RESEARCH ARTICLE

Dehydrated snakes reduce postprandial thermophily

Jill L. Azzolini*, Travis B. Roderick and Dale F. DeNardo

ABSTRACT

Transient thermophily in ectothermic animals is a common response during substantial physiological events. For example, ectotherms often elevate body temperature after ingesting a meal. In particular, the increase in metabolism during the postprandial response of pythons – known as specific dynamic action – is supported by a concurrent increase in preferred temperature. The objective of this study was to determine whether hydration state influences digestion-related behavioral thermophily. Sixteen (8 male and 8 female) Children's pythons (*Antaresia childreni*) with surgically implanted temperature data loggers were housed individually and provided with a thermal gradient of 25–45°C. Body temperature was recorded hourly beginning 6 days prior to feeding and for 18 days post-feeding, thus covering pre-feeding, postprandial and post-absorptive stages. Each snake underwent this 24 day trial twice, once when hydrated and once when dehydrated. Our results revealed a significant interaction between temperature preference, digestive stage and hydration state. Under both hydrated and dehydrated conditions, snakes similarly increased their body temperature shortly after consuming a meal, but during the later days of the postprandial stage, snakes selected significantly lower (~1.5°C) body temperature when they were dehydrated compared with when they were hydrated. Our results demonstrate a significant effect of hydration state on postprandial thermophily, but the impact of this dehydration-induced temperature reduction on digestive physiology (e.g. passage time, energy assimilation) is unknown and warrants further study.

KEY WORDS: *Antaresia*, Digestion, Thermoregulation, Water balance, Pythons

INTRODUCTION

One of the most widely supported tenets of thermal biology is that at all levels of biological organization performances are influenced by temperature, and that performances are executed optimally at a specific temperature or narrow temperature range (optimal temperature, T_o; Brattstrom, 1965; Huey and Bennett, 1987; Block, 1994). Thus, there is an incentive for animals to regulate their body temperature (T_b) so that they can perform optimally in their environment and, in doing so, increase their likelihood of survival and reproduction (Huey and Hertz, 1984; Huey and Bennett, 1987). As the optimal temperature for different performances can differ, the target temperature often fluctuates based on current physiological demands (Brett, 1971; Claireaux et al., 1995; Blouin-Demers and Weatherhead, 2001). Optimal temperature for critical physiological processes can be higher than it is during standard metabolism when the organism is supporting

embryonic development (Wallman and Bennett, 2006; Lourdais et al., 2008; Lorioux et al., 2012) and digestion (Witters and Sievert, 2001; Wang et al., 2002; Tattersall et al., 2004; Wall and Shine, 2008; Raviv and Gefen, 2021) or lower when supporting sperm production (Cejko et al., 2016) and torpor (Gaertner et al., 1973; McAllan and Geiser, 2014).

While there are clear performance benefits of careful regulation at an optimal temperature, conflicts can influence the extent to which T_o and T_b are matched. Thermal heterogeneity and other environmental limitations are known to impact heat exchange and thus thermal optimization of a performance (Brett, 1971; Blouin-Demers and Weatherhead, 2001). Additionally, thermophilic behavior to accommodate physiological activities that have higher optimal temperatures may be impacted by limited capabilities or tradeoffs with other physiological needs (Stephens and Krebs, 1986; Secor and Diamond, 2000; Sunday et al., 2014). For example, given that T_b and evaporative water loss are highly correlated (Mautz, 1982; Guillon et al., 2014), reduced water availability may create a tradeoff between thermal optimization of physiological performance and limiting water loss. Despite the well-established relationship between water loss and T_b, most studies of ectotherm thermoregulation have not tested for the presence of synchronous thermo-hydroregulation processes (Rozen-Rechels et al., 2019). Accordingly, limited water availability may play a large role in an animal's dynamic thermophilic response to optimize a particular performance.

