Metabolic response to feeding in the Chinese striped-necked turtle, *Ocadia sinensis*

Zhi-Chong Pan [a], Xiang Ji [b,c,*], Hong-Liang Lu [c], Xiao-Mei Ma [c]

[a]*Department of Biology, School of Life Sciences and Biotechnology, Ningbo University, Ningbo 315211, Zhejiang, People's Republic of China*
[b]*Jiangsu Key Laboratory for Bioresource Technology, College of Life Sciences, Nanjing Normal University, Nanjing 210097, Jiangsu, People's Republic of China*
[c]*Department of Environmental Sciences and Natural Resources, School of Life Sciences, Hangzhou Normal College, Hangzhou 310036, Zhejiang, People's Republic of China*

Abstract

We measured oxygen consumption in juvenile Chinese striped-necked turtles (*Ocadia sinensis*) after they ingested food, either as a single meal or as double meals, to examine the influence of meal type and feeding frequency on specific dynamic action (SDA). Temporal variation in oxygen consumption after feeding was evident in the ingesting turtles but not in the unfed control turtles. In the single-meal experiment, the peak metabolic rate and the integrated SDA response (the whole energetic cost for the processes of digestion) both did not differ between turtles ingesting mealworms and shrimps when the influence of variation in ingested energy was removed, and the time to reach peak metabolic rate was not affected by meal type and the amount of food ingested. Turtles in the double-meal experiment ingested more energy and hence had a prolonged duration of SDA response than did those in the single-meal experiment, but the integrated SDA response did not differ between both experimental treatments when the influence of variation in ingested energy was removed. Our results show that meal type and feeding frequency have important consequences on the SDA response of juvenile *O. sinensis*. As the integrated SDA response remained remarkably constant either between turtles ingesting different food or between turtles ingesting the same food but at different frequencies when the influence of variation in ingested energy was removed, we therefore conclude that the energetic cost associated with ingestion is primarily determined by energy content of food ingested in juvenile *O. sinensis*.
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1. Introduction

The energy ingested by animals is used for basic or standard metabolism, activity, growth and reproduction, as well as digestive processes of absorption and assimilation of food (Bartholomew, 1977). The increase in oxygen consumption that follows feeding, commonly referred to as specific dynamic action (SDA), has been described for many invertebrates and vertebrates (e.g. Janes and Chappell, 1995; Guinea and Fernandez, 1997; Rosen and Trites, 1997; Secor and Diamond, 1997a, 1999, 2000; Hailey, 1998; Thor, 2000; Secor and Faulkner, 2002; Sigsgaard et al., 2003; Pan et al., 2004, 2005). The energetic cost of SDA can be substantial and therefore should be accounted for in the construction of energy budget (Bartholomew, 1977). The general pattern of SDA is similar in most animals, and is characterized by a rapid increase in metabolic rate soon after feeding, followed by a gradual decline to the prefeeding values (e.g. Jobling, 1981; Chapelle et al., 1994; Guinea and Fernandez, 1997; Secor and Phillips, 1997; Robert and Thompson, 2000; Secor and Diamond, 2000; Whiteley et al., 2001; Pan et al., 2005). However, the time it takes to

reach peak metabolic rate, the value of peak metabolic rate as well as the duration of SDA response may vary among and within species. This is primarily because these variables are affected by numerous external and internal factors such as temperature, size, quantity and composition of the meal, and feeding frequency (Jobling, 1983; Secor and Diamond, 1999, 2000; Andrade et al., 1997; Wang et al., 2001, 2003; Whiteley et al., 2001; Secor and Faulkner, 2002; Iglesias et al., 2003; Toledo et al., 2003).

