

Mammals as Prey: Estimating Ingestible Size

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ABSTRACT Most mammals have deformable bodies, making it difficult to measure the size of living or freshly killed ones accurately. Because small rodents are common prey of many snakes, and because nearly all snakes swallow their prey whole, we explored four methods for determining the ingestible size (the smallest cross-sectional area that the largest part of the rodent can be made into without breaking bones or dislocating joints) of 100 intact rodents, including 50 *Mus musculus* and 50 *Rattus norvegicus*. Cross-sectional areas derived from maximal height and width of specimens at rest or the same specimens wrapped snout to pelvic girdle are roughly 1.5× higher than areas calculated either by the height and width of the same specimens rolled into cylinders or by volumetric displacement. Rolling rodents into cylinders reduces cross-sectional area by straightening the vertebral column, lengthening the abdominal cavity, elevating the sternum, compressing the thoracic cavity, and protracting the shoulder joint, that is, changes similar to those seen in rodents eaten by snakes. Reduced major axis regression of the smallest attainable cross-sectional area, y , on mass, x , shows that y (in $\log \text{mm}^2$) approximates $1.53x$ (in $\log \text{grams}$)^{0.69} for rats and $1.63x$ ^{0.64} for mice. Our results suggest that visual cues provided by live rodents might lead most predators, like snakes, to overestimate ingestible size and hence rarely attack prey too large to ingest. *J. Morphol.* 273:1042–1049, 2012. © 2012 Wiley Periodicals, Inc.

KEY WORDS: scaling; shape; cross-sectional area; Muridae

INTRODUCTION

Accurate, repeatable measures of animals that lack either a rigid integument or rigid musculoskeletal bauplan, such as mammals, are difficult to obtain (Jewell and Fullagar, 1966). Studies of mammalian life history traits have long been plagued by the problem of body size, and these problems are most evident when trying to scale linear dimensions to mass (Silva, 1998). Iskjaer et al. (1989) stated that body size in mammals was a “nebulous quantity to measure,” and suggested a multivariate approach to the problem of measuring size in relation to mammalian life history traits. Dobson (1992) pointed out that rates of change in mass are really functions of both structural size, defined as the size of the supporting tissues, and physiological condition, which is dependent on the size of energy reserves. In each case, mass is of limited value to studies using structural size comparisons because the factors that either contribute to or result from changes in mass are

labile. While the difficulty of measuring deformable body forms is rather obvious, it is easily overlooked in much of the ecological literature.

Vezina (1985) demonstrated that among predatory animals, the prey-to-predator mass ratio is highest among carnivores when compared to piscivores and insectivores. Prey size is extremely important to carnivores that ingest their food whole. For snakes, the predator’s maximal gape determines the size of the largest prey that can be consumed (Greene, 1983), and the critical feature of mammal prey is the smallest attainable cross-sectional area of the largest part of the body (Arnold, 1983; Cundall and Greene, 2000). The problem, then, for both snakes and biologists interested in measuring mammals eaten by snakes, is estimating that variable.

Arnold (1993) reviewed much of the existing literature on predator and prey size relationships in snakes. Prey size was typically extracted from one or several measurements including mass, length (snout–vent length, total body length, or standard length), width (or diameter), and/or volume. The condition of material available determined sample sizes and the measures used. Most studies relied on measurements of intact prey, a rare occurrence in predator stomach or fecal contents. When prey species in stomach or fecal contents could be identified, measures of prey size were sometimes gained from conspecific museum specimens. Recent studies incorporate average conspecific prey mass, length, and width/diameter (Rodríguez-Robles et al., 1999a,b; Rodríguez-Robles, 2002; Glaudas et al., 2008) to arrive at prey size estimates, but the relationships among all measures of size used are rarely reported. Mass is the most widely used measure of the size of mammals used in the laboratory studies of snake feeding behavior (Mori, 1991; Forsman and Lindell, 1993), but prey height, width (diameter), and length (measured as either

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snout to anus length or head and body length) have been used to test the correlations with a particular measure of feeding performance (Pough and Groves, 1983; Mori, 1991; Shine, 1991). Predator-prey mass ratios (Greene, 1983; Pough and Groves, 1983; Kley and Brainerd, 2002; Mehta, 2009) and ingestion ratios (Greene, 1983), such as prey caliber to head caliber (Loop and Bailey, 1972), prey mass to head length (Shine, 1991), and prey height to lower jaw length (Cundall and Deufel, 2006), have been used less frequently.