Digestion is a vital physiological process as it enables an organism to obtain energy and other important nutrients (Lignot et al., 2005; Ott and Secor, 2007; Cox et al., 2008). During digestion, ectothermic animals have an elevated metabolism (Secor and Diamond, 1998), which is referred to as 'specific dynamic action' (SDA; McCue, 2006; Fig. 1) and, concomitantly, there is often a postprandial elevation in T_b (Secor and Phillips, 1997). This postprandial elevation in T_b likely results from a combination of metabolic heat production associated with the increase in metabolism and altered behavioral thermoregulation (Witters and Sievert, 2001; Wang et al., 2002; Wall and Shine, 2008; Raviv and Gefen, 2021). As an animal will lose more water as T_b increases, postprandial thermophily may exaggerate the physiological conflict between energy balance and water balance, especially if water availability is limited. As the majority of terrestrial environments inhabited by organisms experience some degree of water limitation, at least at a seasonal scale (Hao et al., 2018), it is essential to understand the tradeoff between energy and water balance, and to what extent, if any, dehydration influences the thermal response to feeding. While there is evidence that some insectivores and herbivores gain a hydric benefit from eating (Cooper, 1985; Degen et al., 1997; Ostrowski et al., 2002), the opposite has been shown for binge-feeding reptiles. Despite the considerable water content of large whole-animal meals, consuming such meals does not benefit (Wright et al., 2013) and may even worsen (Murphy and DeNardo, 2019) dehydration in binge-feeding squamates. Consistent with this finding, snakes provided with ready access to water drink more after

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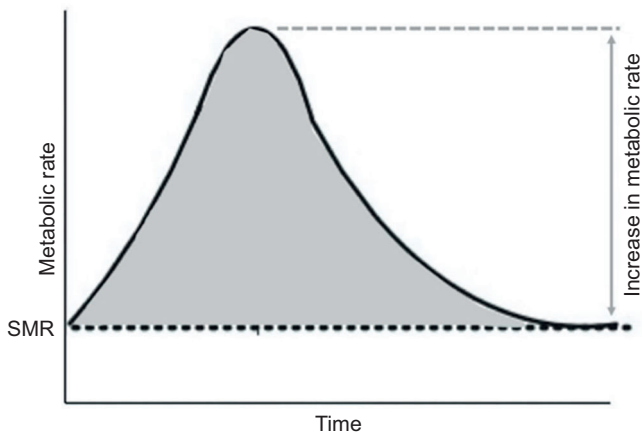
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Fig. 1. Visual representation of the rise in metabolic rate following meal ingestion in ectothermic animals. The total increase in metabolism over baseline (shaded area) is known as the specific dynamic action (SDA). Time zero is the time of meal consumption. The dashed line indicates standard metabolic rate (SMR). Modified from McCue (2006).

consuming a meal (Lillywhite, 2017), further indicating a potential hydric cost of digestion.

Children's pythons serve as an excellent study system for understanding the extent to which hydration state can influence thermophilic responses to optimize specific physiological performance. This species naturally experiences extended annual dry seasons that can lead to dehydration (Brusch et al., 2017), and thus faces the need to perform while in a dehydrated state. Additionally, Children's pythons are binge feeders that only intermittently consume relatively large meals, providing the opportunity to easily evaluate individuals under distinct postprandial and post-absorptive conditions.

This study addressed whether hydration state influences the dynamics of thermal adjustments made during digestion. We hypothesized that dehydration suppresses a thermophilic response during digestion. We predicted that T_b throughout digestion would mimic the shape of the SDA curve; that is, pythons would have the highest T_b during the first several days following a meal and then this would steadily decrease as digestion approaches completion. Furthermore, we predicted that throughout digestion, pythons would prefer higher temperatures when in a hydrated state compared with when they are dehydrated.