Of the variables involved in the SDA response, the integrated SDA response (total oxygen consumed during the SDA response) is the variable that directly reflects the whole energetic cost for the processes of digestion, absorption and assimilation of food. Where variation in the integrated SDA response is determined by variation in ingested energy, we hypothesize that animals ingesting food of different types or ingesting food at different frequencies may not differ in the energetic cost of SDA when the influence of variation in ingested energy is removed. Here, we used juvenile Chinese striped-necked turtles (*Ocadia sinensis*) that feed frequently (Pan et al., 2003) as the experimental model to test our hypothesis. Specifically, our study aims to answer the two questions: Does meal type affect the energetic cost of SDA? Does feeding frequency affect the energetic cost of SDA?

2. Materials and methods

2.1. Animals

Ocadia sinensis is a medium-sized (up to 260 mm carapace length) omnivorous freshwater turtle, that is distributed in the southeastern provinces (including Taiwan and Hainan) of China and northern Vietnam (Zong, 1998). It is currently cultured and harvested by local people for food and traditional medicine. In late July 2004, we obtained 30 unsexed juvenile *O. sinensis*, with body mass varying 17.3–20.2 g, from a private hatchery in Hangzhou (Zhejiang, eastern China). The turtles were transported to our laboratory in Hangzhou, where they were housed 10 in each of the three $1000 \times 600 \times 500$ (length $\times$ width $\times$ height) mm glass cages placed in a constant temperature room at 30 °C. Room lights were set to 12 light : 12 dark; the lights were switched on at 07:00 h (Beijing time). Prior to experiments, we fed turtles on a daily basis with mealworms (larvae of *Tenebrio molitor*) and commercially sold shell-free shrimps for a week to allow habituation to the two types of food.

2.2. Methods

First, we conducted the single-meal experiment to examine the influence of food type on SDA, and then the double-meal experiment to examine the influence of feeding frequency on SDA. Turtles ($N = 30$) used in the single-meal experiment were divided equally into three (one unfed control and two experimental) groups. After the single-meal experiment, we randomly divided the 20 experimental turtles equally into two (one control and one experimental) groups for the double-meal experiment.

Prior to each experiment, food was withheld for 3 days to ensure a uniform post-absorptive state. At the end of the 3-day fast, we allowed the experimental turtles in the single-meal experiment to consume either mealworms or shrimps as much as they wanted for 1 h. Turtles were fed individually, so that the amount of consumed by each individual could be monitored. The first two pieces of food ingested each contained a 3 mm blue plastic thread (diameter 0.2 mm), which was used as a marker to assess passage time. Food passage time was defined as the period between swallowing to the appearance of the first plastic thread in the turtles' feces (Ji et al., 1995). Following feeding, turtles were placed individually into 300 ml closed-system respiratory chambers and housed in a constant-temperature room at 30 °C. Respirometry chambers were constructed with a 5-ml scaled tube and contained a packet of 30% sodium hydroxide to absorbed expired carbon dioxide. Rates of oxygen consumed were calculated from the volume of air lost within the scaled tube over a ten-minute span (Wang and Ji, 1997). We measured rates of oxygen consumption of experimental and control turtles at 4.5 to 15-h intervals for 72 h after feeding.

After the single-meal experiment, we fasted turtles for three more days and then conducted the double-meal experiment. We firstly allowed turtles to consume meal-worms for 30 min and then 22 h later allowed them to eat the same food for 1 h. We measured oxygen consumption of both experimental and control turtles over 96 h at time intervals varying from 3–12 h after the first feeding following the procedures described above.

We extracted non-polar lipids from dried samples of food in a Soxhlet apparatus for a minimum of 10 h using absolute ether as the 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 the energy density (kJ/g) of dried samples of food using a WGR-1 adiabatic bomb calorimeter (Changsha Bente Instruments, China).

2.3. Statistical analyses

All analyses were performed using the statistical package Statistica (Version 5.0). Data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (Bartlett test), and where Log_e transformed when it was necessary to satisfy the assumptions for parametric tests. We used one-way analyses of variance (ANOVA), one-way analysis of covariance (ANCOVA) and repeated measures ANOVA to analyze the corresponding data. Nonparametric analyses (Mann–Whitney U-test) were used when the assumptions for parametric analyses were violated. The

integrated SDA response was estimated by calculating 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 standard metabolism). Descriptive statistics are presented as mean ± 1 standard error, and the significance level is set at $\alpha = 0.05$.

