Acta Scientiarum

http://www.uem.br/acta
ISSN printed: 1679-9283
ISSN on-line: 1807-863X
Doi: 10.4025/actascibiolsci.v38i1.28774

Single large or several small? The influence of prey size on feeding performance of *Philodryas nattereri* (Squamata: Serpentes)

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ABSTRACT. This study aimed at evaluating the energetic return and feeding time on *Philodryas nattereri* kept in captivity. Snakes were fed biweekly for 60 days (four feeding trials), in two different feeding treatments (single and multiple prey items). The energetic return revealed no significant difference between the feeding treatments; however, we found a negative relationship between snake size and prey handling time during a feed using multiple prey items. In *P. nattereri*, when large preys are as easy to find as small ones, there seems to be no difference in energetic return.

Keywords: captivity, energetic return, feeding behaviour, handling time, snakes.

Uma presa grande ou várias pequenas? A influência do tamanho da presa no desempenho alimentar de *Philodryas nattereri* (Squamata: Serpentes)

RESUMO. O objetivo deste estudo é avaliar o retorno energético e o tempo de alimentação em serpentes *Philodryas nattereri* mantidas em cativeiro. As serpentes foram alimentadas a cada duas semanas por 60 dias (quatro eventos alimentares) em dois tratamentos de alimentação diferentes (uma única presa e múltiplas presas). Não houve diferença significativa no retorno energético entre os tratamentos alimentares. No entanto, encontramos uma relação negativa entre o tamanho da serpente e o tempo de manipulação da presa durante uma alimentação usando várias presas. Em *P. nattereri*, parece não haver diferença no retorno energético quando presas grandes são tão fáceis de encontrar quanto presas pequenas.

Palavras-chave: cativeiro, retorno energético, comportamento alimentar, tempo de manipulação, serpentes.

Introduction

According to the Optimal Foraging Theory (OFT), animals search, capture, and consume prey containing the maximum nutritional value, spending the least energy as possible during this process (MacArthur & Pianka, 1966; Pyke, 1984). Large animals tend to ingest large prey, except when smaller prey is abundant (Schoener, 1971). However, this tendency of animals to ingest larger prey does not seem to be general in snakes, an exception that seems to occur due to low handling costs for large and small prey, allowing snakes to consume items found regardless of their size (Shine, 1991).

Handling and eating time may present negative relationship to head length and body size in most snakes (Shine, 1991; Vincent & Mori, 2008; Vincent, Vincent, Irschick, & Rossell, 2006). A possible explanation would be that small snakes are eating preys almost as large as their maximum prey size, which is limited by gape size, while it is not a problem for the large ones (Shine, 1991). Furthermore, large snakes do not have difficulty in handling and ingesting small prey (Shine, 1991). Hence, it is expected that larger animals, which are less affected by gape limitation than the smaller ones, could manipulate prey faster than smaller individuals.

Philodryas nattereri snake (Steindachner 1870) is distributed along the Caatinga and Cerrado from Central Brazil to Paraguay (Vanzolini, Ramos-Costa, & Vitt, 1980). Because of its high abundance, foraging abilities, and fecundity, *P. nattereri* is classified as a key predator in the Brazilian semi-arid region (Mesquita, Borges-Nojosa, Passos, & Bezerra, 2011). It is diurnal, semi-arboreal, and active throughout the year, presenting a generalist diet and activity peak during periods of rainfall and maximum temperature (Mesquita et al., 2011).

This study aimed at comparing the energetic return and feeding time of *P. nattereri* in captivity by analyzing whether single and multiple prey are equally profitable to individual snakes when search time is reduced. Our objective was also to evaluate the influence of snake size and head length on the prey handling time.

Material and methods

We used 17 snakes (nine females and eight males), with an average snout-vent length (SVL) of 99.29 ± 10.21 cm (mean ± standard deviation) and average head length (HL) of 3.02 ± 0.33 mm. Snakes were housed at the "Núcleo Regional de Ofiologia da Universidade Federal do Ceará" (NUROF-UFC) and kept in wooden vivariums (51 x 37 x 37 cm) with water offered *ad libitum* and clay pots that were used as refuges where animals could hide in. The snakes were taken from the wild and held in captivity during a period of between two and seven years.