MATERIALS AND METHODS
Study organism
The Children's python, *Antaresia childreni* (Gray 1842), is a medium-sized (up to 1.2 m snout-to-vent length, SVL; 600 g mass) constrictor native to the wet–dry tropics of northern Australia (Wilson and Swan, 2003), where they experience natural annual fluctuations in water resource availability. Free-standing water can be locally absent for 3–4 months at a time, typically between May and August (Taylor and Tulloch, 1985). All Children's pythons used in this study were captive-bred individuals that have been maintained as part of a long-standing colony at Arizona State University. All experimental procedures were approved by the Arizona State University Institutional Animal Care and Use Committee (protocol 20-1740R).

Experimental design
The experiment was designed to examine the effect of dehydration on T_b when the snakes were post-absorptive (i.e. not digesting a

meal) and postprandial (i.e. during meal digestion). Sixteen adult Children's pythons (n=8 males; mean±s.e.m. mass 506±3 g, range 494–520 g; mean±s.e.m. SVL 95.9±1.5 mm, range 90.6–102.4 mm; n=8 females; 550±5 g, 531–571 g; 95.7±1.6 mm, 89.3–100.9 mm) were housed individually in semilucent plastic drawer cages that had tops made of expanded metal (30 cm×18 cm×10 cm D×W×H; Freedom Breeder, Turlock, CA, USA). Room temperature was set at 25±0.5°C and subsurface heating (Flexwatt, Flexwatt Corp., Wareham, MA, USA) was provided at the rear of each cage so that the cage had a 25–45°C thermal gradient. A piece of semi-rigid, highly absorbent paper (Techboard, Shepherd Specialty Papers, Watertown, TN, USA) covered the bottom of the cage so that the snake could choose to be exposed on the surface or secluded under the paper regardless of the temperature selected. The snakes were randomly distributed among six rows of a rack, three cages per row, with an additional row of cages above and below these six rows to ensure that, for consistency, all snakes had a cage row above and below them. Prior to the start of the experiment, all snakes were provided with water *ad libitum* but were not fed once placed on the experimental rack.

Snakes were given a week to acclimate to their cages, and then temperature loggers (Thermochron iButtons #DS 1922L, Maxim Integrated Products, San Jose, CA, USA) programmed to record temperature (±0.05°C) hourly and coated with Plasti-Dip (PDI Inc., Woodcliff Lake, NJ, USA) were implanted intracoelomically following the methods of Lourdais et al. (2008). While the snakes were under isoflurane anesthesia, a logger was secured to the body wall just caudal to the gall bladder using non-absorbable suture (Braunamid, B. Braun Medical, Melsungen, Germany) to ensure the logger remained stationary.

Snakes were given 2 weeks to recover from their surgeries before beginning the experimental trials. They were weighed using a platform scale and then assigned to two groups using mixed dispersion to ensure balance in size and sex between the groups. Snakes of each sex were ordered from heaviest to lightest and then alternatingly assigned to the two groups. That is, the heaviest male was assigned to group 1 (G1), the second and third heaviest to group 2 (G2), the fourth and fifth heaviest to G1, etc. This was repeated for females, so that there were 4 males and 4 females in each group. The two groups were differentiated by the order in which they would experience the two hydration states (i.e. G1 snakes experienced the hydrated condition first, whereas G2 snakes experienced the dehydrated condition first). Once assigned to their groups, each snake was randomly assigned to a location on the housing rack.

Dehydration was accomplished by withholding food and water for 30 days. This duration was chosen as it causes a moderate level of dehydration and would enable the ensuing 24 day feeding cycle to be completed in a total of 54 days without water, which approximates the duration of water deprivation for Children's pythons in a previous study (Dupoué et al., 2014). As G2 underwent the dehydrated conditions first, they were given 6 days of water access between ending the dehydrated cycle and beginning the hydrated cycle. Throughout the 54 day dehydration period, snakes were weighed weekly to ensure body mass did not drop more than 15%. During the hydrated cycle, water bowls were checked daily to ensure water was always available.

