REPTILES & AMPHIBIANS

Big Pythons, Big Gape, and Big Prey

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Abstract.—Knowing the size of prey that predators can consume facilitates understanding and predicting their ecological impact. Burmese Pythons (*Python bivittatus*) are apex predators that are larger than all but a few snake species, and their prey, which is swallowed whole, cannot exceed the size of their maximal gape. However, prey sizes smaller than maximal gape can occur because of what prey snakes encounter or select or if capturing or swallowing certain prey is prohibitively difficult. Our study quantified the maximal gape of three large Burmese Pythons (SVLs 410–520 cm), including the longest individual captured in Florida (where they are invasive) and one snake that was captured while eating a deer. All three snakes had maximal gape diameters of 26 cm that exceeded the previously reported maximal value of 22 cm, and the soft tissues between the lower jaws accounted for 56–59% of the maximal gape area. Combining our new data with previous data significantly affected the scaling equations' predicted maximal gape. The smallest snake in our study ate a 35-kg deer, which was 93% of its maximal gape area. Hence, in addition to eating prey of large absolute size, Burmese Pythons in nature also eat prey with a size near the limit imposed by gape, but how frequently this occurs remains unclear.

For snakes and other predators that swallow their prey whole, the maximal size of the mouth opening (gape) imposes an anatomical limit on maximum prey size. The overall size of snakes is also important for understanding their feeding ecology, and size varies considerably among different species and ontogenetically within single species (Feldman and Meiri 2013; Esquerre et al. 2017). Consequently, quantifying the scaling relationships between maximal gape and overall size provides useful insights into the range of prey sizes that snakes of different sizes could exploit. Despite its widely acknowledged importance for understanding feeding in snakes (Greene 1983; Cundall and Greene 2000), maximal gape has been quantified for only 13 (Jayne 2023) of the more than 3,500 species of extant snakes (Pough et al. 2016), and accompanying data for the size of prey relative to maximal gape are available for only five species (Jayne et al. 2018; Gripshover and Jayne 2021). Hence, how often snakes in nature consume prey near the limit imposed by their maximal gape remains a largely unanswered question.

To date, the largest species of snake for which gape has been quantified (Jayne et al. 2022) is the Burmese Python (*Python bivittatus*), which is an apex predator with well-documented detrimental effects to the ecology of southern Florida, where it is an invasive species (Dorcas et al. 2012). Two key findings of this recent study of gape in Burmese Pythons were that their relatively large maximal gape was mainly a result of greater stretching of the soft tissues in the intermandibular (IM) region and, even after accounting for overall snake size, interindividual variability in maximal gape was substantial (Jayne et al. 2022). This interindividual variation in gape combined with a paucity of data for very large individuals contributed to considerable uncertainty in predicting the maximal gape size and maximal prey size near the upper limit for the size of Burmese Pythons. For many species with indeterminate growth, including pythons, the rarity of extremely large individuals in natural populations contributes to the challenge of studying and understanding their biology. For example, of more than 9,501 Burmese Pythons captured in Florida, only 72 and 31 individuals had snout-vent lengths (SVL) greater than 420 and 440 cm, respectively (Guzy et al. 2023).

In this study we quantified the maximal gape of three very large Burmese Pythons. We then combined those data with previous data (Jayne et al. 2022) to assess the effects on the scaling relationships between gape, cranial anatomy, and the overall size of this species. We also report a field observation of a large Burmese Python consuming a large deer and compare its size to the maximal prey size permitted by maximal gape.

Methods

The new data and observations of this study were from three large adult female Burmese Pythons captured in southern Florida (Table 1). Python A was captured by searching the area in which a telemetered male was located during the breeding season (Smith et al. 2016; Bartoszek et al. 2021; Guzy

Table 1. Anatomical measurements of three large Burmese Pythons (*Python bivittatus*) in this study (snakes A–C) and the snake with the largest gape in a previous study (Jayne et al. 2022). Abbreviations: SKL, skull length; LJL, lower jaw length; G_{diam}, gape diameter; G_{area}, gape area; IM, percent of gape area from distension of the intermandibular soft tissues (see also Fig. 1).