All snakes were fed four times with intervals of fifteen days. Along the experiments, all the objects, such as the recipient with water and the clay pots, which could cause distractions to the snakes, were removed from the enclosure. All of the snakes had been subjected to a 15-day fasting and in the first feeding trail were weighed and fed with one live adult mouse that was approximately ten percent of the snake mass. After fifteen days, the snakes were fed again, but with three live subadult mice that together weighed approximately 12.5 percent of the total *P. nattereri* weight. We offered the small mice consecutively: the following prey was offered as soon as the snake had eaten the previous prey. All of the *P. nattereri* used in this study were usually fed with an adult mouse weighing approximately 10-12.5 percent of their mass in NUROF-UFC. Therefore, the prey weight percentage used in this study was based on a feeding protocol previously used by NUROF-UFC, in order to prevent the animals from having additional stress. The two types of procedures were repeated in the second month, numbering four feeding trials. We measured the time required for the animal to recognise, capture, and ingest the prey using seconds in a stopwatch, ranging from the time of the first introduced prey to each snake in the wooden box until the snake finished eating the whole last prey to be offered. The snakes were left with their prey for a maximum of 40 minutes in order to avoid discrepancy in sampling times. We carried out all of the feeding events between 8:00 and 12:00h a.m., respecting the *P. nattereri* diurnal activity patterns (Mesquita et al., 2011).

We estimated the energy return using a simplified form of the formula proposed by (Schoener, 1971). Total prey mass was used as a measure of its "potential energy". Time and costs related to pursuit were strongly reduced in our sampling design because of the restricted space of the vivarium (snakes rapidly found and captured the mice as soon as they were introduced into the vivarium); therefore, we did not consider these variables when calculating energetic return. Furthermore, handling and eating costs use to be very low in snakes (below one percent of the energy provide through prey ingesting) (Cruz, Andrade, & Abe, 1999; Feder & Arnold, 1982; Shine, 1991) and were not considered in this approximation either. Accordingly, energy return was calculated as total ingested prey mass divided by feeding time.

The energetic returns in both of the feeding procedures were compared through paired Wilcoxon tests for each month since data was not normally distributed. Since difference in time between the second and third feeding was similar to the difference in the trials for each month, we also compared these events using the paired Wilcoxon test. The relationships between feeding time and snake size (SVL) and between feeding time and HL were assessed using Spearman Rank correlations per feeding trial. The reasons to use HL were that the snake feeding process is gape limited due to head measurements and it is the measure more commonly applied in studies regarding feeding performance of snakes (Shine, 1991; Vincent & Mori, 2008). We also performed analyses using SVL instead of only HL, since *P. nattereri* may use constriction when handling its prey. For the statistical analyses, we converted time measurements in seconds into minutes in order to reduce data variance. When a snake had not consumed its prey during the allotted time, it was removed from the trial statistical analysis. We performed the analyses using R software ver. 2.15.3 (R Devepolment Core Team, 2014) with a significance level of five percent ($p < 0.05$).

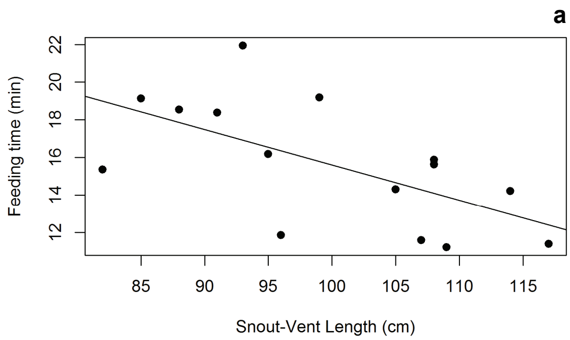
Results and discussion

Following, the energy return in snakes according to the feeding: first (1.70 ± 0.80 g $min.^{-1}$, n = 14); second (1.66 ± 0.67 g $min.^{-1}$, n = 15); third (1.64 ± 0.83 g $min.^{-1}$, n = 17), and fourth (1.65 ± 0.38 g $min.^{-1}$, n = 12). We found no significant difference between the single prey and multiple prey feeding groups in the first month ($U = 53.5$, $p = 0.27$) nor in the second ($U = 32$, $p = 0.62$). Likewise, we observed no significant difference in energy return between the second and third feeding trials either ($U = 47$, $p = 0.49$).

We found negative correlations between feeding time and snake size and between feeding time and head length only in the second round of feedings, corresponding to a multiple prey feeding (Table 1, Figure 1).

Table 1. Relationships between the morphological measurements (snout vent length - SVL and head length) and the feeding times in the four feeding events of *P. nattereri* kept in captivity. Feedings 1 and 3 correspond to single prey feedings, 2 and 4 to multiple prey feedings.

