO_2}\right)}{\left(1-(1-RE)F_{EndO_2}\right)}\right)}{t}$$

where $V_{chamber}$ is the volume of the respirometer (minus the volume of the animal assuming a density of 1 g mL^{-1} for the snake) and t is the duration of the closed period. The respiratory exchange ratio (RE) was assumed to be 0.85 throughout the digestive period (Overgaard et al., 2002a; Wang et al., 2003b). Later, the same snakes underwent a regime of voluntary ingestion of mice allowing us to compare the SDA responses of voluntary ingestion and force-feeding.

The SDA response was also characterised in five Burmese pythons used for organ harvest (433 ± 35 g). These snakes were placed in 3 L respirometers at 25 °C 1 h after ingestion of 25% of body mass and VO_2 was measured until these snakes were sacrificed 48 h after ingestion. VO_2 was determined by closed respirometry using an in-house constructed experimental set-up allowing for simultaneous measurements of the five snakes. In this set-up, a LabVIEW programme controlled a Parker pneumatic manifold via a NI 9181 relay to switch air flows through the respirometers. First, an air sample from each respirometer was passed through the gas analyzer to determine the initial oxygen fraction ($F_{startO2}$). Then the respirometer was closed for 15 min and the gas from the respirometer by the end of the closed period was passed through the oxygen analyzer to determine F_{endO2}. Using this automated design, VO_2 of each snake was measured every 48 min.

2.3. Determination of cardiac right-to-left-shunt in fasting and digesting ball pythons

Four fasting ball pythons (606 ± 107 g) were anaesthetised with 2% Isoflurane (Baxter, Allerød 3450, Denmark) and intubated for artificial ventilation with a HI 665 Harvard Apparatus Respirator (Holliston, MA, USA) at 20 breaths min^{-1} and tidal volume of 50 mL kg^{-1}. Lidocaine was injected subcutaneously before incisions were made to place catheters containing heparinised saline in the dorsal aorta approximately 5 cm above the cloaca (PE-50), as well as in the left and right atria (PE-74). The aortic cannulation was occlusive, while the catheters of the atria were cannulated using the Seldinger technique. All catheters were secured to the back of the snake by sutures. The catheters had been coated internally with TDMAC (TriDodecylMethylAmmonium Chloride heparin complex, PolySciences Inc, Warrington, PA USA) to reduce clotting. Snakes were allowed to recover for 24 h after surgery in a climatic chamber at 30 °C where they had access to water. We have previously shown that blood pressure, heart rate and catecholamines return to pre-operative levels in this period (Olesen et al., 2008). On the following day the catheters were externalised from the chamber, so blood samples could be removed without disturbing the snakes. Having determined blood gases in the fasting condition, the snakes were force-fed a meal equivalent to 11 ± 4% of body mass and measurements of blood gases were repeated 24 and 48 h into the postprandial period.

Blood oxygen concentrations were measured according to Tucker (1967) and hematocrit was determined after blood samples were centrifuged for 3 min at 12,000 rpm in glass capillaries.

In three of the four snakes we also measured total CO_2 concentration as described by Cameron (1971) and pH using a capillary pH electrode connected to a PHM 73 (Radiometer, Copenhagen, Denmark) thermostatted at 30 °C. Plasma bicarbonate concentration ($[HCO_3^-]$) was calculated as $[HCO_3^-] = Cpl_{CO2} - (P_{CO2} \cdot \alpha_{CO2})$ using an α_{CO2} (CO_2-solubility in blood) of 0.0366 mmol l^{-1} (Heisler, 1984), and the partial pressures of CO_2 (P_{CO2}) were calculated on the basis of the Henderson–Hasselbalch equation: $P_{CO2} = Cpl_{CO2}/[\alpha_{CO2} \cdot (1 + 10^{(pH-pK')})]$, assuming $pK' = -0.0763 \cdot pH + 6.7283$ as determined previously for *Python* plasma at 30 °C (Overgaard and Wang, 2002).

From the oxygen concentrations $[O_2]$ of the blood sampled from the left and right atria ($[O_2]_{LAt}$ and $[O_2]_{RAt}$, respectively), as well as mixed arterial blood from the dorsal aorta ($[O_2]_a$), the relative volume contribution of systemic venous blood to the systemic arterial blood (R–L shunt, pulmonary bypass) was calculated from the standard shunt equation (Berggren, 1942):

$$\text{R–L shunt } (\%) = \left([O_2]_{LAt} - [O_2]_a\right) / \left([O_2]_{LAt} - [O_2]_{RAt}\right) \cdot 100\%.$$

2.4. Echocardiography of anaesthetised ball pythons

Two ball pythons were anaesthetised with isoflurane and intubated for artificial ventilation with room air (10 min^{-1}, 50 mL kg^{-1}) containing 1.5% isoflurane. One snake (1278 g) had fasted for 3 weeks while the other (1526 g) had ingested 168 g of mice 24 h prior to imaging. Images were obtained while the snakes were at room temperature, but body temperature of the snake was maintained at 25 °C using a heating pad.

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