

## Influence of food type on specific dynamic action of the Chinese skink *Eumeces chinensis*

Zhi-Chong Pan<sup>a</sup>, Xiang Ji<sup>b,c,\*</sup>, Hong-Liang Lu<sup>b</sup>, Xiao-Mei Ma<sup>b</sup>

<sup>a</sup>Department of Biology, School of Life Sciences and Biotechnology, Ningbo University, Ningbo 315211, Zhejiang, People's Republic of China

<sup>b</sup>Department of Environmental Sciences and Natural Resources, School of Life Sciences, Hangzhou Normal College, Hangzhou 310036, Zhejiang, People's Republic of China

<sup>c</sup>Jiangsu Key Laboratory for Bioresource Technology, School of Life Sciences, Nanjing Normal University, Nanjing 210097, Jiangsu, People's Republic of China

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### Abstract

We used the Chinese skink (*Eumeces chinensis*) as an experimental model to study influence of food type on specific dynamic action (SDA) of feeding. Thirty-three adult males collected from a natural population were divided equally into three (one control and two experimental) groups. We starved all skinks at 30 °C for 3 days and then provided the experimental skinks with a single meal consisting of either mealworms or meat [the flesh of the bullfrog (*Rana catesbeiana*)]. Food ingested by skinks of the two experimental groups differed in lipid content and lean dry mass but not in total dry mass and energy. Defecation following feeding occurred slightly earlier in skinks ingesting mealworms (mean=41.7 h) than in those ingesting meat (mean=47.7 h), but the difference was not significant. Analyses of variance (ANOVAs) with repeated measures showed that temporal variation in oxygen consumption over 72 h after feeding was evident in the experimental skinks but not in the control ones. Oxygen consumption was higher in the experimental skinks than in the control ones during the time interval between 4.5 and 36 h after feeding. The peak metabolic rate was greater but occurred later in skinks ingesting meat than in those ingesting mealworms. The estimated amounts of oxygen consumed by mealworm-fed, meat-fed and unfed skinks at 30 °C over 72 h after feeding were 356.5, 393.8 and 295.2 mL, respectively. Our results provide a support for the previous prediction that SDA is affected by types of food ingested by animals as skinks ingesting mealworms and meat differed in the time to reach a peak metabolic rate, the level of the peak metabolic rate and the magnitude of the SDA effect.

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### 1. Introduction

Animals obtain energy through feeding, and, for those that are carrying out a normal pattern of activities, the obtained energy is used not only for basal or standard metabolism, thermoregulation, activity and production (tissue growth and offspring production) but also for the

processes of digestion, absorption and assimilation of food (Kleiber, 1961; Bartholomew, 1977; Jobling, 1981, 1983; Cruz-Neto et al., 2001; Secor, 2001; Iglesias et al., 2003). The postprandial increase in metabolic rate, commonly called for historical reasons specific dynamic action (SDA), has been found in all animals so far studied (e.g., Jobling, 1981, 1983; Chapelle et al., 1994; Peck, 1996; Guinea and Fernandez, 1997; Rosen and Trites, 1997; Secor and Diamond, 1997a,b; Secor and Phillips, 1997; Cruz-Neto et al., 1999; Overgaard et al., 1999; Sievert and Andreadis, 1999; Robert and Thompson, 2000; Iglesias et al., 2003; Sigsgaard et al., 2003; Pan et al., 2004). SDA is of sufficient magnitude that it must be taken into account in all analyses

\* Corresponding author. Department of Environmental Sciences and Natural Resources, School of Life Sciences, Hangzhou Normal College, Hangzhou 310036, Zhejiang, People's Republic of China. Tel.: +86 571 88989878; fax: +86 571 28865337.

