Specific dynamic action and postprandial thermophily in juvenile northern water snakes, *Nerodia sipedon*

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Received 25 July 1998; accepted 12 September 1998

**Abstract**

1. We measured oxygen consumption of seven juvenile Northern water snakes, *Nerodia sipedon*, at 3, 19, 41, and 89 h after feeding. 2. Oxygen consumption 19 h after eating was significantly higher than at 3, 41, and 89 h after feeding and the values at 3 h post-feeding were significantly higher than those at 41 and 89 h. 3. We monitored substrate temperature preference in nine juvenile *N. sipedon* at 2000, 0000, 0800, 1200, and 1600 h for 3 days.

4. After feeding and at night snakes selected warmer substrate temperatures. © 1999 Elsevier Science Ltd. All rights reserved.

**1. Introduction**

Heterotrophs are characterized by the need to consume, digest, and assimilate food. Eating provides the energy and raw materials requisite to survive and obtain the building blocks needed for growth, tissue maintenance and reproduction. While the meal ingested provides fuels for metabolism, processing of food itself has an energy cost. This cost is most commonly manifested in an elevation of oxygen consumption known as specific dynamic action (SDA). The magnitude and duration of the elevated oxygen consumption depends on the size of the meal, body temperature (\(T_b\)) of the animal, type of prey eaten, the antideigestive defences of the food, the body mass of the animal, and amount of protein in the meal. As meal size and amount of protein in the meal increase so does the magnitude of SDA (Coulson and Hernandez, 1979; Chakraborty et al., 1992; Janzen, 1981; Secor and Diamond, 1997). As the \(T_b\) of an animal increases the duration of SDA decreases (Kalorarani and Davies, 1994). When *Caiman crocodilus* was fed rodents it displayed an SDA that lasted longer, but had a lower amplitude than was displayed when the meal consisted of fish (Gatten, 1980). For *Python molurus* body mass affected SDA (Secor and Diamond, 1997).

In endotherms the calorogenic effect of food may contribute to thermal homeostasis when the animal is below its thermonutral zone (Costa and Kooyman, 1984). In ectotherms this is generally not the case, however, the presence of food in a reptile's digestive tract is one of the factors important in temperature selection. Snakes that select \(T_{bs}\) of less than 28°C when fasted tend to elevate their \(T_{bs}\) after feeding, presumably to enhance digestion (Touzeau and Sievert, 1993). Conversely, *Nerodia taxispilota* has a preferred fasting temperature that maximizes digestive efficiency and therefore this species does not elevate \(T_b\) after a meal (Goodman, 1971). The function of postingestive thermophily may be to enhance digestive efficiency. For example, *Natrix maura* had lower absorption efficiencies between 10 and 25°C than between 30 and 35°C. In addition, as \(T_b\) increased in *N. maura* so did the rate of digestion (Hailey and Davies, 1987b). Although higher \(T_{bs}\) increase metabolic rates, they also speed digestive processes and enhance absorption.

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Because of this there should be a strong link between behavioral thermoregulation and digestive function in snakes.

If young individuals can speed digestion and increase digestive efficiency by elevating $T_b$, it would allow them to take more meals and grow more rapidly than by maintaining constant, lower $T_b$s. We measured $T_b$ of juvenile Northern water snakes, *Nerodia sipedon*, before and after feeding. Our goals were to determine if these snakes demonstrated postprandial thermophily and to determine the time course of SDA. An ancillary opportunity afforded by our design was to measure oxygen consumption of these snakes during and between shedding periods. Because growth is at a particular premium for young animals, postprandial thermophily may be more pronounced in neonates and juveniles.

2. Materials and methods

Juvenile Northern water snakes, *Nerodia sipedon* (Colubridae), were collected in May–July, 1994 in Blount County, TN and maintained at $24 \pm 1.5^\circ C$ in the animal facility at Maryville College. Body mass averaged 12.76 g (range = 6.50–19.65 g). Snakes were individually housed in plastic shoe boxes with screening in the lids to provide ventilation. They were provided with a large water dish, water ad lib, and a retreat in which to hide. Throughout the time the snakes were in captivity, and during the experiment, the photoperiod was 13L:11D with scotophase starting at 1900 h.