		Snake		
Measurement	previous	A	B	C
SVL (cm)	397	410	462	520
TotalL (cm)	451	450	515	579
mass (kg)	62.3	52.3	52.7	56.3
SKL (cm)	10.2	10.4	11.2	12.2
LJL (cm)	12.8	12.0	13.0	13.8
G_{diam} (cm)	22	26	26	26
G_{area} (cm^2)	380	531	531	531
IM (%)	51.4	59.2	57.8	57.1

et al. 2023), and it was caught at 1330 h on 19 December 2022. This snake was within an agricultural water retention feature dominated by Coastal Plain Willow (*Salix caroliniana*) and Bent Alligator Flag (*Thalia geniculata*). Immediately after being euthanized, the head and approximately 20 cm of neck of this snake was placed in a plastic bag filled with water to prevent freeze drying when it was subsequently frozen. After thawing the specimen, gape was measured on 10 July 2023. Python B was caught and euthanized at 1700 h on 20 July 2023 and it was refrigerated (but not frozen) until its gape was measured during the afternoon of 21 July 2023. Python C was caught and euthanized on 10 July 2023 and kept refrigerated for three days before the head and neck were frozen in ice on 14 July and its gape was measured during the afternoon of 21 July. This extraordinarily large snake was the longest but not the heaviest individual captured in Florida (Table 1). Pythons B and C were caught at different locations on a paved road surrounded by cypress swamp.

The procedures for measuring maximal gape followed those described in more detail in Jayne et al. (2022). In brief, for the head and a length of neck between one to two skull lengths, maximal gape diameter (G_{diam}) was determined by inserting the hemispherical end followed by the cylindrical shaft of successively larger 3D-printed probes until they were too large to be inserted without damaging the tissues of the snake. Maximal gape area (G_{area}) was calculated for a circle with a diameter equal to G_{diam}. The incremental increases in probe diameters were 1 and 2 cm for probes with diameters from 10–14 and 16–28 cm, respectively. For additional procedures the specimens were stored with a cylindrical spacer that had the same diameter as the probe at maximal gape (Fig. 1). All procedures were in compliance with the Institutional

Animal Care and Use Committee of the University of Cincinnati (protocol number 21-05-26-02).

We measured skull length (SKL) as the straight-line distance from the snout to the posterior margin of the parietal crest, and lower jaw length (LJL) as the distance from its joint with the quadrate bone to the distal tip of the dentary. After inserting pins at the proximal and distal ends of the lower jaw, we took anterior-view photographs of specimens for which we subsequently used a graphics program to determine the contributions of the circular gape area by: (1) the intermandibular soft tissues (IM), (2) the lower jaws (LJ), and (3) the structures between the distal ends of the left and right quadrates (Fig. 1).

We performed linear ordinary least squares (Kilmer and Rodriguez 2016) regression analyses of $\log_{10}$-transformed values of lengths (cm) and areas (cm^2). The criterion for a calculated slope differed significantly from that expected from geometric similarity (isometry; Table 2, column 3) whether or not the 95% confidence limits (CL) of the calculated slope encompassed the expected value for isometry. For the scaling regressions, we also calculated the 95% prediction limits for a single observation of SVL (Sokal and Rohlf 1981, p. 474). We calculated the residual values (observed-expected) to quantify how much each observed value differed from the value predicted by the regression at a given SVL.
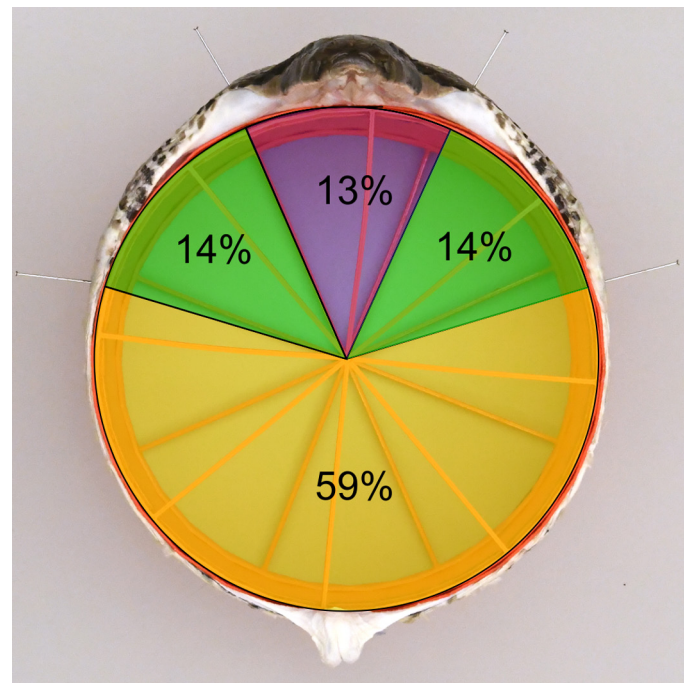