T_b assessment
Once all snakes had completed testing under both the hydrated and dehydrated conditions, the temperature loggers were removed following the anesthesia and surgery protocol described for the implantation surgery except that, once the coelomic cavity had been

entered, the anchoring suture was cut and the logger removed from the snake. The hourly temperature data were downloaded from the loggers and then parsed down to the relevant time frames described below. We compared the average T_b of multiple digestive stages during both hydrated and dehydrated states (Fig. 2). We assigned five stages of the feeding cycle for use in our analyses. 'Pre-feeding' data were defined as the average hourly T_b for the 6 days immediately preceding the day of feeding. 'Postprandial' data were collected for 12 days after the snake was fed a 30±1 g thawed mouse (5.9% body mass of male snakes, 5.5% body mass of female snakes). Our rationale for the allotted 12 days was that metabolism in pythons, as in many snakes, rises relatively rapidly after consumption of a meal and then tapers off more slowly over subsequent days, reaching pre-feeding levels approximately 12 days post-feeding (Ott and Secor, 2007). We divided the first 12 days post-meal consumption into three 4 day stages: postprandial days 1–4, postprandial days 5–8 and postprandial days 9–12. This separation of postprandial time points incorporated peak digestive effort (days 1–4 post-feeding), a time when metabolism can be tenfold more than pre-feeding levels (McCue, 2006; Fig. 1), as well as the gradual decline from peak effort to baseline. Following the completion of postprandial days 9–12, we collected 'post-absorptive' data, which consisted of the average hourly T_b collected on days 13–18 post-feeding. This 24 day cycle breakdown into five stages was then duplicated for the data collected when the snake was under the alternative hydration state (dehydrated for G1 and hydrated for G2).

Statistical analysis

We performed all statistical analyses using RStudio version 1.0.153. We chose a linear mixed effects model using the 'lme4' package as our data contained continuous covariates and possible non-linear relationships. We set our statistical significance at 0.05 for all models and *post hoc* analyses. We tested for an interaction between average temperature, feeding stage and hydration status. We included sex and body condition index (BCI; calculated as residuals of a body mass versus SVL regression) as fixed effects. We also included snake ID as a random effect. We tested for normality using the Shapiro–Wilk test ($P=0.56$) and assessed multicollinearity using variance inflation factors (all VIFs<2.5, 'car' package). We used estimated marginal means (aka least-squares means, 'emmeans' package) for *post hoc* testing of pairwise comparisons between digestive stage and hydration status.

To evaluate intra-individual thermoregulatory precision, we evaluated the standard error of the mean (s.e.m.) of each animal's T_b over the course of each feeding stage as a dependent variable. The model used for this analysis had the same fixed and random effects as the model used to analyze inter-individual temperature preference. Again, we tested for normality by using the Shapiro–Wilk test ($P=0.87$), tested multicollinearity using VIFs (all VIFs<2.5), and used estimated marginal means for *post hoc* testing comparisons.

RESULTS

Body mass

Throughout the dehydration process, G2 snakes lost 63±9 g (range 23–103 g), or 13% body mass, while G1 snakes lost an average of 58±5 g (range 43–72 g), or 11% body mass. Upon being given water at the end of the dehydration cycle, G2 snakes returned to within 30±11 g (range 4–56 g; 94%) and G1 snakes returned to within 36±2 g (range 29–44 g; 93%) of their pre-water deprivation mass within 24 h of being provided with water but no food. This supports previous work indicating that the vast majority of mass lost during water deprivation in snakes is due to water loss (Dupoué et al., 2015). Following the completion of the hydrated feeding cycle, G1 snakes were at 98% (12±6 g, range −9–30 g) and G2 snakes within 99% of their initial body mass (7±4 g, range −29–5 g).

