

Sexual variation in assimilation efficiency: its link to phenotype and potential role in sexual dimorphism

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Abstract Sex-specific variation in morphology (sexual dimorphism) is a prevalent phenomenon among animals, and both dietary intake and resource allocation strategies influence sexually dimorphic traits (e.g., body size or composition). However, we investigated whether assimilation efficiency (AE), an intermediate step between dietary intake and allocation, can also vary between the sexes. Specifically, we tested whether sex-based differences in AE can explain variation in phenotypic traits. We measured morphometric characteristics (i.e., body length, mass, condition, and musculature) and AE of total energy, crude protein, and crude fat in post-reproductive adult Children's pythons (which exhibit a limited female-biased sexual size dimorphism) fed both low and high dietary intakes. Meal size was negatively related to AE of energy. Notably, male snakes absorbed crude protein more efficiently and increased epaxial (dorsal) musculature faster than females, which demonstrates a link between AE and phenotype. However, females grew in body length faster but did not absorb any nutrient more efficiently than males. Although our results do not provide a direct link between AE and sexual size dimorphism, they demonstrate that sexual variation in nutrient absorption exists and can contribute to other types of sex-based differences in phenotype (i.e., sexual dimorphism in growth of musculature). Hence, testing the broader applicability of AE's role in sexually dimorphic traits among other species is warranted.

Keywords Dietary intake · Digestive efficiency · Growth rate · Python · Resource allocation · Snake

Introduction

Sexual variation in morphology (sexual dimorphism) is widespread among animals and the evolutionary interpretation of this phenomenon has long attracted scientific attention (e.g., Darwin 1871; Cox and Calsbeek 2010). Sexual size dimorphism (SSD) is particularly prevalent, and it may ultimately be explained by sexual selection for large male size to improve intra-sexual combat success (male-biased SSD) or natural selection for large female size to increase reproductive capacity (female-biased SSD) (reviewed in Fairbairn et al. 2007). However, other aspects of body plan may also vary between the sexes. For example, males have greater muscle mass than females in many species (e.g., fish: Casselman and Schulte-Hostedde 2004; snakes: Bonnet et al. 1998; rodents: Schulte-Hostedde et al. 2001; humans: Wells 2007). Although sexual dimorphism may be the result of underlying genetic differences between the sexes (reviewed in Fairbairn et al. 2007), a variety of proximate mechanisms including growth characteristics and timing of maturity can influence sexually dimorphic traits (reviewed in Shine 1990).

Recently, investigation into the role of resource dynamics in SSD has garnered considerable attention (e.g., Bonduriansky 2007; Cox et al. 2008). Specifically, researchers have posited that SSD is influenced by two sources of variation. First, dietary intake strongly influences SSD dynamics (Taylor and DeNardo 2005; Cox et al. 2006, 2008; Bonduriansky 2007). In fact, SSD can be eliminated in some species when individuals are raised in

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captivity with ample food availability (Taylor and DeNardo 2005; Cox et al. 2006; but see Cox et al. 2008). Second, sexual variation in resource allocation strategy may contribute to SSD. Individuals use resource allocation strategies to navigate tradeoffs between competing life-history traits (e.g., growth and storage) given finite available nutrients (Glazier 1999; Boggs 2009). Even when both sexes have equivalent dietary intakes, sex-specific allocation strategies can result in sexual variation in body size, mass, or musculature. For example, male-biased SSD could result from males preferentially investing absorbed resources into lean body mass (e.g., muscular and skeletal growth) to put them at a combative advantage, whereas female-biased SSD may be due to size-dependent fecundity in females.

Assimilation efficiency (AE; the efficiency by which animals absorb ingested nutrients) rests at the interface between dietary intake and allocation. AE typically refers to the absorption efficiency of energy, in general, and is influenced by dietary intake (Brown and Downs 2003; Maxwell et al. 2009). Yet, adequate AE of specific macronutrients (e.g., protein) is necessary for maintenance and growth. Further, AE of certain macronutrients may co-evolve with other aspects of life history. For example, in the snowy plover (*Charadrius alexandrinus*), relatively high-protein AE may have co-evolved with a specialized high-protein dietary intake of polychaete worms (Castro et al. 2008). Similarly, a co-evolution of allocation strategy and AE of energy, crude protein, crude fat or some combination thereof may play a proximate role in sexual dimorphism. However, such relationships between allocation strategy and AE have not been examined to our knowledge.