Researchers interested in studying gape-limited predators that feed on mammals are thus faced with the following problems: The relative size of prey influences predator performance, but the linear dimensions, and thus absolute size, of mammals are changeable. Mass is an unchanging measure of a body's absolute size, but alone it provides little information about the linear dimensions of an elastic body simply because a single change in one dimension will result in a change in at least one other dimension. Therefore, we test the relationship between a mammal's mass, linear dimensions, and ingestible size, defined as the smallest attainable cross-sectional area of the largest part of the body. To determine the effect of deformability on estimated cross-sectional area, we first explore differences among cross-sectional area estimates of freshly killed rodents derived from four different measurement protocols. Specifically, we test the hypothesis that measures of freshly killed, resting rodents give estimates of cross-sectional area higher than measures of the same rodents rolled tightly into cylinders. We then ask which musculoskeletal features change when rodents are rolled into cylinders and whether this deformation approximates what occurs when a snake swallows a rodent. Finally, we determine the scaling relationships between measures of mass, length, height, and width of unmanipulated rodents and the smallest attainable cross-sectional area in order to generate a method of estimating rodent ingestible size from single mass or linear measurements alone.

METHODS

To estimate relationships between cross-sectional area and other measures of rodents, the senior author measured 50 juvenile to adult Norway rats (*Rattus norvegicus*) and 50 juvenile to adult house mice (*Mus musculus*) of both sexes. Because pregnancy causes significant changes in the body form of female rodents, no conspicuously gravid females were used (Dewsbury, 1992). All rodents were reared and housed in the laboratory under normal light and temperature conditions with ad libitum access to food and water. All animals were humanely sacrificed prior to measuring using CO₂ anesthesia to cessation of heartbeat. Methods were approved under Lehigh University IACUC protocol 66.

Cross-sectional Area Estimates

Cross-sectional area was estimated for each rodent from four different manipulations (see later). For three manipulations,

cross-sectional area (A) was derived as the area of an ellipse using the following equation:

$$A = \frac{\pi ab}{4}$$

where major (a) and minor (b) axes were derived from height and width measurements, respectively, described later. For the fourth manipulation, cross-sectional area was derived as the area of a cylinder of a given length (L) and fixed volume (V) using the following equation:

$$A = \frac{V}{L}$$

All linear measurements were taken to the nearest 0.1 mm using dial calipers. Measurements of mass were made to the nearest 0.1 g.

Height width (HW) method. Height and width of rodents were taken at approximately the highest and widest points of the prey following Cundall and Deufel (2006) for height and Pough and Groves (1983) for width. For all specimens we measured, the widest point occurred at the level of the pelvic girdle (Fig. 1A) and the highest point lay at the middle of the trunk (Fig. 1B).

Rolled (Ro) method. To test the effect of uniform pressure along the entire length of a rodent body on cross-sectional area, as possibly experienced by rodents following complete engulfment, rodents were rolled tightly into cylinders using pieces of 70 lb. paper cardstock (Fig. 1C,D). Prey height and width (usually the same) were measured from the inner height and width of the paper cylinder.

Wrapped (Wr) method. Rodents were tightly wrapped from the snout to the pelvic girdle using surgical gauze (Fig. 1E,F). This procedure simulates the effect snakes have on prey form during ingestion, shifting much of the visceral volume caudally and enlarging the caudal end relative to the head and trunk (Fig. 2). Height and width of the caudal end of the prey were measured at the level of the pelvic girdle just past the end of the gauze (Fig. 1E,F).

Volumetric (Vo) method. Assuming that rodent bodies could be viewed as cylindrical masses, we derived cross-sectional area using rodent length and the volume of the head and trunk. Length was measured as the distance from the tip of the snout to the base of the tail using calipers for mice and small rats and a ruler for large rats. Rodents were laid on their backs to reduce the effects of the curvature of the spine (Jewell and Fullagar, 1966). Rodent head and body volume was measured to the nearest 1 mL by volumetric displacement. To take volume readings, rodents were dipped to the base of the tail after being completely immersed several times in a graduated cylinder to remove as much air as possible from the fur.