T_b within a given hydration state

All 16 snakes completed the hydrated feeding cycle. We found that hydrated snakes had significantly elevated T_b during postprandial days 1–4 compared with pre-feeding T_b ($P=0.0072$; Fig. 2), as expected given the increased metabolic demands of digestion. T_b during postprandial days 5–8 was intermediate in that it was not significantly different from that of any of the other stages (all $P>0.10$). The average T_b during postprandial days 1–4 was marginally higher than that during postprandial days 9–12 ($P=0.074$) and significantly higher than in the post-absorptive stage ($P=0.013$). Average T_b during postprandial days 9–12 and the post-absorptive average T_b were not significantly different from pre-feeding T_b ($P=0.99$, $P=1.000$).
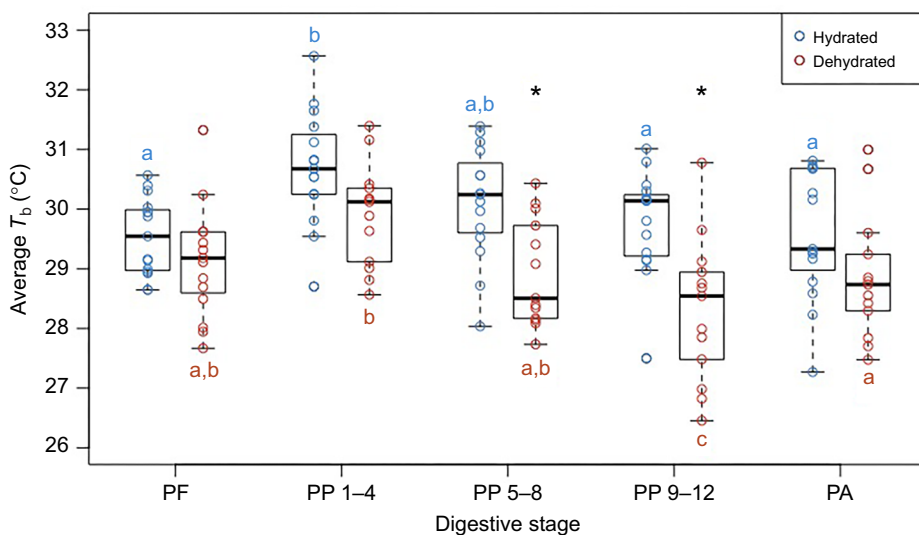

Fig. 2. Average T_b of all pythons in the two hydration states during the various feeding stages. Data are for snakes in the hydrated (*n*=16, blue data points) and dehydrated (*n*=13, orange data points) condition. The bold line inside each box represents the mean; the top and bottom of each box represent the 75th and 25th quartiles, respectively; whiskers denote the s.e.m. The blue letters reflect significant differences among the hydrated measurements, while the orange letters show significant differences among the dehydrated measurements. Asterisks denote significant differences between hydrated and dehydrated animals at a given feeding stage. PF, pre-feeding; PP, postprandial days 1–4, 5–8, 9–12; PA, post-absorptive.

Only 13 snakes completed the dehydrated feeding cycle. One snake died shortly after the end of the hydrated conditions phase. The cause of death was unknown; however, it did not appear to be linked to the assigned treatment as the snake had only been without water for 8 days. We also had two snakes that refused to eat during their dehydrated feeding cycle. All three snakes were in G1, the group that experienced the hydrated feeding cycle before the dehydrated feeding cycle.

Postprandial thermal dynamics during dehydration were similar to those when hydrated (Fig. 2). Dehydrated snakes chose significantly warmer T_b during postprandial days 1–4 than they did during postprandial days 9–12 ($P<0.0001$) and post-absorptive ($P=0.047$) stages (Fig. 2). T_b on postprandial days 1–4 was not significantly different from that on postprandial days 5–8 ($P=0.086$), and post-absorptive T_b was not significantly different from pre-feeding T_b ($P=0.99$). Unlike when they were hydrated, the average pre-feeding T_b when the snakes were dehydrated was not significantly different from T_b during postprandial days 1–4 ($P=0.23$).

T_b between hydration states

There was a significant effect of both hydration status ($P<0.0001$) and digestive stage ($P<0.0001$) on T_b. The average T_b during the last postprandial segments (days 5–8 and 9–12) was lower when snakes were dehydrated compared with when they were hydrated ($−1.1°C$, $P=0.027$ and $−1.5°C$, $P=0.0006$, respectively; Fig. 2). Thus, snakes reduced their postprandial T_b more quickly when dehydrated.