We used the Children's python (*Antaresia childreni*) as a model to address several hypotheses related to resource dynamics. First, we hypothesize that dietary intake affects AE of total energy, crude fat, and crude protein. Specifically, we predict snakes to generally assimilate less efficiently on a high dietary intake (two mice once every week for 2 weeks) relative to a low dietary intake (one mouse every week for 4 weeks). Second, we hypothesize sexual variation in nutrient absorption and phenotypic growth exists. Due to female-biased SSD theory (i.e., larger size confers greater reproductive capacity), we predict female *A. childreni* increase body length faster than males and exhibit higher AE for total energy, crude fat, or both. Third, we hypothesize a link between sexual variation in AE and sexual variation in phenotype. For example, we predict males exhibit higher AE of crude protein which corresponds with increased musculature growth because *A. childreni* exhibit male–male agonistic behaviors (Z.R.S. and D.F.D. unpublished) and other male snakes exhibit greater muscle mass than their female counterparts (e.g.,

Bonnet et al. 1998). Together our results will shed light on the interactive roles of dietary intake and AE on phenotype, which may provide new insight into the underlying mechanisms of sexual dimorphism.

Materials and methods

Subjects

We used a colony of *A. childreni* maintained at Arizona State University, Tempe, AZ, USA. *Antaresia childreni* is a medium-sized (≤ 1.2 m snout-to-vent length and 650 g body mass), non-venomous, constricting pythonid snake from northern Australia (Wilson and Swan 2003). Like other pythons (e.g., Shine et al. 1998; Aubret et al. 2005), *A. childreni* exhibits female-biased SSD in which females are typically longer and heavier-bodied than males (Z.R.S. and D.F.D. unpublished). Reproduction in this species entails an extended period of negative energy balance because little to no food intake for several months is coupled with considerable energy investment into courting behavior by males or egg production by females (Z.R.S. et al. unpublished). Because the post-reproductive period is a critical period for energy replenishment, we used immediately post-reproductive individuals to assess sexual differences in AE and resource allocation.

During the study, we housed all snakes individually at $25 \pm 2^\circ\text{C}$ in $91 \times 71 \times 46$ cm cages (Freedom Breeder, Turlock, CA, USA) with continuous access to supplemental heat via sub-surface heating elements under one side of each cage (Flexwatt, Flexwatt Corp., West Wareham, MA, USA). We maintained a 12 h photoperiod and provided all animals with water ad libitum throughout the study. All procedures abided by Arizona State University's Institutional Animal Care and Use Committee protocol #08-967R.

Experimental design

At 0, 4, 8, 12, and 16 weeks into the study, we measured several relevant morphological characteristics of 8 male and 15 female *A. childreni*. We determined snout-to-vent length (SVL, ± 0.5 cm) and body mass (± 0.1 g). We created a regression line between SVL and body mass from the best fit of pooled data from week 0. We then compared this line to subsequent measurements of SVL and body mass to create residuals, which we used to determine body condition for weeks 4, 8, 12, and 16. We also measured the mean width of epaxial (dorsal) muscles (± 0.01 mm) which is strongly associated with contraction strength in *A. childreni* and other snakes (Lourdais et al. 2005, unpublished). Briefly, we used digital calipers (± 0.0005 mm, FB-2400; Frei and Borel, Oakland, CA, USA) to repeatedly measure epaxial muscle

width (3–5 times) at three locations along each snake (i.e., 25, 50, and 75% of SVL). We averaged the measurements of each location and determined mean epaxial muscle width for each snake to be the grand mean of these three values.

We fed all snakes one mouse weekly for the first 4 weeks of the study and then fasted snakes for 2 weeks to allow complete digestive clearing, which takes 7–14 days in other pythons (Secor 2003). Next, we randomly assigned each snake to a low (one mouse once per week for 4 weeks) or high (two mice once per week for 2 weeks) dietary intake treatment. We collected all feces from the cages during dietary intake treatments and throughout a subsequent 2-week fasting period. After this second fasting period, we switched animals in the low dietary intake treatment to the high dietary intake treatment (and vice versa) before collecting feces as before. Prior to nutrient analyses, we stored fecal samples at -20°C in individual plastic bags.