E-mail address: xji@mail.hz.zj.cn (X. Ji).

of energy metabolism (Bartholomew, 1977). The general pattern of SDA seems to be similar in most animals and is characterized by a rapid increase in metabolic rate soon after feeding to a peak followed by gradual decreases to the prefeeding values (e.g., Jobling, 1981; Chapelle et al., 1994; Guinea and Fernandez, 1997; Secor and Phillips, 1997; Robert and Thompson, 2000; Iglesias et al., 2003; Pan et al., 2004). However, the time it takes to reach a peak metabolic rate, the level of the peak metabolic rate and the duration and the magnitude of the SDA effect may vary, in various degrees, among and within species primarily because the traits involved in the SDA effect are affected by numerous external and internal factors such as temperature, reproductive condition, size, quantity and composition of the meal and forage mode (and thus, feeding frequency) (Bennett and Dawson, 1976; Greene, 1983; Jobling, 1983; Schwarzkopf, 1991; Secor and Diamond, 1995; Andrade et al., 1997; McKinon and Alexander, 1999; Robert and Thompson, 2000; Wang et al., 2001, 2002; Whiteley et al., 2001; Iglesias et al., 2003; Toledo et al., 2003). For example, an increased food intake prolongs the duration of SDA in *Pygoscelis adeliae* (Adélie penguin; Janes and Chappell, 1995), increases the magnitude of the SDA effect in *Python molurus* (Albino Burmese python; Secor and Diamond, 1997a,b) and *Crotalus durissus* (Neotropical rattlesnake; Andrade et al., 1997) and postpones the time it takes to reach a peak metabolic rate in *Pleuronectes platessa* (European plaice; Jobling and Davies, 1980). Animals that ingest food containing more proteins have a greater magnitude of the SDA effect (Bartholomew, 1977; Coulson and Hernandez, 1979; Janzen, 1981; Blaxter, 1989; Houlihan, 1991; Chakraborty et al., 1992; Secor and Diamond, 1997b).

As the metabolic response of fasted animals to a single meal often accurately reflects energetic costs of digestion, absorption and assimilation of food, measuring temporal variation in oxygen consumption after feeding is a commonly used method to test for the SDA effect in animals (Jobling, 1981; Janes and Chappell, 1995; Sievert and Bailey, 2000). In the present study, we investigate the differential postprandial metabolic response (SDA) of Chinese skinks (*Eumeces chinensis*) to different food. Our experimental model is a medium-sized (up to 134 mm SVL) ground-dwelling oviparous scincid lizard, which is one of most conspicuous lizard species in the southern provinces (including Taiwan and Hainan) of China (Zhao and Adler, 1993; Lin and Ji, 2000; Ji et al., 2002). Our aims are (1) to show the general pattern of SDA in *E. chinensis*, (2) to examine influence of food type on SDA and (3) to compare our data with those collected in other parallel studies.

## 2. Materials and methods

Thirty-three adult male *E. chinensis* were collected in early August 2003 from a population in the vicinity of Lishui (Zhejiang, eastern China), with body mass varying from 21

to 38 g and snout-vent length from 100 to 110 mm. The captured skinks were transported to our laboratory at Hangzhou Normal College, where they were divided equally into three [one (unfed) control and two (fed) experimental] groups of which each was housed in a 1000×600×500 (length×width×height) mm<sup>3</sup> glass cage. We placed the cages in a constant temperature room at 30 °C, thereby controlling the mean body temperature of skinks at the corresponding level (Ji et al., 1995). Room lights were set to a cycle of 12 light:12 dark. Prior to measuring oxygen consumption, we starved all skinks for 3 days to ensure a uniform postabsorptive state (Ji et al., 1995; Xu et al., 1999). At the end of the 3-day fast, we housed skinks individually in 300 mL closed-system respiratory chambers inside which the temperature was controlled at 30 °C, and then measured oxygen consumption ( $\dot{V}O_2$ ) for each skink based on the reduced air space in a calibrated tube during 10 min (Wang and Ji, 1997). After measurements, we provided the experimental skinks with a single meal consisting of either mealworms (larvae of *Tenebrio molitor*) or meat [the flesh of the bullfrog (*Rana catesbeiana*)]. Our skinks need not to be trained to eat mealworms and frog meat, although the two types of food are novel to them. We allowed the experimental skinks to eat voluntarily as much as they wanted for 1 h, thereby avoiding force-feeding. The first two pieces of food ingested by the experimental skinks each contained a 3-mm blue plastic thread (diameter 0.2 mm), which was used as a mark. The food passage time was defined as the lapsed time from swallowing to appearance of the first plastic thread (Ji et al., 1995). We measured oxygen consumption of both experimental and control skinks over 72 h at time intervals varying from 4.5 to 12 h after the event of feeding using the same respiratory chambers described above.