There was also a significant effect of digestive stage ($P=0.0029$) and hydration ($P=0.0099$) on the precision of intra-individual T_b over time. That is, T_b showed significantly less within-individual variation during the dehydrated pre-feeding measurements than during the dehydrated postprandial days 5–8 ($P=0.042$) and at every stage during the hydrated postprandial period (days 1–4, $P=0.0009$; days 5–8, $P=0.0029$; days 9–12, $P=0.017$).

T_b between sexes

We found a significant effect of sex ($P=0.018$) on T_b that persisted regardless of hydration state. In all stages other than postprandial days 1–4 and whether hydrated or dehydrated, males were, on average, 0.63°C warmer than females (Fig. 3).

DISCUSSION

In both hydrated and dehydrated conditions, python T_b peaked during postprandial days 1–4, supporting our prediction that pythons would choose the highest T_b during the first 96 h following a meal regardless of hydration state (Fig. 2). Our results complement existing research regarding behavioral thermophily during digestion in ectotherms. This phenomenon has been documented in a variety of different snake species, including rat snakes (*Elaphe obsoleta obsoleta*), carpet pythons (*Morelia spilota*), common water snakes (*Nerodia sipedon*) and common garter snakes (*Thamnophis sirtalis*) (Blouin-Demers and Weatherhead, 2001). In another carnivorous, binge-feeding ectotherm, the Gila monster (*Heloderma suspectum*), postprandial thermophily was positively correlated with meal size (Gienger et al., 2013). Gila monsters not only had higher T_b as their meal size increased but also they maintained higher T_b for up to twice as long when given a meal that was 20% of their body mass versus a meal that was only 5% of their body mass (Gienger et al., 2013). These meal size effects are consistent with meal size effects on SDA, providing complementary evidence that SDA and post-prandial thermal dynamics are synchronized. Furthermore, as larger meals lead to increased SDA and thermophilic responses, further studies should investigate whether dehydration induces an even greater suppression during digestion of larger meals.

Beyond squamates, there is substantial diversity in species that become thermophilic during digestion. For example, sculpin (*Cottus extensus*: Wurtsbaugh and Neverman, 1988) migrate to warmer water after feeding, and Woodhouse's toads (*Bufo woodhousii*) increase T_b following meals whereas fasted toads do not change T_b over time (Witters and Sievert, 2001). Postprandial thermophily has also been documented in invertebrates such as leeches (*Hirudo verbena*: Petersen et al., 2011) and scorpions (*Hottentotta judaicus*: Raviv and Gefen, 2021).

As predicted, after peaking there followed a progressive decrease in T_b through postprandial days 5–8 and 9–12 (Fig. 2). The trend in our temperature data mimics the metabolic curve seen in a typical SDA response (Fig. 1), where the peak metabolic rate is reached within 4 days of meal consumption. Following this peak, the metabolic rate slowly returns to the baseline rate (Secor and Diamond, 1998). In one study that compared metabolic rates between eight species of snakes, some of which naturally are frequent feeders and others, like Children's
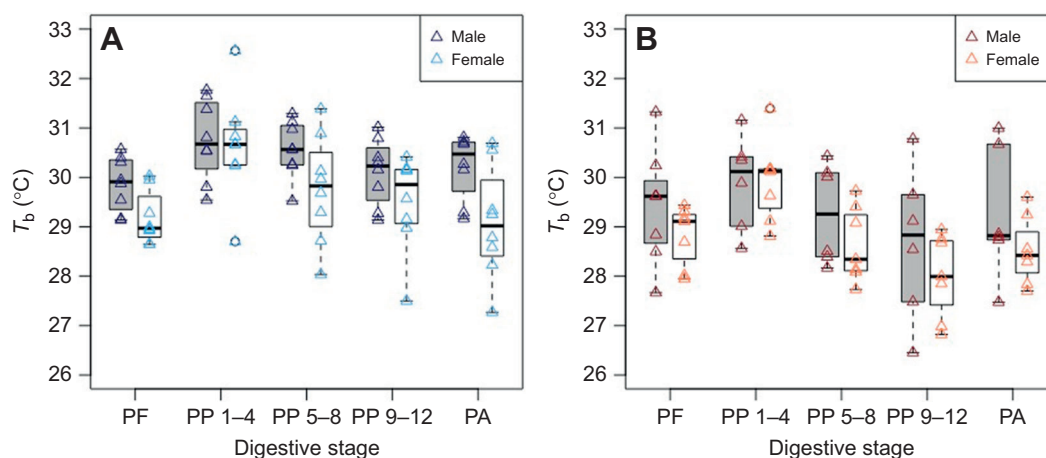
Fig. 3. T_b differences between the sexes for pythons in the two hydration states during the various feeding stages. (A) Hydrated ($n=8$ males, $n=8$ females) and (B) dehydrated ($n=6$ males, $n=7$ females) snakes. The bold line within each box represents the mean; the top and bottom of each box represent the 75th and 25th quartiles, respectively; whiskers denote the s.e.m. Gray boxes show the cumulative data for males, whereas white boxes show the cumulative data for females, at each digestive stage and hydration state. The triangles aligned with the gray and white boxes represent individual animals (blue when hydrated, brown when dehydrated).