Figure. 1. Anterior view of Burmese Python (*Python bivittatus*) A preserved at maximal gape. The areas shaded yellow, green and purple represent the contributions to maximal gape area (G_{area}) of the intermandibular (IM) soft tissues, the lower jaw from its joint with the quadrate to the distal tip of the dentary, and the structures between the distal ends of the of the left and right quadrate bones, respectively. Photograph by Bruce Jayne.

Table 2. Least squares regression statistics (± 95% CL) for the scaling equations of $\log_{10}$-transformed values of morphology and maximal gape in Burmese Pythons (*Python bivittatus*). Values in italics are from the 43 snakes in Jayne et al. (2022), whereas the values in boldface include the three snakes in the present study (N = 46). Slopes expected from geometric similarity are indicated by "exp." Observed slopes (obs.) that conformed to isometry (based on 95% CL) or had negative or positive allometry are indicated by =, –, and +, respectively. Abbreviations: SVL = snout-vent length; G_{diam} = maximal gape diameter; G_{area} = maximal gape area; SKL = skull length; LJL = length of the entire lower jaw. Units of distance, area, and mass are cm, cm², and g, respectively.

| Variables | | | | | Regression | |
independent	dependent	exp.	obs.	slope	intercept	r^2
SVL	$\mathbf{G_{diam}}$	**1**	**=**	**0.927 ± 0.075**	**-1.178 ± 0.174**	**0.934**
SVL	*G_{diam}*	*1*	*–*	*0.870 ± 0.067*	*-1.055 ± 0.154*	*0.944*
SVL	$\mathbf{G_{area}}$	**2**	**=**	**1.854 + 0.150**	**-2.461 + 0.350**	**0.934**
SVL	*G_{area}*	*2*	*–*	*1.739 ± 0.134*	*-2.215 ± 0.308*	*0.944*
SVL	**SKL**	**1**	**–**	**0.748 ± 0.035**	**-0.977 ± 0.080**	**0.977**
SVL	*SKL*	*1*	*–*	*0.732 ± 0.036*	*-0.942 ± 0.084*	*0.976*
SVL	**LJL**	**1**	**–**	**0.761 + 0.038**	**-0.948 + 0.089**	**0.974**
SVL	*LJL*	*1*	*–*	*0.750 ± 0.042*	*-0.925 ± 0.096*	*0.970*
SKL	$\mathbf{G_{area}}$	**2**	**+**	**2.481 + 0.158**	**-0.043 + 0.123**	**0.958**
SKL	*G_{area}*	*2*	*+*	*2.366 ± 0.155*	*0.030 ± 1.117*	*0.959*

Results

The maximal gape diameter (G_{diam}) of all three large specimens was 26 cm, and the contributions of their IM soft tissues to G_{area} ranged from 57.1–59.2% (Table 1; Figs. 1–2A). For the combined sample of the three specimens in this study and the 43 snakes examined by Jayne et al. (2022), the slopes of G_{diam} and G_{area} did not differ significantly from the values of 1 and 2, respectively, that were expected from isometry (Table 2). By contrast, skull length and lower jaw length both had significant negative allometry with SVL (observed slope < isometric expectation), and G_{area} had significant positive allometry with skull length (observed slope > isometric expectation) (Table 2).