Analyses of nutrient content and assimilation efficiency

We analyzed the nutrient content (i.e., kilocalories, crude protein, and crude fat) of fecal samples and 30 mice. First, we dried fecal samples and mice to a constant mass at 95°C in a vacuum oven and then ground samples to a fineness of 0.75–1.0 mm. We then determined caloric content of a 2 g subsample of each sample using an Adiabatic bomb calorimeter following the American National Standards Institute/American Society for Testing and Materials method D2015-77. We also determined crude fat content using the Randall modification of the standard Soxhlet extraction (following Association of Analytical Communities (AOAC) method 920.39c). Briefly, we extracted the dried and ground test portion by a 2-step process. First, we placed the test portion in a cellulose thimble and immersed this into boiling hexanes (Fisher Scientific, H291-20) to ensure rapid solubilization of extractables. Then, we raised the thimble above the solvent and the test portion was further extracted by continuously evaporating and condensing the solvent across the samples. We determined the resulting crude fat residue gravimetrically after drying. Using a 2 g sample, the lowest confidence level of this method was 0.1% fat. We also determined protein content by converting protein in the sample to ammonium sulfate by digesting the sample with sulfuric acid containing a potassium sulfate/titanium dioxide/cupric sulfate catalyst mixture. We made the acid digest alkaline before distilling and titrating the ammonia with

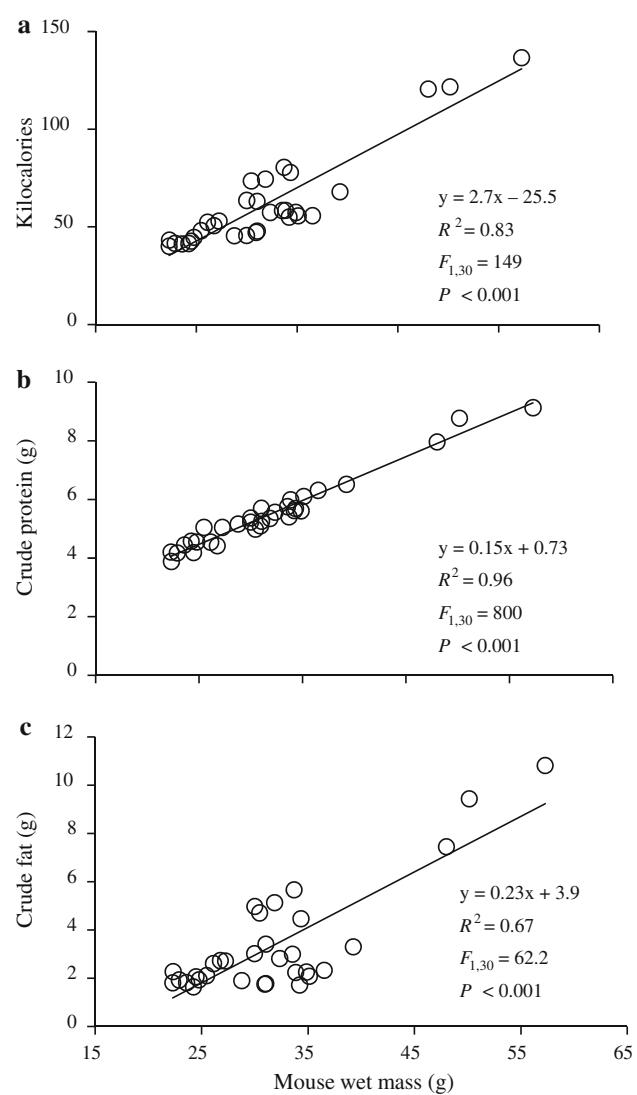


Fig. 1 The linear relationships between mouse wet mass and nutrient content ($n = 30$) were used to predict the (a) energy, (b) crude protein, and (c) crude fat content of each mouse fed to snakes in the study

standard acid. Then, we determined percent nitrogen and converted to crude protein using the factor 6.25 (AOAC method 990.03). Using a 1 g sample, the lowest confidence level of this method was 0.1% protein (0.02% nitrogen).