pythons, are infrequent feeders, all snakes reached their peak metabolic rate within 4 days of meal consumption (Secor and Diamond, 2000). The similar shapes of the T_b response curve in our study and the classic SDA curves are likely related, at least in part, to endogenous heat production associated with digestive activity. While thermogenesis during digestion has not been documented in Children's pythons, increased metabolic heat production during digestion in the South American rattlesnake, Crotalus durissus, increased T_b by 1.2°C (Tattersall et al., 2004). While increased metabolism likely accounts for some increase in T_b, behavioral thermophily likely provides a significant contribution to increased T_b during digestion. For example, wild rattlesnakes (Crotalus atrox, Crotalus molossus and Crotalus tigris) fitted with intracoelomic temperature-sensing radio transmitters were observed retreating into a shelter immediately following meal consumption, but within 24–72 h most snakes were found fully basking (Beck, 1996). The few snakes in this study that were not basking had adjusted their position within their shelter so that they were partially exposed to sunlight. Basking snakes had an average T_b of 31°C, whereas the unfed snakes' average T_b was only 25°C. Unlike physiological processes related to locomotion, which can have a broad range of optimal temperatures, the T_o for energy assimilation tends to require more precise thermoregulation (Angilletta, 2001). In frequently feeding ectotherms such as eastern fence lizards (Sceloporus undulatus), the preferred T_b of ~33°C is very close to the T_o for digestive efficiency (Angilletta, 2001). Further, lizards captured from locations in Utah, South Carolina and New Jersey, USA, were found to have similar T_b despite the differing climates, indicating that the lizards must behaviorally thermoregulate in order to maintain the preferred temperature. Both endogenous heat production related to metabolic activity and behavioral thermophily likely contribute to increased postprandial T_b in ectotherms, but the relative importance of metabolic heat production in binge-feeding ectotherms warrants further investigation.

Our final prediction that throughout digestion, pythons would prefer higher temperatures when in a hydrated state compared with when they are dehydrated was mostly supported. When dehydrated, snakes were significantly cooler during postprandial days 5–8 and 9–12 (Fig. 2). It is notable that T_b was not significantly different between hydration states during postprandial days 1–4, when T_b was highest. Although our findings were statistically significant, the physiological significance of a 1.5°C reduction in T_b requires further investigation. Pythons have approximately 96% digestive efficiency at a range of temperatures from 24 to 33°C (Bedford and Christian, 2000), so a 1.5°C temperature reduction may seem insignificant from a functional standpoint. However, elevations in T_b require an investment of energy (e.g. for endothermy) and a commitment of time (e.g. for basking), and/or are associated with additional predation risks (e.g. during basking efforts), so thermophily, even at a finer scale, must convey benefits. Irrespective of the thermal sensitivity of energy assimilation, lower T_b may extend gastrointestinal passage time (Angilletta, 2001; Raviv and Gefen, 2021). Digestion is a vulnerable state for many vertebrate species (Claireaux et al., 1995; Wang et al., 2001), so even a slightly prolonged digestive process could make wild animals more at risk of predation. Additionally, longer passage time may force longer durations between meals and, for ectothermic animals living in seasonal climates, the ability to consume frequent meals in a limited time window is especially crucial (Secor and Phillips, 1997), and more frequent meals have been shown to improve body condition and reproductive success (Tattersall et al., 2004; Taylor et al., 2005).

