The postabsorptive and postprandial metabolic rates of praying mantises: Comparisons across species, body masses, and meal sizes

Marshall D. McCuea,⇑, Isabella Salinasa, Gabriella Ramirez a, Shawn Wilderb

a Department of Biological Sciences, St. Mary’s University, San Antonio, TX, United States
b Department of Integrative Biology, Oklahoma State University, Stillwater, OK, United States

ARTICLE INFO

Article history:
Received 11 July 2016
Received in revised form 19 August 2016
Accepted 20 August 2016
Available online 24 August 2016

Keywords:
Specific dynamic action
Energetics
Standard metabolic rate
Arthropods
Nutrition
Heat increment of feeding
Respirometry
Carbon dioxide
Body mass
Arachnids

ABSTRACT

The metabolic rate of an animal affects the amount of energy available for its growth, activity and reproduction, and, ultimately, shapes how energy and nutrients flow through ecosystems. Standard metabolic rate (SMR; when animals are post-absorptive and at rest) and specific dynamic action (SDA; the cost of digesting and processing food) are two major components of animal metabolism. SMR has been studied in hundreds of species of insects, but very little is known about the SMR of praying mantises. We measured the rates of CO₂ production as a proxy for metabolic rate and tested the prediction that the SMR of mantises more closely resembles the low SMR of spiders – a characteristic generally believed to be related to their sit-and-wait foraging strategy. Although few studies have examined SDA in insects we also tested the prediction that mantises would exhibit comparatively large SDA responses characteristic of other types of predators (e.g., snakes) known to consume enormous, protein-rich meals. The SMR of the mantises was positively correlated with body mass and did not differ among the four species we examined. Their SMR was best described by the equation

\[ \text{W} = 1526 \times g^{0.745} \]

and was not significantly different from that predicted by the standard ‘insect-curve’; but it was significantly higher than that of spiders to which mantises are ecologically more similar than other insects. Mantises consumed meals as large as 138% of their body mass and within 6–12 h of feeding and their metabolic rates doubled before gradually returning to prefeeding rates over the subsequent four days. We found that the SDA responses were isometrically correlated with meal size and the relative cost of digestion was 38% of the energy in each meal. We conclude that mantises provide a promising model to investigate nutritional physiology of insect predators as well as nutrient cycling within their ecological communities.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Measures of metabolic rates when animals are post-absorptive and at rest (i.e., standard metabolic rate [SMR] of ectotherms, or basal metabolic rate [BMR] of endotherms) are commonly used for comparisons among species and are thought to reflect the energetic cost of maintenance metabolism (McNab, 1999; Frappell and Butler, 2004; Hulbert and Else, 2004; Careau et al., 2014). This energetic cost can represent a significant proportion of an animal’s total energy budget – especially in less active species (Calder, 1987; Lovegrove, 2000; Terblanche et al., 2004; Montes et al., 2007). The cost of digesting and assimilating food (specific dynamic action; SDA) represents another large component of an animal’s energy expenditure. Typically about 10–30% of the total energy budget is spent processing food (McCue, 2006; Secor, 2009). Quantifying both maintenance costs and SDA are critical for understanding how much energy is available to allocate to other functions such as growth, activity, and reproduction (Weiner, 1992; Reinhold, 1999).

Arthropods represent some of the most abundant organisms in many ecosystems in terms of both abundance and biomass (McGavin, 2001). Hence, understanding arthropod metabolism is critical for understanding the flow of energy and nutrients through ecosystems (Teal, 1962). While metabolic rates have been measured in a wide variety of insects, very little is known about the metabolic rates of some insect families, notably praying mantises (Order: Mantodea, Family: Mantidae). In fact a comprehensive review of SMRs of 391 species of insects did not include any mantis species (Chown et al., 2007), and there only appears to be one published study that reports metabolic rates of praying mantises (Paratenodera angustipennis) (Matsura, 1981).

Mantises are an interesting group in which to examine metabolic rates as they are one of the few insect orders that consists...
of exclusively sit-and-wait or ambush foragers. While Odonata (e.g., dragonflies) is another exclusively predatory order, they differ in that they tend to be highly active foragers. Spiders (Order: Araneae), on the other hand, are also exclusively predatory and like mantises primarily use a sit-and-wait foraging strategy. They are also well known for having SMRs that are substantially lower than those of insects in general (Anderson, 1970; Wilder, 2011; Schmitz, 2016). Hence, it remains unclear if praying mantises are more similar in their metabolic rates to other insects or have diverged to be more similar to spiders to which they are more ecologically similar.

Very little is known about the SDA of insects compared to other groups of animals [reviewed in (McCue et al., 2016)] and no studies have examined SDA in praying mantises. For mantises, SMR and SDA likely represent the majority of an individual’s energy budget and nutrient availability in nature. Studies of SDA in a variety of other animals have shown that processing of protein requires a larger amount of energy than that of other macronutrients (Hailey, 1998; McCue et al., 2005; Tentolouris et al., 2008; Henrikson et al., 2015) and thus mantises may exhibit comparatively large SDA responses. Moreover, many predatory arthropods including mantises have been shown to be food-limited in nature (Wise, 1975, 1993; Greenstone and Bennett, 1980; Eisenberg et al., 1981; Barry, 1997, 2013; Overgaard and Wang, 2012) and high costs of SDA could further reduce energy availability to mantises. Hence, understanding the energetic costs of processing meals in mantises can provide insight into the consequences of changes in prey size and abundance for energy and nutrient availability in nature.