We created regression lines between mouse wet mass (g) and each nutrient (kcal or g) to predict the nutrient composition of each mouse fed to a snake (Fig. 1). We then determined AE of each nutrient using the following equation:

$$AE (\%) = 100 \times \frac{\text{Predicted ingested nutrient(kcal or g)} - \text{Defecated nutrient(kcal or g)}}{\text{Predicted ingested nutrient(kcal or g)}}$$

Statistical analyses

We transformed data that failed to meet the assumptions of parametric tests as necessary, and we analyzed the data using SPSS version 13 (SPSS Inc. 2004, Chicago, IL, USA). We tested for the effects of time and sex on morphometric growth using repeated-measures analyses of variance with time as the within-individual effect, sex as the between-individual effect, and time \times sex as an interaction. In analyses with significant sphericity, we used χ^2 tests with epsilon adjusted Greenhouse–Geisser tests. To test for the effects of sex and dietary intake on each nutrient's AE, we used analyses of covariance (ANCOVA) with sex and dietary intake as main effects, individual snake identification (ID) number as a random effect, sex \times dietary intake as an interaction, and age, week 8 mass, and week 8 SVL as covariates. For all ANCOVA tests, we initially ran the complete model (i.e., all effects, interactions, and covariates) and parsimoniously removed variables of $\alpha > 0.10$. We then re-analyzed our data using the remaining variables to create the most robust model possible, which we report. We determined significance at $\alpha < 0.05$ and display all values as mean \pm 1 SEM.

Results

Relative to males, females were significantly longer (females 98.4 ± 1.5 cm, males 92.9 ± 1.3 cm, $t_{21} = 2.1$, $P = 0.044$) at the onset of the study. Due to females' larger investment of body reserves during reproduction, there were no initial sex differences in body mass (females 353.1 ± 16.1 g, males 342.6 ± 25.5 g, $t_{21} = 0.36$, $P = 0.72$) or mean epaxial muscle width (females 7.12 ± 0.17 mm, males 7.37 ± 0.18 mm, $t_{21} = 0.94$, $P = 0.36$). Also, there were no differences in age between females (7.0 ± 0.9 years) and males (7.6 ± 1.5 years, $t_{21} = 0.36$, $P = 0.72$).

Over the course of the study, both sexes consumed similar numbers of mice (females 11.9 ± 0.1 , males 11.5 ± 0.3 , $t_{21} = 1.6$, $P = 0.12$), kilocalories (females 531.5 ± 15.9 , males 497.5 ± 26.5 , $t_{21} = 1.2$, $P = 0.26$), crude protein (females 56.6 ± 0.8 g, males 54.0 ± 1.6 g, $t_{21} = 1.7$, $P = 0.11$), and crude fat (females 24.0 ± 0.8 g, males 22.2 ± 1.4 g, $t_{21} = 1.2$, $P = 0.12$). Snakes exhibited increased body mass, SVL, body condition, and mean epaxial muscle width over the course of the study (Fig. 2; Table 1). During the study, females exhibited greater SVL growth rates while males increased mean epaxial muscle width at a greater rate than females (Fig. 2; Table 1).

Both sex and dietary intake independently affected some aspects of AE, but no significant sex \times dietary intake interactions existed (Fig. 2e–g). Snakes digested energy more efficiently during the low dietary intake treatment