2.1. Oxygen consumption

Seven snakes were weighed to the nearest 0.01 g. In the lab, water snakes show a strong tendency to feed in the hour after lights out, even when fed ad lib. (P. Andreidis, unpub. data). Approximately one hour after lights out, snakes were fed one fathead minnow (*Pimephales promelas*) equal to about 10% of its body mass. Ninety min before we started measuring oxygen consumption we gently placed snakes individually into the 250 ml reaction vessels of a Gilson Differential Respirometer. The bottom of the vessel was covered with a disk of filter paper soaked with 2 ml of 10% KOH. The snake was suspended 1 cm above the KOH on a plastic mesh platform. The reaction vessels were submerged into the water bath of the respirometer and the snakes were left undisturbed for 90 min. After habituation oxygen consumption was measured for six 3 min periods. All oxygen consumption values were converted to STPD. Oxygen consumption of each snake was measured at 27°C at 3, 19, 41, and 89 h after feeding.

Mean values for $\mu l g^{-1} min^{-1}$ of oxygen consumed were calculated for each snake. A one-way repeated measures ANOVA was used to determine if the time since the meal affected oxygen consumption. This was followed by a Student–Newman–Keul stepwise comparison test. Values were considered significant at $P < 0.05$. Values are reported as mean ± SD.

We also compared five snakes in ecdysis (cloudy eye cups) with five snakes that were not shedding to see if ecdysis had a significant effect on metabolism. This was done at 32°C and a paired t-test was used to compare the means.

2.2. Temperature selection

Substrate temperature preference was recorded for nine snakes in a linear thermal gradient with an aluminum floor that measured 210 x 18 cm. The gradient had 18 cm walls and was covered by a clear acrylic lid. Floor temperatures ranged from 12 to 45°C. Two heating pads on the underside of the aluminum floor maintained a linear thermal gradient. The gradient was placed in a walk-in cold chamber set at 10°C which kept the cold end of the gradient at 12°C. The floor of the gradient was covered with an unbroken sheet of thin, cloth toweling to provide traction for the snakes when they moved. A 4 cm wide strip of cardboard ran the length of one side of the gradient, extending out from the junction of the wall and floor at a 45° angle to the floor along one of the long walls of the gradient. This structure provided a retreat that offered temperatures from 12 to 45°C, but did not allow the snakes to be off the floor. Water was provided ad lib in a container too small for the snakes to climb into. During scotophase a red 25 W light bulb pointed away from the thermal gradient allowed us to see the snakes and take substrate temperature readings.

A snake was placed in the thermal gradient on the morning prior to the first night of the experiment and allowed to habituate. At 2000 h that night the substrate temperature under the snake's stomach was measured with a Chromega-Alomega (Omega Engineering, Inc) thermocouple connected to a Kane May 1242 Digital Data Logger. This was repeated at 0000, 0800, 1200, and 1600 h. These five measurements were labeled day 1. Night consisted of the mean of the 2000 and 0000 h recordings and day consisted of the mean of the 0800, 1200, and 1600 h recordings. Just before scotophase on day 2 each snake was given a minnow (*Pimephales*) equal to about 11% of its body mass (range = 9.7–12.7%). Substrate temperatures were measured at the same time as on day 1 for days 2 and 3.

The data points for each individual from each night and each day the snake was in the thermal gradient were pooled to yield 6 data points per animal (3 night
values and 3 day values). These values were analyzed with a one-way repeated measures ANOVA to assess the effect of day vs night and feeding on temperature selection. The ANOVA was followed by a Student–Newman–Keul stepwise comparison test. We used a paired t-test to compare the average selected temperatures at night with those selected during the day. We took the mean $T_b$ of a snake each night and calculated a 3 night average for each individual. A daytime average was calculated similarly. Thus, each snake contributed one night value and one day value. Values were considered significant at $P \leq 0.05$.