3. Results

3.1. Metabolic response to a single meal

The three groups did not differ in body mass ($F_{2, 27} = 2.28$, $P = 0.122$). Food ingested by turtles of the two experimental groups differed significantly in wet mass, dry mass, lipid content and energy content but not in lean dry mass (Table 1). Food passage time was significantly longer in the turtles ingesting mealworms than in the turtles ingesting shrimps (42.9 ± 0.9 vs. 39.8 ± 0.5 h; $F_{1, 18} = 10.01$, $P < 0.01$), but the mean time to reach peak metabolic rate did not differ between turtles ingesting different types of food (12.9 ± 2.0 vs. 12.3 ± 2.8 h; $F_{1, 18} = 0.05$, $P = 0.828$) (Fig. 1). Peak metabolic rate was greater in the turtles ingesting mealworms than in the turtles ingesting shrimps (3.8 ± 0.1 vs. 3.3 ± 0.1 ml O_2/h; $F_{1, 18} = 7.24$, $P = 0.015$) but this difference was absent when the influence of variation in ingested energy was removed (ANCOVA: $F_{1, 17} = 2.14$, $P = 0.162$).

The three groups had the same metabolic rates prior to feeding ($F_{2, 27} = 1.38$, $P = 0.270$). Temporal variation in oxygen consumption over 72 h after feeding was evident in the experimental turtles (repeated measures ANOVA: mealworm: $F_{8, 72} = 32.81$, $P < 0.0001$; shrimp: $F_{8, 72} = 26.18$, $P < 0.0001$), but not in the control turtles (repeated measures ANOVA: $F_{8, 72} = 1.44$, $P = 0.195$). Oxygen consumption of the control turtles averaged 2.1 ± 0.1 ml O_2/h (Fig. 1). Oxygen consumption was significantly higher in the
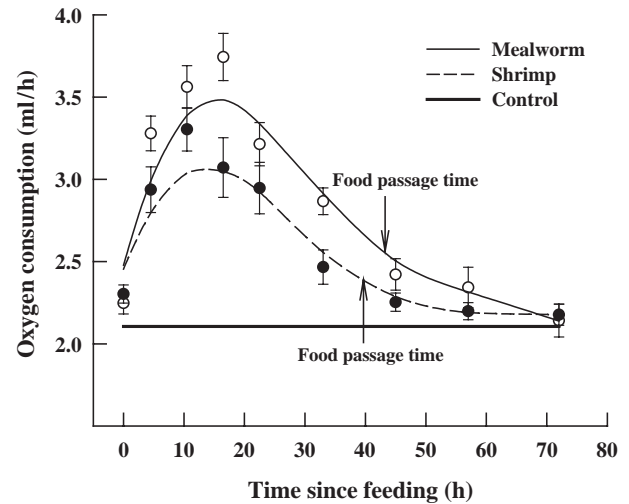

Fig. 1. Temporal changes in oxygen consumption at 30 °C for juvenile *Ocadia sinensis* after ingestion of a meal experiment. The curves are generated from a fit of least squares on the original data, and the horizontal line represents the mean oxygen consumption of the control turtles. Data are expressed as mean ± 1 standard error. Arrows show the means of food passage time. Body masses of control, mealworm-fed and shrimp-fed turtles were 19.0 ± 0.2, 18.8 ± 0.3 and 18.7 ± 0.3 g, respectively.

experimental turtles than in the control ones within the time interval from 4.5–45 h after feeding (one-way ANOVA: all $P < 0.05$) (Fig. 1).