We extracted nonpolar lipids from dried samples of food in a Soxhlet apparatus for a minimum of 5.5 h using absolute ether as solvent. The amount of lipids in each sample was determined by subtracting the lipid-free dry mass from the total sample dry mass. We determined energy density of dried samples of food using a WGR-1 adiabatic bomb calorimeter (Changsha Bente Instruments, China). Titrations were performed on the residue after calorimetry to correct for nitrogenous wastes. Further corrections were performed for fuse wire burning.

All data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (Bartlett test), and Log<sub>e</sub> transformations were performed when necessary to satisfy the assumptions for parametric tests. We used one-way analyses of variance (ANOVA) and repeated-measures ANOVA to analyze the corresponding data when the assumptions of parametric analyses were met. Nonparametric analyses (Mann–Whitney *U*-test) were used when these assumptions were violated. The magnitude of the SDA effect was estimated to be equal to the area under the curve from a fit of least squares on the original data of the experimental group (i.e., total oxygen consumed) minus the area under the curve of the control group (i.e., oxygen

consumed due to resting metabolism). Descriptive statistics are presented as mean $\pm$ 1 standard error, and the significance level is set at  $\alpha=0.05$ .

### 3. Results

Skinks of the three groups did not differ in size (snout-vent length) and mass (one-way ANOVA, both  $P>0.921$ ). Food ingested by skinks of the two experimental groups differed considerably in wet mass, lipid content and lean dry mass but not in total dry mass and energy content (Table 1). Food passage time (an indicative of defecation following feeding) was apparently shorter in skinks ingesting mealworms (41.7 $\pm$ 4.1 h,  $N=11$ ) than in those ingesting meat (47.7 $\pm$ 3.2 h,  $N=11$ ), but the difference was not significant ( $F_{1, 20}=1.32$ ,  $P=0.264$ ). The peak metabolic rate was greater (8.3 $\pm$ 0.4 vs. 6.3 $\pm$ 0.2 mL/h O<sub>2</sub>;  $F_{1, 20}=16.81$ ,  $P<0.001$ ) but occurred about 5 h later (14.3 $\pm$ 0.8 vs. 19.4 $\pm$ 1.2 h;  $F_{1, 20}=11.78$ ,  $P<0.003$ ) in skinks ingesting meat than in those ingesting mealworms (Fig. 1).

Neither body size nor body mass was correlated with oxygen consumption measured at each time interval in both control and experimental skinks (all  $P>0.05$ ), so the two potential covariates were excluded from considerations. ANOVAs with repeated measures showed that temporal variation in oxygen consumption over 72 h after feeding was evident in the experimental skinks (mealworm:  $F_{10, 100}=12.44$ ,  $P<0.0001$ ; meat:  $F_{10, 100}=21.76$ ,  $P<0.0001$ ), but not in the control ones ( $F_{10, 100}=0.40$ ,  $P=0.942$ ). Oxygen consumption of the control skinks averaged 4.1 mL/h O<sub>2</sub> (Fig. 1). During the time interval between 4.5 and 36 h after feeding, oxygen consumption was significantly higher in the experimental skinks than in the control ones (one-way ANOVA, all  $P<0.05$ ), and, within the interval, skinks ingesting meat consumed significantly more oxygen than did those ingesting mealworms measured at 18, 24 and 30 h after feeding (one-way ANOVA, all  $P<0.03$ ) (Fig. 1).