3. Results

3.1. Oxygen consumption

The time since feeding had a significant effect on oxygen consumption ($P < 0.0001$). The highest oxygen consumption value was measured 19 h after the meal. This was significantly higher than the values measured at other times. The values measured 3 h after the meal were significantly higher than those measured 41 and 89 h after feeding. The values at 41 and 89 h did not differ significantly (Fig. 1).

Ecdysis did not have a significant effect on $O_2$ consumption ($P = 0.205$). Snakes with cloudy eye caps and ventral scales had an $O_2$ consumption of $4.07 \pm 1.65 \mu l g^{-1} min^{-1}$ while snakes not undergoing ecdysis had a rate of $3.22 \pm 1.20 \mu l g^{-1} min^{-1}$.

3.2. Temperature selection

There was a significant effect of time on selected substrate temperature ($P \leq 0.02$). On night 2 the snakes selected significantly higher ($P = 0.01$) substrate temperatures than on day 3 ($P < 0.05$). None of the other time blocks differed significantly (Fig. 2).

The mean nighttime selected $T_b$s of the nine snakes were significantly higher ($P \leq 0.016$) than the mean daytime selected $T_b$s. When we compared the pooled nighttime selected substrate temperatures with the pooled daytime temperatures we found that snakes selected substrates that were 3°C higher at night. When mean selected substrate temperatures were compared for each individual, out of 27 possible comparisons (nine snakes x 3 day–night pairs), only five had higher day temperatures than night temperatures.

4. Discussion

Specific dynamic action and post-ingestive thermodilution occurred in our juvenile water snakes. SDA has been documented in a wide variety of reptiles including other snakes, *Natrix maura* (Hailey and Davies, 1987b), *Crotalus durissus* (Andrade et al., 1997), and *Python molurus* (Secor and Diamond, 1997); crocodilians, *Caiman crocodilus* (Gatten, 1980) and *Alligator mississippiensis* (Coulson and Hernandez, 1979); lizards, *Sceloporus merriami* (Beaupre et al., 1993) and *Varanus albifasciatus* (Secor and Phillips, 1997); and turtles *Chrysemys picta* (Sievert et al., 1988).

We chose to measure oxygen consumption of our snakes at 27°C because it was near the preferred fasting $T_b$ measured in our juvenile snakes and in adult $N$. 
sipedon (Lutterschmidt and Reinert, 1990). In general, the time course of SDA decreases as ambient temperature increases (Hailey and Davies, 1987b; Kalaram and Davies, 1994). Had we tested the time course of SDA at the T\textsubscript{SA} chosen during night 2 (30.5°C) it would undoubtedly have decreased the length of SDA.

Our results were similar to those of Hailey and Davies (1987b) with N. maura. Their juvenile snakes (25–35 g) fed slightly more than 10% of their body mass in a fish meal displayed an SDA at 25°C that lasted 3 days. Their peak of SDA occurred at 24 h. Our SDA did not last as long as it did in N. maura possibly because we tested our snakes at a slightly higher temperatures and because the masses of snakes and meals were absolutely larger for N. maura than for N. sipedon even though both species ate a meal equal to approximately 10% of their body mass. To ascertain that the values obtained at 41 and 89 h were indeed postdigestive values, we also measured oxygen consumption of six snakes at 144 h after feeding. The values observed at 144 h were not significantly different from those at 41 and 89 h.

We fed our snakes relative meal sizes which were comparable to what they would take in the field (King, 1992). Compared to our snakes, other snakes may have a greater range in relative prey size. *Python molurus*, a sit-and-wait predator, eats large, infrequent meals. When given a meal of 100% its body mass this species increased its oxygen consumption by 1,170% and had a scope of peak oxygen consumption of 44. These high values reflect the fact that between meals there is some atrophying of the digestive tract and the high oxygen consumption of SDA is caused in part by the necessary regeneration of the digestive tract requisite for digestion and absorption (Secor and Diamond, 1997). General scaling principles would dictate that smaller snakes eat more frequently. Unlike *P. molurus* our snakes had a scope of peak oxygen consumption of only 32.