For the greatest observed value of SVL (520 cm), the scaling regressions predicted values of G_{diam} and G_{area} of 21.9 cm and 376 cm², respectively, and the upper 95% prediction

Table 3. Values predicted for maximal gape with lower and upper 95% predication limits based on log-log scaling equations with SVL for the previous and present studies of Burmese Pythons (*Python bivittatus*).

| | Jayne et al. (2022) N = 43 G_{diam} (cm) | | | This study N = 46 G_{diam} (cm) | | |
SVL (cm)	predicted	lower	upper	predicted	lower	upper
100	4.8	3.8	6.2	4.7	3.5	6.4
200	8.8	7.0	11.2	9.0	6.8	12.0
300	12.6	9.9	15.9	13.1	9.9	17.5
400	16.1	12.7	20.5	17.2	12.8	22.9
500	19.6	15.4	25.0	21.1	15.7	28.3
520	20.3	15.9	25.9	21.9	16.3	29.4
	G_{area} (cm²)			G_{area} (cm²)		
100	18.4	11.4	29.7	17.7	9.9	31.7
200	61.3	38.2	98.3	63.9	36.1	113.3
300	124.1	77.1	199.8	135.5	76.3	240.9
400	204.7	126.5	331.5	231.0	129.2	413.0
500	301.8	185.2	492.0	349.4	194.2	628.8
520	323.1	198.0	527.5	375.8	208.6	677.1
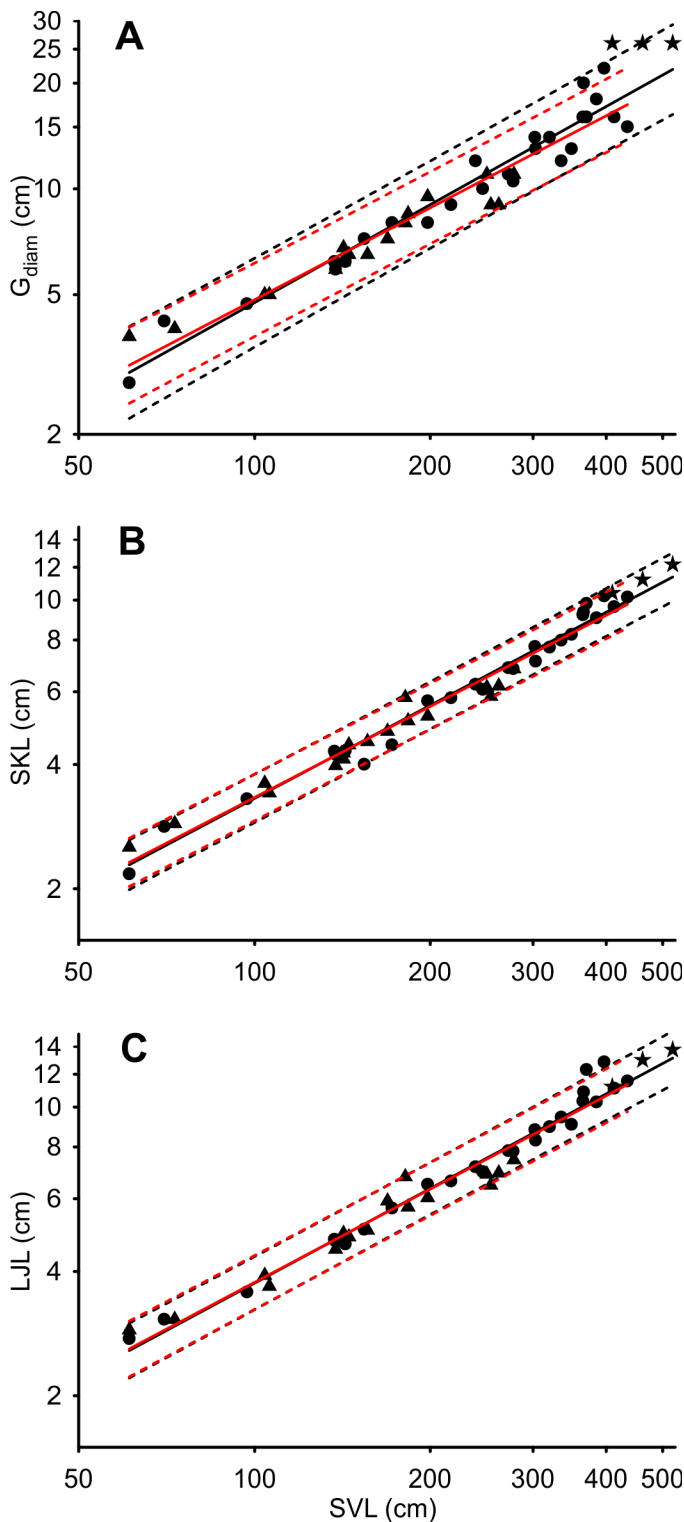
Figure 2. Log-log plots of the scaling relationships between maximal gape, cranial dimensions, and snout-vent length (SVL) in Burmese Pythons (*Python bivittatus*). The solid lines are the least-square regressions, and the dashed lines are the associated 95% prediction limits. The red lines are for the 43 snakes in Jayne et al. (2022), and the black lines include those data plus the three snakes in this study (stars). Triangles are males, and the other symbols are females. (A) Maximal gape diameter versus SVL. (B) Skull length versus SVL. (C) Lower jaw length versus SVL. See Table 2 for regression statistics.