Feeding	Correlation between feeding time and SVL	Correlation between feeding time and head length
Feeding 1	$r_s = 0.1$, N = 14, p = 0.73	$r_s = -0.04$, N = 14, p = 0.88
Feeding 2	$r_s = -0.64$, N = 15, p = 0.01	$r_s = -0.62$, N = 15, p = 0.01
Feeding 3	$r_s = -0.15$, N = 17, p = 0.56	$r_s = -0.21$, N = 17, p = 0.42
Feeding 4	$r_s = -0.31$, N = 12, p = 0.31	$r_s = -0.06$, N = 12, p = 0.83



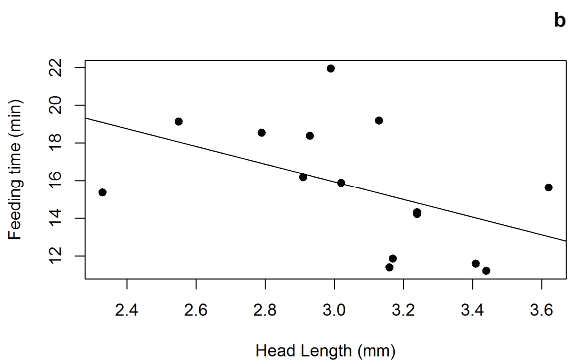


Figure 1. Relationships between feeding time and morphological measurements of *P. nattereri* from the second feeding trial. a) Negative correlation between feeding time and snout-vent length; b) Negative correlation between feeding time and head length. Both figures indicate that feeding time was reduced for snakes with larger body size and head length. min = minutes.

Despite the high diversity of snakes in Brazil and extensive natural history studies on these animals, to the best of our knowledge, this was the first time that predictions from foraging theory have been experimentally tested using a Brazilian snake species. *P. nattereri* has a generalist diet and explores many different microhabitats (Mesquita et al., 2011), which characterises an opportunistic predator. Our results indicate that the presence of several small preys that are more accessible than a large one in a given environment is a possible and viable option for *P. nattereri*.

Feeding time is known to have a negative association with the body size and head length of snakes (Shine, 1991; Vincent & Mori, 2008; Vincent et al., 2006). This pattern has been found, for example, in terrestrial diurnal snakes (*P. porphyriacus* and *M. spilota*; Shine, 1991) and even in aquatic species (*Nerodia fasciata*; Vincent et al., 2006), reinforcing its generality. However, this effect was only observed for the multiple prey feeding treatment. According to Shine (1991), large snakes are able to handle prey of different sizes better than smaller snakes, a statement that is corroborated in our results. Feeding time commonly increases with prey size, which probably occurs due to a general positive correlation between prey size and number of upper jaw movements used to ingest the prey and to gape size limitation (Hampton, 2013; Shine, 1991). This difference in handling seems to be sufficiently high to allow large snakes to have these advantages. Such a result was not observed in the fourth feeding routine, where the smallest snakes did not eat, reducing the sample size and possibly affecting the lack of significance in the comparisons between morphological measurements (SVL and HL) and feeding time in this trial. The high similarity between the results using HL and SVL is expected since they were highly correlated (Pearson correlation: r = 0.80, df = 15, p < 0.001; data were normally distributed).

Animals in captivity can sometimes show different behaviours, which do not correspond to the behavioural repertoire of the species in nature. For example, in the wild, hunting three underweight preys may probably require more time and energy than hunting a single prey with an "ideal weight". Thus, further studies in natural conditions are important to assess the results found in this paper.

Conclusion

Finally, for *P. nattereri*, single and multiple prey feedings have equal energy return when search costs are reduced. Abundant small prey can be as energetically viable as scarce large prey. Therefore, these animals can choose their prey based on availability and practicality. We also found a negative relationship between feeding times and the body size as well as head length of snakes. Hence, the larger size in this species (in both the body size and the head length) may provide it with energetic advantages related to the handling time of small prey.

Acknowledgements

We would like to thank the staff of NUROF-UFC for the logistical support, Alice Frota Feitosa for contingently helping with data collection, Paulo Cesar Mattos Dourado Mesquita, and an anonymous reviewer for providing valuable comments to a previous version of this manuscript, Stephen Patrick John Read for helping with English review, and Ibama for providing the licence for us to keep snakes in NUROF-UFC (LO no. 011/2004 – Protocol Number 02007.000921/87-71).

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Received on August 5, 2015.
Accepted on December 15, 2015.

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