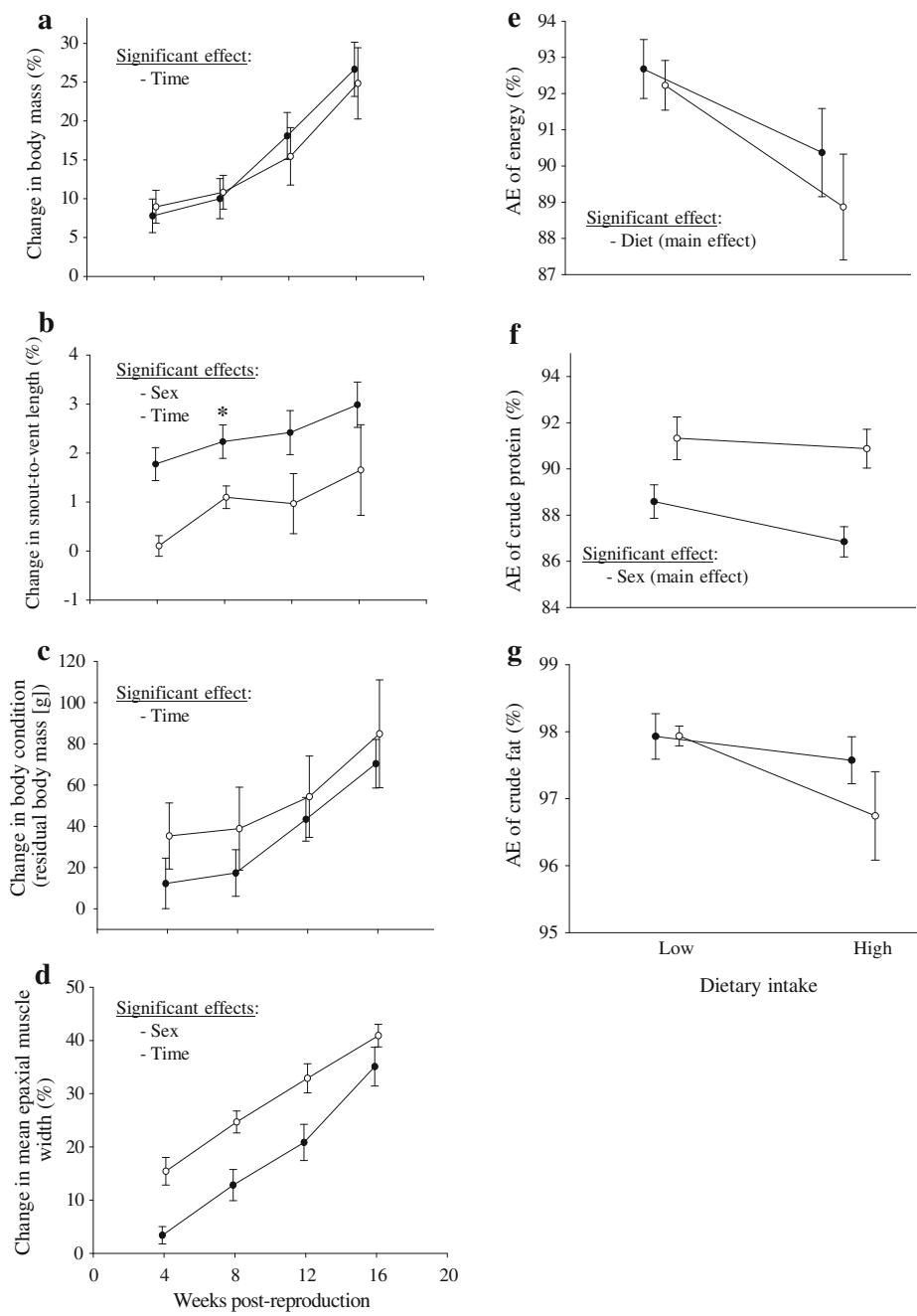
(Fig. 2e) because dietary intake significantly affected AE of energy ($F_{1,46} = 5.9$, $P = 0.019$). Also, females were less efficient at digesting crude protein than males (Fig. 2f) because sex significantly affected AE of crude protein ($F_{1,46} = 16.9$, $P < 0.001$). Body size, body mass, and age did not significantly covary with any nutrient's AE.

Discussion

In partial support of our first hypothesis, dietary intake was negatively related to AE of total energy in *A. childreni* (Fig. 2). Adults of other vertebrate taxa similarly demonstrate shifts in digestive performance due to increased dietary intake [e.g., decreasing AE of fat in seals (Trumble et al. 2003) or increasing digestive clearing duration in sunbirds (Markman et al. 2006)]. In accordance with our results, sex-specific variation in AE of total energy does not exist in other systems of female-biased SSD (e.g., Markman et al. 2006; Santiago-Quesada et al. 2009). However, these researchers corrected for body size whereas we found no main or interactive effects of body size or mass on any nutrient's AE. In contrast to our results (Fig. 2f), birds exhibiting female-biased SSD demonstrated no sexual differences in AE of protein (Castro et al. 2008). Conflicting results may be due to differences in phylogeny, sex-specific selection, and/or nutritional ecology.