limits for these same variables were 29.4 cm and 677 cm^2, respectively (Table 3). The variation in gape among snakes with a given SVL is shown in Fig. 2A.

The observed values of G_{diam} (26 cm) and G_{area} (531 cm^2) for python A were large for its SVL. For example, the residual value of G_{diam} based on the SVL exceeded those of all other individuals, and it was 8.5 cm greater than the value of 17.5 cm predicted for SVL = 410 cm (Fig. 2A). However, compared to python A, two specimens had greater residual skull lengths and nine specimens had greater residual values of lower jaw length predicted from SVL. Consequently, unusually large cranial dimensions for its overall size were not sufficient to explain the impressively large gape of python A, which also had the greatest value (59%) for the proportion of gape area from the soft IM tissues (Fig. 1; Table 1), which emphasizes their important role in affecting maximal gape.

Python A was found while it was swallowing an adult White-tailed Deer (*Odocoileus virginianus*) that was measured after the snake was palpated, causing regurgitation after the prey had been completely swallowed. This deer had a maximum circumference (in the mid-thoracic region) of 78.5 cm,

Figure 3. Burmese Python (*Python bivittatus*) A in the field soon after being found while consuming a 35-kg White-tailed Deer (*Odocoileus virginianus*). The white arrow indicates the distal end of the lower jaw. At rest the dorsal scales overlap and completely cover the skin between scales. However, when swallowing large prey, the distance between adjacent dorsal scales can exceed their width (yellow arrow). Photographs by Ian Bartoszek.

and this circumference corresponds to that of a circle with a diameter of 25 cm and an area of 491 cm^2. Thus, the maximal diameter and cross-sectional area of the deer were 96.2% and 92.5% of the corresponding maximal values of G_{diam} and G_{area} of this snake. The 35-kg mass of the deer was 66.9% of the snake's mass.

When python A was found, its head was near the pelvis of the deer (Fig. 3), which was approximately two-thirds of the total distance from the nose of the deer to the tips of its fully retracted and extended hindlimbs; so, the location of the snake's head was past the region of the deer with the greatest circumference and a posterior portion of the snake's body was coiled around the hindlegs of the deer and anchored the prey as the python maneuvered its mouth around the deer. Necropsy of the deer revealed it was a male, and the tooth marks on the neck suggest this is where the snake first seized the prey. The overall direction of swallowing was from head to tail. However, one of the forelimbs of the deer was extended straight forward beyond the head of the deer, which is contrary to the expectation of headfirst swallowing with limbs folded back against the body that becomes increasingly common as relative prey sizes of snakes increase (Loop and Bailey 1972; Cundall and Greene 2000). The snake completely swallowed the remainder of the deer (hips to the ends of its hindlimbs) in 21 min.

Discussion

The large gape observed for python A raises the interesting possibility that ingesting a large meal could somehow affect the soft tissues relevant to the gape of snakes and perhaps contribute to interindividual variability in gape for a given overall size. In contrast to python A, pythons B and C had empty digestive tracts that suggested a lengthy time since the last feeding. Compared to pythons B and C, the greater ease of inserting submaximal probe sizes in python A suggests that recent ingestion can at least decrease the stiffness of soft tissues. However, to enhance gape the soft tissues also must be able to tolerate greater strain (stretch) before the tissues fail, and this mechanical property can vary independently from the stiffness of the material.