The total amount of oxygen consumed, estimated by the area under the curve of the experimental group, was 356.5 mL in skinks ingesting mealworms and 393.8 mL in those

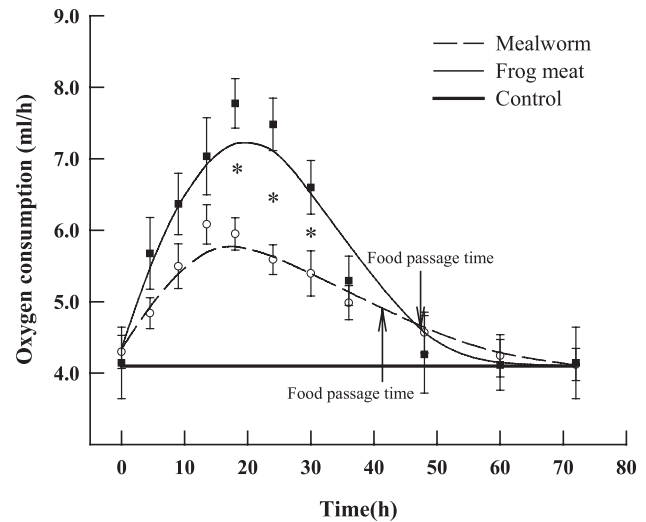


Fig. 1. Oxygen consumption (measured at 30 °C) of adult male *E. chinensis* after a single meal. Error bars are  $\pm$ 1 standard error. The differences in oxygen consumption between the two experimental groups are examined at each time interval using a one-way ANOVA, and the two means differing significantly are marked by an asterisk ( $\alpha=0.05$ ). The curves in the figure are generated from a fit of least squares on the original data, and the horizontal line represents the mean oxygen consumption of the control skinks. Arrows show the means of food passage time.

ingesting meat; the total amount of oxygen consumed by the control skinks was 295.2 mL (4.1 mL/h $\times$ 72 h) (Fig. 1). Thus, the estimated magnitude of the SDA effect was 61.3 mL O<sub>2</sub> in skinks ingesting mealworms and 98.6 mL O<sub>2</sub> in those ingesting meat. Assuming that 1 mL O<sub>2</sub> releases 20.08 J (Schmidt-Nielsen, 1990), energy expended due to SDA was about 1.2 kJ (8.5% of the gross energy content of the meal) in skinks ingesting mealworms and about 2.0 kJ (16.9% of the gross energy content of the meal) in skinks ingesting meat.

### 4. Discussion

The pattern of SDA in *E. chinensis* is similar to that reported for numerous other animals so far studied using the method of a single meal in that metabolic rate increases

Table 1  
Major components of food on which skinks fed in a single meal

	Mealworm (larvae of <i>Tenebrio molitor</i> ( $N=11$ ))	Meat (flesh of <i>Rana catesbeiana</i> ) ( $N=11$ )	Significant levels of Mann-Whitney <i>U</i> -test
Food wet mass (g)	1.49 $\pm$ 0.10 0.99–1.92	2.61 $\pm$ 0.04 2.32–2.79	$P<0.0001$
Food dry mass (mg)	542.9 $\pm$ 37.2 359.8–700.8	545.3 $\pm$ 8.3 485.9–584.1	$P=0.922$
Lipid contents (mg)	156.4 $\pm$ 10.7 103.6–201.8	5.3 $\pm$ 0.1 4.8–5.7	$P<0.0001$
Food lean dry mass (mg)	386.6 $\pm$ 26.5 256.2–499.0	540.0 $\pm$ 8.3 481.1–578.4	$P<0.001$
Food energy contents (kJ)	14.1 $\pm$ 1.0 9.4–18.2	11.8 $\pm$ 0.2 10.5–12.6	$P=0.082$

Data are expressed as mean $\pm$ 1 standard error and range.

soon after feeding to a peak and then decreases to the prefeeding values (Fig. 1). However, the time to reach a peak metabolic rate, the level of the peak metabolic rate and the magnitude of the SDA effect differed between skinks ingesting mealworms and meat (Fig. 1). The duration of the SDA effect did not differ between the two experimental groups because the time intervals (4.5–36 h) when the experimental skinks consumed significantly more oxygen than did control ones did not differ between the two groups. Food intake (both dry mass and energy content) did not differ significantly between the two experimental groups (Table 1), so the confounding effect resulting from variation in food intake can be lessened to some extent. As food ingested by skinks of the two experimental groups differed considerably in wet mass, lipid content and lean dry mass, our results therefore add evidence that food type (and thus, source of nutrients) can influence SDA of animals (e.g., Secor and Phillips, 1997; Somanath et al., 2000; Pan et al., 2004).