The estimated integrated SDA response was 48.7 ± 3.7 ml O_2 in the turtles ingesting mealworms and 29.1 ± 5.3 ml O_2 in the turtles ingesting shrimps. Assuming that 1 ml O_2 releases 20.1 J (Schmidt-Nielsen, 1990), the energy expended due to SDA was about 978 J (11% of the gross

Table 1
Major components of food ingested by juvenile *Ocadia sinensis* ($N = 10$ in each of the two food treatments) in the single-meal experiment

	Tenebrio molitor larvae	Shell-free shrimps	Significant levels of Mann–Whitney U-test
Wet mass (mg)	934.3 ± 24.8	418.8 ± 32.4	$P < 0.001$
	842.4–1116.8	263.2–574.3	
Dry mass (mg)	347.3 ± 9.2	254.2 ± 19.7	$P < 0.002$
	313.1–415.1	159.7–348.5	
Lipid content (mg)	74.6 ± 2.0	4.8 ± 0.4	$P < 0.001$
	67.2–89.1	3.0–6.6	
Lean dry mass (mg)	272.7 ± 7.2	249.4 ± 19.3	$P = 0.406$
	245.9–326.0	156.7–341.9	
Energy content (kJ)	8.7 ± 0.2	4.5 ± 0.4	$P < 0.001$
	7.8–10.4	2.8–6.2	

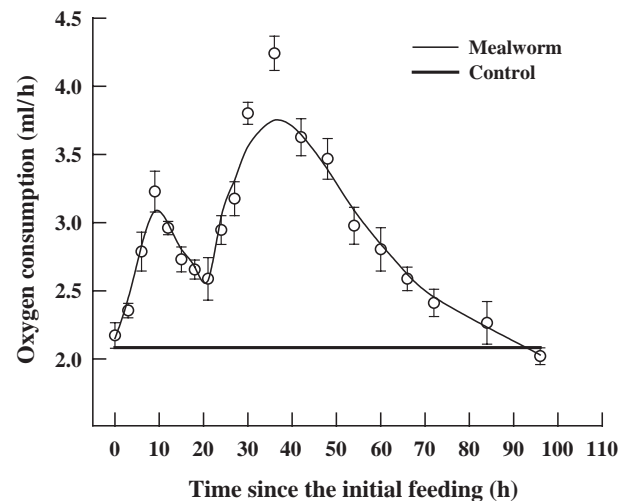Data are expressed as mean ± 1 standard error and range.

Fig. 2. Temporal changes in oxygen consumption measured at 30 °C for juvenile *Ocadia sinensis* in the double meal experiment. Data for the experimental turtles are expressed as mean ± 1 standard error. The curve in the figure is generated from a fit of least squares on the original data, and the horizontal line represents the mean oxygen consumption of the control turtles. Body masses of control and mealworm-fed turtles were 19.0 ± 0.3 and 18.5 ± 0.3 g, respectively.

energy content of the meal) in the turtles ingesting mealworms and about 584 J (13% of the gross energy content of the meal) in the turtles ingesting shrimps. When the influence of variation in ingested energy was removed using an ANCOVA, the estimated integrated SDA response did not differ between the experimental turtles ingesting different food ($F_{1, 17}=1.07$, $P=0.316$).

3.2. Metabolic response to double meals

Neither body mass ($F_{1, 18}=2.39$, $P=0.140$) nor metabolic rate prior to feeding ($F_{1, 18}=0.0006$, $P=0.980$) differed between the control and experimental turtles. Temporal variation in oxygen consumption over 96 h after the first feeding was evident in the experimental turtles (repeated measures ANOVA: $F_{19, 171}=34.28$, $P<0.0001$), but not in the control turtles (repeated measures ANOVA: $F_{19, 171}=1.35$, $P=0.161$). Oxygen consumption of the control turtles also averaged 2.1 ± 0.1 ml O_2/h (Fig. 2). Oxygen consumption was significantly higher in the experimental turtles than in the control ones within the time interval from 6–72 h after the first feeding (one-way ANOVA: all $P<0.05$) (Fig. 2). The first peak metabolic rate (3.3 ± 0.1 ml O_2/h) occurred 9.3 h after the first feeding, whereas the second peak metabolic rate (4.2 ± 0.1 ml O_2/h) occurred 13.4 h after the second feeding (Fig. 2).