Some additional changes in the skin of snakes can occur during feeding. For example, when Burmese Pythons feed, the skin in the gular and ventrolateral regions of the neck rapidly changes from white to a pinkish hue, which suggests an increase in the flow of blood (Fig. 4). Similar changes in color and presumed blood flow associated with feeding have been observed for other species of large snakes eating large prey, including *Boa constrictor*, *Corallus hortulana*, *Malayopython reticulatus*, and *Simalia amethistina* (B. Jayne, pers. obs.; D. Cundall, pers. comm.). How and whether increased circulation affects the mechanical properties of skin remains to be determined. If ingesting prey does indeed affect mechanical

properties of the soft tissues relevant to gape, determining the persistence and timing of this effect and whether the time between euthanasia and feeding also effects the distensibility of the skin would be interesting. Some additional nuances in how our three large specimens were stored before measuring gape could pose a confounding factor for correlating recent feeding to enhanced maximal gape. For example, python C had by far the greatest amount of rigor mortis, python B was intermediate, and python A had barely any discernable rigor mortis. In light of the above, standardizing the time between euthanasia and freezing or measuring gape would also seem to be a best practice for quantifying gape.
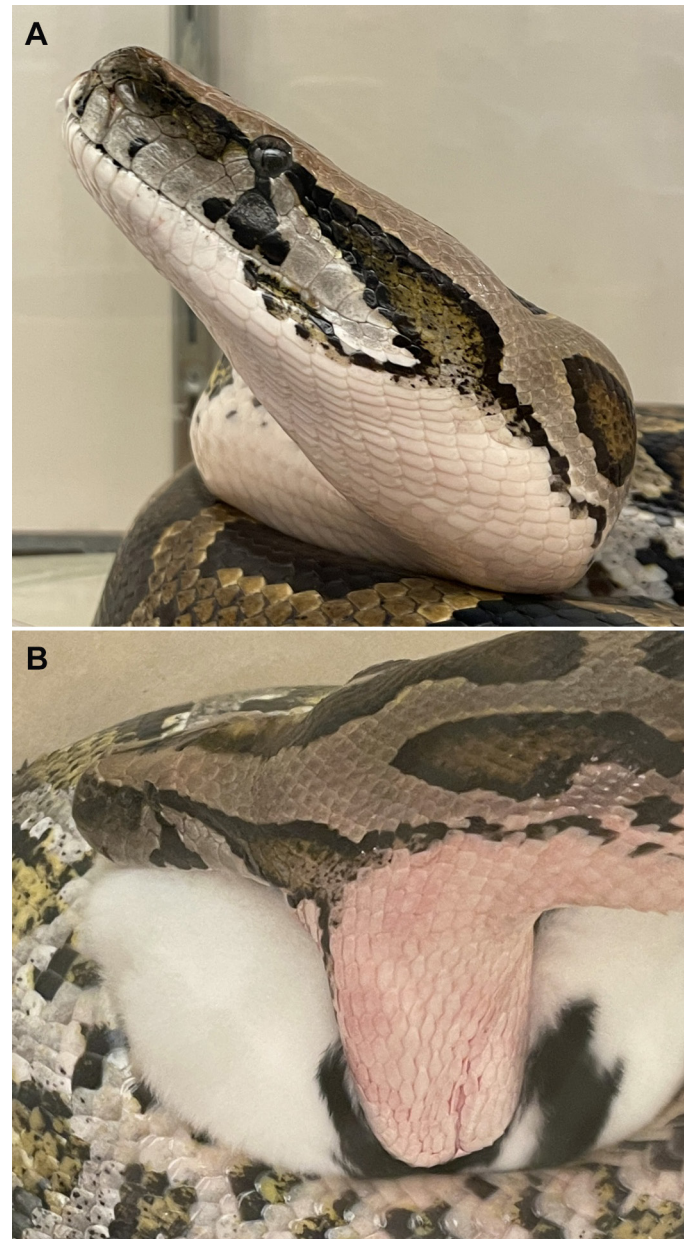

Figure 4. An 18-kg captive Burmese Python (*Python bivittatus*) before feeding (A) and while beginning to swallow a 1.6-kg rabbit (B). Note the change in the color of the gular and ventrolateral skin while the snake is feeding. Photograph by Bruce Jayne.

