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Postprandial responses in the African rhombig egg eater (*Dasypeltis scabra*)

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Abstract

The African rhombic egg eater (*Dasypeltis scabra*) is a colubrid snake feeding exclusively on bird eggs. Frequency of feeding is governed by the seasonal availability of bird eggs; i.e., long fasting intervals change with relatively short periods when plenty of food is available. Intermittent feeding snakes show a remarkable postprandial increase of metabolic rate and digestive organ size. The postprandial increase in metabolic rate (specific dynamic action, SDA) in snakes is affected by meal size, temperature, and meal composition. A major portion of SDA in snakes is allocated to gastric function and the breakdown of the meal. We hypothesize that SDA in egg eaters is lower than in other snake species, because egg eaters feed on ''liquid'' food that does not require enzymatic breakdown in the stomach. We also hypothesized that other components of the postprandial response of egg eaters (e.g., size changes of the intestine and the liver) do not differ from other snakes. The standard metabolic rate and metabolic response to feeding were measured using closed-chamber respirometry. Size changes of small intestine and liver were measured using high-resolution transcutaneous ultrasonography. Standard metabolic rates of fasting egg eaters were in the same range of mass specific values as known from other snakes. Within 24 h after feeding, oxygen consumption doubled and peaked at 2 days after feeding. At the same time, the size of the small intestine and the cross-sectional diameter of the liver increased. Within 2 days after feeding, the size of the mucosal epithelium doubled its thickness. Liver size increased significantly within 24 h reaching maximum size 2–4 days after feeding. The size of both organs returned to fasting values within 7–10 days after feeding. The postprandial response of African rhombic egg eaters shows the same pattern and dynamics as known from other snake species. However, the factorial increase of metabolic rate during SDA is the lowest reported for any snake. A comparison with literature data supports the idea that SDA is mainly determined by gastric function and that it is low in egg eaters because they do not have to break down solid meals in the stomach as other snake species do.

Keywords: Resting metabolic rate; Specific dynamic action; Fasting; Organ size changes

Introduction

The African rhombic egg eater (*Dasypeltis scabra*) is a mid-sized colubrid snake (max. body length of females: 120 cm, of males: 90 cm) that occurs south of the Sahara

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down to the Cape region. Traditionally, the species has been placed among the "Colubrinae" but its phylogenetic position remains obscure. Phylogenies based on morphological and molecular traits render contrasting results (Gravlund, 2001). The species feeds exclusively on freshly laid bird eggs, incubated eggs are not eaten. Young individuals feed on small song bird eggs while fully grown individuals may swallow eggs up to the size of a chicken egg. The species is characterized by a number of morphological adaptations to feeding bird eggs, e.g., reduction of teeth, elongation of cervical hypapophyses to crack eggs, and jaw mechanics (Kathariner, 1898; Gans, 1952). During nocturnal activity the snakes search for bird nests which are approached from nearby branches. Because most bird species breed seasonally, the prey availability of the egg eaters has a distinct seasonal pattern. During the birds' breeding season plenty of prey is available but no prey is available during the rest of the year. Thus, a relatively short feeding season is followed by a long fasting period. Such intermittent patterns of feeding and fasting occur in many snakes and other ambush hunting sauropsids. Morphological and physiological responses to feeding and fasting have mainly been described for boid species (Secor and Diamond, 1995, 1997a, b; Starck and Burann, 1998; Overgaard et al., 1999; Starck and Beese, 2001, 2002; Overgaard et al., 2002; Secor, 2003; Wang et al., 2002; Starck et al., 2004; McCue et al., 2005; Starck and Wimmer, 2005; Lignot et al., 2005; McCue, 2006). Generally, the specific dynamic action, SDA (Benedict, 1932; Brody, 1945; Kleiber, 1975) of boids is high, i.e., after feeding oxygen consumption increases on average 5–18-fold (Secor and Diamond, 1995, 1997a, b, 2000; Overgaard et al., 1999; Secor, 2003; Toeldo et al., 2003; Wang et al., 2002; Starck et al., 2004; McCue et al., 2005). Peak metabolic rates of 17-fold SMR have been reported for individual snakes (Secor and Diamond, 1995). The amplitude of SDA depends on amount of food eaten, environmental temperature, and nutrient components of the food (Zaidan III and Beaupre, 2003; McCue et al., 2005; McCue, 2006). Recent studies suggest that most of the energy investment during SDA is allocated to gastric function and the breakdown of the prey in the stomach (Secor, 2003; Starck et al., 2004) or is attributable to the costs of postprandial protein synthesis (McCue et al., 2005). However, the experimental evidence is not unequivocal. Secor (2003) showed that pythons that had been feeding on homogenized prey have lower SDA than individuals feeding intact prey, but McCue et al. (2005) showed that meal composition has a stronger effect on SDA than the mechanical breakdown of prey in the stomach. The naturally liquid prey of egg eaters offers a non-manipulative comparative test for such ideas. If gastric function and the gastric breakdown of food determines the amplitude of SDA we predict that: (1) mass specific standard metabolic rate of fasting egg eaters should not differ from other (colubrid) snakes; (2) the postprandial up-regulation of oxygen consumption should be lower than in other snakes, because no pre-absorptive breakdown of food is required; and (3) the postprandial up-regulation of organ size should not differ from other snake species feeding approximately the same amount of food. Our study will not be able to differentiate between the effects of breaking down the meal and effects of meal composition. Eggs are rich in lipid (ca. 10% of fresh mass; Mehner, 1983) and protein (ca. 12% of fresh mass) which by itself elicits a relatively small SDA.

The aim of this study was (1) to characterize the morphological and physiological pattern of the postprandial response of egg eaters when feeding on chicken eggs, and (2) to use these data together with comparative information to test the predictions about SDA.

Materials and methods

Animals

African rhombic egg eaters (*D. scabra*) were caught in the field or purchased from a South-African reptile farm. All physiological and morphological measurements were taken from nine snakes maintained at the reptile room at the University of Jena (sex unknown, body mass range 26–85 g, median 47 g). Animals were housed in 50 cm × 50 cm × 80 cm cages, with water, heating, and shelter. Cage temperature ranged from 25 to 30 °C, air humidity was 70%, and day light regime was 12L:12D h. Snakes were fed in biweekly intervals. For feeding, the snakes were intubated with a silicon tube, and stirred chicken egg equivalent to 20% of the snake's body mass was injected directly into the stomach of the snake. We used a repeated measures design with three successive feeding intervals in which all snakes experienced the same conditions and thus each snake could serve as a control of its own.

Ultrasonography

Ultrasonography was performed on live snakes and the animals received no prior treatment. Transcutaneous ultrasonography was performed while snakes were partly submersed in water. We used an ophthalmological ultrasonography device (I3 Innovative Imaging Inc., Sacramento, California), equipped with a 10 MHz concave sector scanner in B-mode (scan angle, 52°; scan speed, 28 frames s^{-1}; frequency, 10 MHz (90 dB); resolution, 0.15 mm axially, 0.2 mm laterally; image depth, 45 mm; gray scale, 256 shades; cross-vector scale, calibrated to 1550 m s^{-1}) or a portable ultrasonograph (Sonosite 180 HF) equipped with a linear broadband