Our first goal was to quantify and compare metabolic rates of four species of praying mantises. We examined the relationship between SMR and body mass in mantises and tested whether it differed among mantis species. These data were then compared to a published dataset (referred to here as the ‘insect-curve’) representing 391 species of insects (Chown et al., 2007) and a dataset that we compiled on 75 species of arachnids – the ‘spider-curve’. Our second goal was to measure the SDA of mantises consuming various sized meals. While the relationships among body mass, meal size, and SDA have been examined in numerous vertebrate species, to our knowledge no study has examined all of these relationships in an insect model.

2. Methods

2.1. Animals

Between 2015 and 2016 we obtained first and second instar praying mantis nymphs representing four species (Tenodera sinensis, Polyspilota griffini, Rhombodera extensicollis, and Proheireodula picta) from private breeders in the USA. The nymphs were fed live crickets (Acheta domesticus) appropriate for their size. Small mantises (i.e., <200 mg) were fed every 4–5 d and larger individuals (i.e., >200 mg) were fed every 5–7 d. The mantises were individually housed inside rectangular cages with linear dimensions (i.e., length × width × height) that were minimally twice that of their body length. Cages were made of plastic food storage containers with the lids replaced with insect netting for ventilation. Pieces of galvanized hardware cloth (5 mm × 5 mm) were placed inside cages to provide three-dimensional structure. The mantises were misted daily and kept at 28 ± 1 °C (except during metabolic measurements, see below) and a photoperiod of 14 h L: 10 h D.

Previous studies have shown that 5 d is sufficient for adult mantids (Paratenundera angustipennis) to become postabsorptive indicated by the cessation of defecation after feeding (Matsura, 1981). Subadult mantises tend to feed more frequently than adults and thus the time required for them to become postabsorptive may be somewhat less than 5 d. To be conservative and ensure that all of the mantises in this study were postabsorptive prior to the respirometry trials, the smaller individuals (i.e., <200 mg) were fasted for 5 d and larger individuals (i.e., >200 mg) were fasted for 7 d. We measured body masses (mb) of postabsorptive mantises (±1 mg) and then offered them an ad libitum meal of appropriately sized crickets for ~1 h. The mantises were reweighed to determine meal masses. We expressed the meal sizes in terms of absolute sized mass (in mg) and the energetic content (in J). The relative prey mass (RPM) was calculated by dividing meal mass by mantis body mass and reported in terms of percent.

2.2. Metabolic rates

After feeding, mantises were placed inside metabolic chambers that were modified from Lock&Lock (Hana Cobi, Korea) containers (i.e., 180 ml or 470 ml). Dry, CO2-free gas was generated using a CO2 adsorber (Puregas, Broomfield, CO; #PCD112P) and pumped through the chambers at constant rates of 50–500 ml min−1 depending on the mb of each mantis. We measured the concentration of CO2 in the gas exiting each chamber using a CO2 analyzer (LiCor Biosciences, Lincoln, NE, USA; model# Li-6262) paired with an 8-channel multiplexer (Sable Systems Inc., Las Vegas, NV, USA) programmed to cycle between all of the metabolic chambers once each hour. Each mantis was measured for at least 5 min with 2-min baseline measurements between each animal. Although these animals are generally sedentary during digestion we minimized the potential effects of activity by using the lowest average CO2 content over a 2-min period during each hourly measurement for calculations of metabolic rate [sensu (Terblanche et al., 2004)]. Rates of carbon dioxide production (VCO2, in ml CO2 h−1) were calculated using the following equation:

\[ V_{\text{CO}_2} = V_l(F_{\text{CO}_2} - F_{\text{CO}_2}) \]

where \( V_l \) is flow rate of dry gas entering each metabolic chamber and the \( F_{\text{CO}_2} \) and \( F_{\text{CO}_2} \) represent the fractional CO2 content of the gas entering and exiting the chambers, respectively. We used a value of 24.65 kJ L−1 of CO2 (Chown et al., 2007) to express CO2 production in terms of energy production (i.e., kJ h−1) and further converted the rates of energy production into power (i.e., μW; \( 1 \text{ kJ} h^{-1} = 2.78 \times 10^3 \mu W \)) to permit comparisons with previously published studies (see below).

The metabolic rates were measured at 25 ± 1 °C for 120 h after feeding. We defined the standard metabolic rates (SMR) as the average hourly metabolic rate (measured as the lowest 2-min moving average as described above) between 96 and 120 h. The SDA was calculated as the cumulative energy expenditure (in kJ) in excess of SMR between 0 and 96 h. The SDA coefficient (SDAcoeff) represents a measure of the fractional CO2 content devoted to SDA, and was calculated as the SDA divided by the energy content (in kJ) of the cricket meals. We found that subsamples of these crickets contained 71.8% water and we used a value of 29.3 kJ/g (dry) to calculate their energy content (Beaupre et al., 1993; Nespolo et al., 2011).

We documented many more feedings than we report here. In this study we only report meal sizes for trials where we also have complete SDA and SMR measurements. In several cases the mantises attempted to moult inside the metabolic chambers within 120 h after feeding. The mantises were usually unsuccessful given the limited space of the metabolic chambers. In any case, those feeding trials were eliminated from the final data sets because of the possibility of confounding the ecdysis activities with digestion.