Adding the three large specimens to the sample of Jayne et al. (2022) increased the slope and decreased the y-intercept of all scaling equations (Table 2). However, the updated scaling equations of skull length and lower jaw length versus SVL had barely perceptible differences with those of the previous sample (Fig. 2A–B). By contrast, the slopes increased so much for maximal gape versus SVL for the combined data that they conformed to isometry, whereas in Jayne et al. (2022), G_{diam} and G_{area} had significant negative allometry (Table 2). This reinforces how even a modest number of observations that expand the range of animal size can have a noticeable effect on scaling regressions.

For the combined data and the maximal observed value of SVL (520 cm), the predicted values of maximal G_{diam} (21.9 cm) and G_{area} (376 cm^2) were approximately 8% and 16% greater than the corresponding values predicted in Jayne et al. (2022), and the 95% prediction limits were G_{diam} = 29.4 cm and G_{area} = 677 cm^2 (Table 3). Thus, a gape diameter of approximately 30 cm seems possible for a Burmese Python approaching the maximal overall size of this species, which is probably greater than that of any snake captured in Florida. Based on the scaling equations for prey size in Jayne et al. (2022), a gape diameter of 30 cm (and G_{area} = 707 cm^2) could allow a snake to swallow a deer with a mass 57.9 kg and an alligator with a mass of 95.6 kg.

For pythons captured in Florida, the heaviest snake (97.7 kg; SVL = 488 cm; IAB, unpubl. data) is 1.74 times heavier than the longest snake (python C); hence, the greater weight of the former snake would substantially decrease relative prey mass (prey mass divided by snake mass) for a prey item with a given mass. However, given the modest differences in length between these two snakes, one would expect reasonably similar values of maximal gape and in turn similar values of prey size relative to the maximal gape size for a given size of prey. Consequently, one should take care to not assume that different relative prey masses equate to different sizes of prey relative to maximal gape.

When large snakes eat prey of impressively large absolute size, one cannot know or reasonably estimate whether prey size is approaching the anatomical limit unless gape has been measured directly or scaling equations are used to predict maximal gape from the overall size of the snake. However, the directly measured prey and gape sizes for python A indicated that it did indeed consume prey near its anatomical limit. Hence, in the vernacular of Hertz et al. (1988), its performance was at the level of an Olympian rather than that of a boy scout.

Clearly, several factors other than maximal gape can limit prey size. For example, snakes simply might refuse to attack prey above a given size that is well within what their gape could accommodate. Furthermore, even if snakes attack prey of sizes near their maximal gape, such large prey could be too difficult to subdue and swallow. For example, in the field, two unrelated species of snakes (*Liodytes rigida* and *Fordonia leucobalia*) eat only hard-shelled crustaceans that are much smaller than their maximal gape (Jayne et al. 2018; Gripshover and Jayne 2023). However, two other unrelated species (*Regina septemvittata* and *Gerarda prevostiana*) often eat freshly molted crustaceans with sizes near their maximal gape, which demonstrates how variation in the formidability of prey can affect maximal prey size (Jayne et al. 2018; Gripshover and Jayne 2023). An interesting related topic for further study would be resolving how often large snakes attack and kill large prey but fail to eat it because its size exceeds maximal gape (Natusch et al. 2021).

Our study focused on maximal prey sizes and maximal swallowing capacity, but Burmese Pythons also eat extremely small prey relative to their overall size (Lord et al. 2023). Hence, a thorough understanding of predator-prey ecology requires accounting for the sizes and frequencies of all prey consumed. Using scaling equations to predict maximal gape from overall snake size can facilitate pooling data from snakes of different sizes to generate the frequency distributions of relative prey sizes (Jayne et al. 2018; Gripshover and Jayne 2021, 2023) that are needed to test the general question of how often animals in nature perform near their maximal capacities (Hertz et al. 1988). Furthermore, such an approach also could facilitate determining whether relative prey size decreases with increased time in which invasive snakes have been established in a particular area and might potentially have depleted larger prey.

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