The total oxygen consumed by the experimental turtles was 275.4 ml, whereas the total oxygen consumed by the control turtles was 201.6 ml (2.1 ml O_2/h × 96 h) (Fig. 2). Thus, the energy expended due to SDA was about 1483 (73.8 ml O_2 × 20.1 J/ml O_2) J (12% of the energy content of the double meals). Turtles in the double-meal experiment consumed more food than did those in the single-meal experiment (Tables 1 and 2) but the estimated integrated SDA response after feeding did not differ between both experiments when the influence of variation in ingested energy was removed using an ANCOVA ($F_{1, 17}=1.06$, $P=0.317$).

Table 2
Major components of food (*Tenebrio molitor* larvae) ingested by juvenile *Ocadia sinensis* ($N=10$) in the double-meal experiment

	The first meal	The second meal	Significant levels of Mann–Whitney U-test
Wet mass (mg)	542.0 ± 3.6	753.8 ± 22.4	$P<0.0001$
	522.6−558.5	675.0−868.8	
Dry mass (mg)	200.5 ± 1.3	277.0 ± 8.2	$P<0.0001$
	193.3−206.6	248.1−319.3	
Lipid content (mg)	52.3 ± 0.3	69.8 ± 2.1	$P<0.0001$
	50.5−53.9	62.5−80.5	
Lean dry mass (mg)	148.2 ± 1.0	207.2 ± 6.2	$P<0.0001$
	142.9−152.7	185.5−238.8	
Energy content (kJ)	5.1 ± 0.1	7.2 ± 0.2	$P<0.0001$
	4.9−5.3	6.4−8.2	

Data are expressed as mean ± 1 standard error and range.

4. Discussion

The postprandial increase in metabolic rate in juvenile *O. sinensis* is similar to the pattern reported for numerous other species of animals where metabolic rate increases soon after feeding to a peak and then decreases to the prefeeding values. When comparing our data to other studies where reptiles have ingested mealworms as a single meal at 30 °C, we find that the SDA response differs among species. For example, the time to reach peak metabolic rate (13 h in this study) varies from 4 h in *Eulamprus tympanum* (southern water skink; Robert and Thompson, 2000) to 15 h in *E. quoyii* (eastern water skink; Iglesias et al., 2003), the maximal metabolic rate following feeding (1.8 times the prefeeding value in this study) varies from 1.4 [*Trachemys scripta elegans* (red-eared slider turtle); Pan et al., 2004] to 2.4 (*E. tympanum*; Robert and Thompson, 2000) times the prefeeding value, and the duration of the SDA effect (40 h in this study) varies from 15 h in *Sphenomorphus indicus* (brown forest skink; Lu et al., 2004) to 48 h in *E. tympanum* (Robert and Thompson, 2000). These comparisons show that the SDA response differs considerably among reptiles ingesting food of the same type.

Differences in SDA are, in fact, very obvious among animals that ingest food differing in quality and/or quantity. For example, feeding can be followed by a 10–44-fold increase in metabolic rate in some infrequently foraging species that ingest very large meals (Secor and Diamond, 1995, 1997a,b, 2000; Andrade et al., 1997; Overgaard et al., 1999, 2002; 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 frequently (Jobling, 1981; Janes and Chappell, 1995; Secor and Diamond, 1999; Robert and Thompson, 2000; Secor and Faulkner, 2002; Iglesias et al., 2003; Lu et al., 2004; Pan et al., 2004, 2005). The general conclusions that have been drawn in this field include: an increased food intake prolongs the duration of the SDA effect (Janes and Chappell, 1995), increases the integrated SDA response (Secor and Diamond, 1997a,b; Andrade et al., 1997) and postpones the time it takes to reach peak metabolic rate (Jobling and Davies, 1980). In addition, meals with a higher content of proteins generate a greater integrated SDA response (Bartholomew, 1977; Coulson and Hernandez, 1979; Janzen, 1981; Blaxter, 1989; Houlihan, 1991; Chakraborty et al., 1992; Secor and Diamond, 1997b; Hailey, 1998).