Metabolic rate rose by up to about 1.5 times prefeeding values within 14.3 h at 30 °C in skinks ingesting mealworms and to about 2.0 times prefeeding values within 19.4 h in skinks eating meat (Fig. 1). This difference results primarily from the differential energetic costs associated with digestion, absorption and assimilation of different food.

As SDA is about 4–30% for carbohydrates, 4–15% for fats and 30–70% for proteins when it is expressed in terms of the energy content of the food ingested (Bartholomew, 1977; Blaxter, 1989), the magnitude of the SDA effect should be therefore more pronounced in animals ingesting more proteins. Given that skinks of the two experimental groups did not differ significantly in the duration of the SDA effect and the total ingested energy, the greater magnitude of the SDA effect in skinks ingesting meat is therefore primarily due to the lower lipid content (and thus, more proteins) in this type of food (Table 1).

When comparing our data with those collected in other parallel studies in which food ingested by reptiles maintained at 30 °C in a single meal consisting of mealworms, we find that the influence of individual variables involved in the SDA effect, in various degrees, differs among species. The time it took to reach a peak metabolic rate was about 4 h in *Eulamprus tympanum* (southern water skink; Robert and Thompson, 2000), 15 h in *E. quoyii* (eastern water skink; Iglesias et al., 2003), 13 h in *Sphenomorphus indicus* (brow forest skink; Lu et al., 2004) and 10 h in hatchling *Trachemys scripta elegans* (red-eared slider turtle; Pan et al., 2004). The maximal metabolic rate following feeding was about 2.4, 1.5, 1.6 and 1.4 times prefeeding values in *E. tympanum* (Robert and Thompson, 2000), *E. quoyii* (Iglesias et al., 2003), *S. indicus* (Lu et al., 2004) and hatchling *T. s. elegans* (Pan et al., 2004), respectively. The duration of the SDA effect (the time interval during which metabolic rate was significantly higher in the experimental animals than in the control ones) was about 32 h in *E. chinensis* (Fig. 1), but it was about 48 h in *E. tympanum*

(Robert and Thompson, 2000), 50 h in *E. quoyii* (Iglesias et al., 2003), 15 h in *S. indicus* (Lu et al., 2004) and 28 h in hatchlings of *T. s. elegans* (Pan et al., 2004). The above comparisons show that the time it takes to reach a peak metabolic rate, the level of the peak metabolic rate and the duration of the SDA effect differ among reptiles even fed with the same food. Actually, inter- and intraspecific differences in the SDA effect are very obvious when comparing data collected in a variety of animals from vertebrates to invertebrates that ingest food differing in both quality (and thus, composition) and quantity (e.g., Jobling and Davies, 1980; Janes and Chappell, 1995; Peck, 1996; Andrade et al., 1997; Rosen and Trites, 1997; Secor and Diamond, 1997a,b; Ferry-Graham and Gibb, 2001; Whiteley et al., 2001; Sigsgaard et al., 2003). For example, feeding can be followed by a 10–45-fold increase in oxygen consumption in some species (such as snakes) that occasionally ingest very large meals (Secor and Diamond, 1995; Andrade et al., 1997; Overgaard et al., 1999; Bedford and Christian, 2001; Toledo et al., 2003), but the elevated metabolic rate after feeding is much less pronounced in animals that ingest small meals or feed more frequently (Overgaard et al., 1999; Bedford and Christian, 2001; Iglesias et al., 2003). However, as food intake was expressed in terms of mass rather than energy in most previous studies, whether variation in the SDA effect reflects the accumulative or the combined effects of individual nutrient components in the ingested food still remains an unanswered question.

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