Previous work on other vital physiological processes, such as reproduction, have shown an extremely sensitive relationship with T_b. In one study where river lamprey were maintained at 14, 10 and

7°C, females held at 14°C were first to release their eggs (Cejko et al., 2016). Even within Children's pythons, a comparative review of existing data reveals a highly sensitive relationship between T_b and gravidity duration. At the pythons' preferred T_b during reproduction (31.3°C), they had an average gravidity duration of 23.1 days (Lourdais et al., 2008). In contrast, Lorioux et al. (2012) maintained reproductive pythons at a slightly higher constant temperature of 31.5°C and found the average gravidity duration to be slightly shorter at 22.5 days. Lastly, we (J.L.A. and D.F.D., unpublished data) held reproductive pythons at a constant temperature of 31.0°C and found a slightly longer gravidity duration of 24.8 days. Together, these results demonstrate that a difference of only 0.5°C in T_b results in a 2 day difference in gravidity duration in this species. Based on this knowledge, the physiological significance of the 1.5°C reduction in T_b during digestion caused by dehydration warrants investigation.

Surprisingly, we found a significant effect of sex on T_b during most digestive states, where males were consistently warmer than females. Whether hydrated or dehydrated, males were, on average, 0.63°C warmer than females at all stages except postprandial days 1–4 (Fig. 3). As reported above, we similarly did not find a significant effect of hydration state on T_b during postprandial days 1–4. Given that postprandial days 1–4 are the time of peak metabolic activity during digestion, it may be critical for pythons to maintain peak T_b during this time regardless of hydration state or sex. While we did not anticipate a sex-based difference, there is pre-existing evidence that sex can affect T_b and digestive physiology. Male and pregnant female Atlantic stingrays (Dasyatis sabina) chose significantly warmer temperatures than did non-pregnant females (Wallman and Bennett, 2006). In Children's pythons, the assimilation efficiency of some nutrients significantly differed between sexes (Stahlschmidt et al., 2011). The authors attributed this to differences in body composition, where females store more energy in the form of fat whereas males prioritize skeletal muscle mass (Stahlschmidt et al., 2011). Perhaps the temperature preference during digestion influences specific nutrient absorption and disposition; however, that is beyond the scope of our study.

Both water balance and digestion are vital performances, and our study demonstrates a likely tradeoff between the two in terms of selected T_b during digestion. Energy and water balance may tradeoff in additional ways. Interestingly, the only two instances where a snake refused a meal were when the individual was dehydrated. Digestion in snakes requires greater water intake (Lillywhite, 2017) and for water-deprived western diamond-back rattlesnakes (C. atrox), consuming a meal worsens their dehydration (Murphy and DeNardo, 2019). Therefore, food refusal by two water-deprived pythons in our study may reflect the tradeoff between energy and water balance in that the opportunity to obtain energy resources was bypassed to avoid exacerbating the current water imbalance. Lastly, it is important to note that our presentation of the thermal gradient provided a predictive daily thermal landscape. It is unknown how animals would respond in an environment that presents higher levels of complexity (Wall and Shine, 2008; Burggren, 2019; Nancollas and Todgham, 2022). Future studies could incorporate added factors for individuals to consider when choosing postprandial T_b, such as proximity of water resources, vulnerability at heat sources and frequency of availability of potential prey.

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