Our morphometric and AE results support our second hypothesis and affirm there can be sexual variation in both nutrient absorption and phenotypic growth (Fig. 2). From an ultimate viewpoint, the higher growth rate by females may be explained by natural selection on females' allocation to body length to increase reproductive capacity as fecundity in this species is size dependent (Fig. 2b). Further, our results indicating sex-specific variation in epaxial muscle growth is an example of sexual dimorphism in body composition (Fig. 2d). Such dimorphisms are common among other taxa and this prevalence may be due to sex-specific reproductive requirements. Although females generally require larger energy reserves (i.e., fat) for yolk production, males often require greater skeletal muscle mass for male–male combat or mate searching (e.g., snakes: Bonnet et al. 1998; rodents: Schulte-Hostedde et al. 2001; fish: Casselman and Schulte-Hostedde 2004; humans: Wells 2007). Notably, sexual variation in muscle mass can be associated with sex-specific differences in performance and/or habitat preference. For example, male sea kraits (*Laticauda* spp.) are heavier-bodied, stronger, and more terrestrial than their female counterparts (Bonnet et al. 2005), which lends support for the idea that sexual variation in epaxial muscle growth in *A. childreni* is due to sexual selection on increased muscular performance in males.

Fig. 2 Phenotypic characteristics of adult female (closed circle) and male (open circle) Children's pythons (*Antaresia childreni*) in the 16 weeks following reproduction. Snakes' (a) body mass, (b) snout-to-vent length, (c) body condition, and (d) mean epaxial muscle width relative to initial (i.e., immediately post-reproductive) measurements for these traits. Complete statistical results can be found in Table 1. Snakes' assimilation efficiencies (AE) of (e) energy, (f) crude protein, and (g) crude fat during low and high dietary intake treatments (see “Methods”)



Our third hypothesis was also supported as we found a link between AE and phenotype because males digested crude protein more efficiently and increased epaxial musculature faster. Testosterone can influence the amount and type of muscle deposition (e.g., Lyons et al. 1986), and it has been implicated as a mechanism underlying variation in body size in male-biased SSD systems (Cox and John-Alder 2005; but see Taylor and DeNardo 2005). Yet, the specific role of testosterone on AE of crude protein is unclear and warrants future study.

We did not identify a direct link between AE and SSD; however, we offer several possible alternate explanations.

First, our results may be due to the degree of SSD in our study species. *Antaresia childreni* exhibits a limited SSD (i.e., females are ~6% longer than males), and other systems with more significant SSD may yield further insight. Next, our results may have been influenced by the constraints of our methods determining AE. Notably, our only significant AE result due to sex involved the nutrient we had the most confidence in predicting the ingested content of (i.e., crude protein: Fig. 1). SSD systems in which animals ingest a more consistent diet (e.g., extruded rodent diet) may clarify this potential confound. Also, sexual variation in metabolism due to variation in resting

Table 1 Variables significantly affecting changes in post-reproductive Children's python (*Antaresia childreni*) body mass, snout-to-vent length (SVL), body condition, and mean epaxial muscle width over time through repeated-measures analyses of variance, where time was the within-individual effect, sex was the between-individual effect, and time \times sex was an interaction

	df	F	P
Change in body mass			
Time	2, 44	58	<0.001
Change in SVL			
Sex	1, 21	6.9	0.016
Time	2, 41	5.7	0.0060
Change in body condition			
Time	2, 49	56	<0.001
Change in mean epaxial muscle width			
Sex	1, 21	4.6	0.045
Time	2, 40	95	<0.001

In analyses with significant sphericity, χ^2 tests with epsilon adjusted Greenhouse-Geisser tests were used

metabolic rate or activity may explain AE variation because it occurs in other snakes (Crews et al. 1987; Peterson et al. 1998; but see Hailey and Davies 1986), but was not measured in our study. Last, variation in the rate of SVL change may be explained by the AE of other important compounds involved in growth [e.g., vitamins and minerals (calcium or phosphorus)] which we did not measure.

Further investigation into the dynamics of AE may elucidate mechanisms underlying sexual dimorphism of other traits and in other animal systems. We were able to discern sex-specific differences in nutrient absorption and phenotype by adults undergoing an annual period of positive energy balance. However, because the timing of maturity influences sexually dimorphic traits (e.g., body size: Shine 1990), AE and allocation should also be examined in juvenile pythons or other taxa to investigate ontogenetic differences between the sexes. Given the robust link between AE and phenotype, systems of sexual dimorphism should be investigated to further explore the relationships among known proximate factors such as testosterone and both nutrient absorption and resource allocation. Future research should also examine other aspects of resource dynamics. For example, patterns of resource allocation could be clarified through the use of magnetic resonance technologies, which can provide non-invasive time-series analyses of whole-animal fat and protein deposition. In sum, we provide the initial step to investigating AE as a proximate mechanism in sexual dimorphism by demonstrating a link between sexual variation in AE and phenotype.

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