Many physiological functions of reptiles, including digestive rate (Stevenson et al., 1985) and efficiency (Goodman, 1971; Hailey and Davies, 1987b) are temperature dependent. Most such functions have a thermal optimum, the rate decreasing above or below this optimum. Raising T\textsubscript{A} from suboptimal to more nearly optimal temperatures can enhance digestive functions and improve locomotor speed (Stevenson et al., 1985). A disadvantage of attempting to maintain a constantly high T\textsubscript{A} is that it increases the snake’s metabolic cost (Stevenson et al., 1985) and in some environments may increase exposure to predators. The increased metabolic rate caused by high T\textsubscript{A}s also means the snake must consume more prey and hunting could expose a snake to its predators. Therefore, snakes must select appropriate T\textsubscript{A}s while balancing conflicting selection pressures. This can be done by elevating T\textsubscript{A} after feed-

ing and dropping T\textsubscript{A} if the animal is fasting. Basking may increase the risk of predation, but conductive heating by sitting on or under a warm rock may allow the snake to heat and still remain concealed. It would also allow nocturnal snakes to warm after the sun had set. *Nerodia fasciata* move from air to water once the temperature of air drops below water after sunset (Osgood, 1970).

The tendency for juvenile *N. sipedon* to select higher T\textsubscript{A}s at night than during the day was unexpected. Snakes normally do not show diurnal rhythms of T\textsubscript{A} selection in thermal gradients (Touzeau and Sievert, 1993). *Nerodia sipedon* active in the field at night does avoid cooling by staying in the water when water temperature exceeds air temperatures and is found perching on vegetation when air temperature exceeds water temperature (P. Andreidis unpub. data). It would make sense for juvenile snakes to attempt to stay warm during their nocturnal activity period since warmer T\textsubscript{A}s increase the digestive rate of snakes (Dorcas et al., 1997). A more rapid digestive rate would allow a juvenile snake to eat more frequently and grow more quickly. A higher T\textsubscript{A} would also allow a reptile to have increased locomotor performance (Crowley, 1985) which would be helpful in evading predators.

Many snake species seem heat after feeding particularly if they maintain low, fasting T\textsubscript{A}s (Touzeau and Sievert, 1993). Hailey and Davies (1987b) noted that basking *N. maura* were more likely to have food in their stomachs than non-basking snakes. One of us (P. Andreidis, unpub. data) has observed that *N. sipedon* perching on vegetation at night typically has conspicuous bulges from food in the stomach. Juvenile *Thamnophis sirtalis sirtalis* fed meals equal to 1/3 their mass increased use of a hot shelter after feeding (Gibson et al., 1989). In contrast to juveniles, adult *T. s. sirtalis* in a thermal gradient did not display thermophily after feeding, but in the same study *T. s. parietalis* did show postigestive elevation in T\textsubscript{A} (Lyserenko and Gillis, 1988). Lyserenko and Gillis attributed the difference to differences in the habitat of these two subspecies. The more northerly *T. s. parietalis* had a great deal to gain by being able to digest meals rapidly whereas in the more southerly *T. s. sirtalis* the exposure from basking combined with the cost of locomotor speed which occurs after feeding put the animal at a greater risk of predation.

Postigestive thermophily is not consistently found within the genera of *Nerodia* or *Thamnophis*. Adult *N. sipedon* elevated T\textsubscript{A} after being fed either fish or transmitters (Lutterschmidt and Reinert, 1990). In contrast, *N. tissipilota* (Goodman, 1971) and *N. rhombifer* lacked postigestive thermophily (Tu and Hutchison, 1995). *Nerodia sipedon* has a much more northerly distribution than either *N. tissipilota* or *N. rhombifer* and may have stronger pressures to digest rapidly than the
more southerly distributed congenericapters. *Nerodia taxispilota* and *N. rhombifer* are sister taxa and *N. sipedon* is part of a different species group (Lawson, 1987). Elevation of T_b after feeding is found in both small and large snakes, snakes that have eaten small meals as well as snakes that have eaten large meals, and in both frequent and infrequently feeding species (Touzeau and Sievert, 1993) even though it is not a universal feature of snake thermal ecology (Lillywhite, 1987).

References


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