In this study, an increase in food intake did increase the integrated SDA response (single-meal vs. the first meal in the double-meal experiment; mealworm-fed vs. shrimp-fed turtles in the single-meal experiment), postpone the time to reach peak metabolic rate (single-meal vs. the initial meal in the double meal experiment), and prolong the duration of the SDA effect (single-meal vs. double-meal experiment). Moreover, the proportion of energy expended due to SDA was slightly greater in the turtles ingesting shrimps (13% of

the gross energy content of the meal) than in the turtles ingesting mealworms (11% of the gross energy content of the meal), presumably because shrimps contain more proteins (*c.* 75% in the dried sample, based on the commercially reported ingredient table) than do mealworms (*c.* 55% proteins in the dried sample, Ji et al., 1996). Thus, our results generally support the aforementioned conclusions. However, as food intake was expressed in terms of mass rather than energy in most previous studies, whether variation in SDA primarily reflects variation in ingested energy remains unclear.

In our single-meal experiment, metabolic rate rose by up to about 1.8 times the prefeeding value in the turtles ingesting mealworms, and to about 1.6 times prefeeding value in the turtles ingesting shrimps (Fig. 1). These two values are both smaller than those reported for *Chelydra serpentina* (3.4 times), *Sternotherus odoratus* (2.1 times) and *Trachemys scripta* (2.7 times) that were fed small pieces of beef (Secor and Diamond, 1999), but it is difficult to interpret these differences because of the pronounced differences in animal size (mean body mass: *c.* 19 g vs. 65 – 325 g), mass-specific mean food intake (less than 5.0% of body mass vs. 5.5 – 10.0% of body mass) and food type (mealworms or shrimps vs. beef). As food ingested by our turtles differed between the two experimental groups in mass, structural property (presence or absence of exoskeleton), composition and energy content (Table 1), our results therefore add evidence that meal type can influence peak metabolic rate after feeding (Secor and Phillips, 1997; Somanath et al., 2000; Pan et al., 2004, 2005). It should be noted, however, that peak metabolic rate after feeding did not differ between the two experimental groups when the influence of variation in ingested energy was removed. This finding is of interest, because it suggests that peak metabolic rate following feeding is more heavily dependent on energy content rather than on gross mass or composition of food ingested. This result is inconsistent with that reported for the marine toad (*Bufo marinus*), where different meals generate different levels of metabolic peak even though they were of the same energy content (Secor and Faulkner, 2002). In our double-meal experiment, metabolic rate rose by up to about 1.5 times the prefeeding value after the first feeding, and to about 2.0 times prefeeding value after the second feeding (Fig. 2), with the two lower-to-higher digestive metabolic peaks being parallel with less-to-more food ingested in the two fore-and-aft feedings (Table 2). This result provides further evidence for the conclusion that peak digestive metabolic rate is mainly determined by energy ingested.

Collectively, juvenile *O. sinensis* ingesting different food or ingesting food at different frequencies differed considerably in the integrated SDA response (Figs. 1 and 2). These results support the previous conclusions that meal type and feeding frequency have important consequences on SDA (e.g. Hailey, 1998; Secor and Faulkner, 2002; Iglesias et al., 2003; Toledo et al., 2003; Pan et al., 2004, 2005). However, as the integrated SDA response remained remarkably

constant either between turtles ingesting different food or between turtles ingesting the same food but at different feeding frequencies when the influence of variation in ingested energy was removed, we therefore conclude that, in at least juvenile *O. sinensis*, the energetic cost associated with ingestion is more heavily determined by energy content rather than gross mass or composition of food ingested.

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