Analyses

Differences among means of cross-sectional area estimates derived from the four methods were tested with one-way Analysis of Variance (ANOVA) using PASW Statistics 18 for Windows. Raw data for both *Rattus* and *Mus* failed to meet the assumption of homogeneity of variance (Levene's test) primarily because variances for HW and Wr were 2–6× times higher than those for Ro and Vo (Table 1). Therefore, data were log transformed, and homogeneity of variance was retested prior to the ANOVA. The log-transformed data for *Rattus* met the assumption of homogeneity of variance (Levene's test, $P > 0.05$) and differences among means were compared post hoc using Fisher's least significant difference (LSD) test. The log-transformed data for mice failed to meet the assumption of homogeneity of variance and differences among means were compared post hoc using Dunnett's C test. To determine how the smallest cross-sectional area estimate (Ro method) scaled to mass and the various

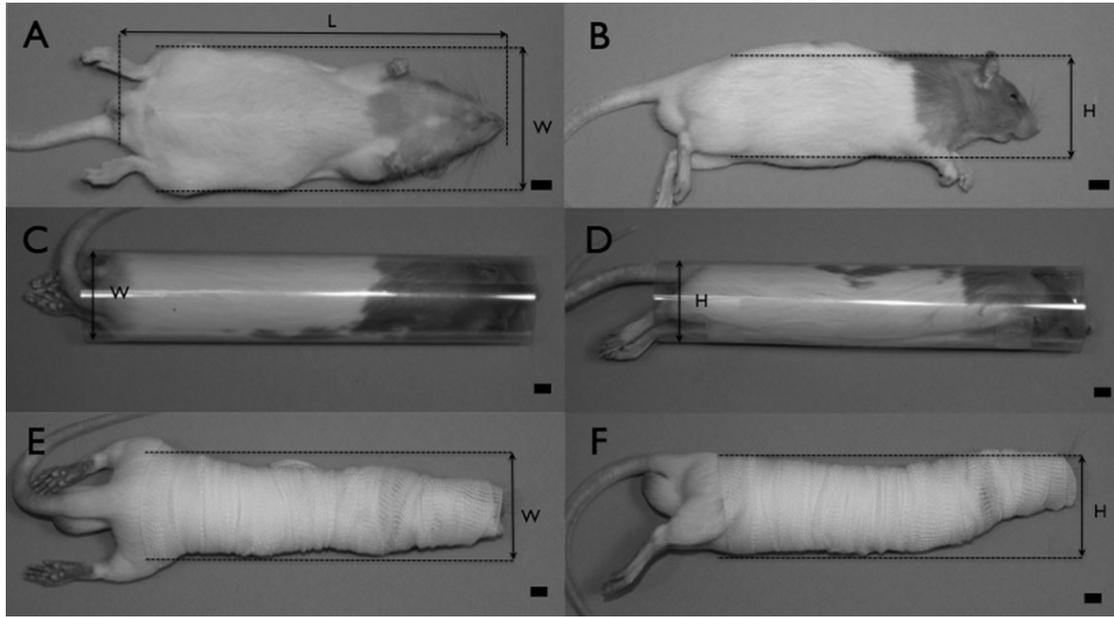


Fig. 1. Photographs of a Norway rat with dimensions measured under different manipulations. HW is represented by (A) and (B). A: Ventral view and B: lateral view. Ro is represented by (C) and (D). C: Dorsal view and D: lateral view. Mylar used to allow prey to be viewed within cylinder. Wr is represented by (E) and (F). E: Dorsal view and F: lateral view. Scale bar = 10 mm.

linear measures commonly used to measure rodents, we used reduced major axis regression (Sokal and Rohlf, 1995). All variables were log transformed prior to the analysis. Homogeneity of slope between variables was tested using methods reviewed by McArdle (1987).

Radiography

An adult male rat was sacrificed using the methods previously described and X-rayed in lateral and ventral views, first in its resting state, and then after rolling it into a cylindrical shape (Ro method). To determine effects of ingestion on prey form, radiographs were also taken of a second adult rat (400g) following its ingestion by a 1,400 g reticulated python (*Broghammerus [Python] reticulatus*). To facilitate imaging in lateral and ventral planes, the python was anesthetized with 15 mg/kg methanohexital 30 min prior to radiography.



Fig. 2. Photograph a 1,400 g reticulated python (*B. reticulatus*) swallowing an 800 g Norway rat at a late stage of oral transport (dorsal view).

RESULTS

Average cross-sectional area differed significantly across methods of measurement for both *Rattus* ($F_{(3,196)} = 10.18$, $P < 0.001$) and *Mus* ($F_{(3,196)} = 14.29$, $P < 0.001$). Post hoc comparisons (Table 2) showed that average cross-sectional areas derived from HW and Wr methods were not significantly different ($P = 0.41$ for *Rattus* and $P = 0.99$ for *Mus*) despite the superficial impression that both the Wr method (Fig. 1E,F) and the effect of being swallowed (Fig. 2) similarly enlarged the caudal end of the prey relative to the head and body. In *Rattus*, average cross-sectional areas derived by both HW and Wr were higher than those by both Vo ($P < 0.01$) and Ro ($P < 0.05$). In *Mus*, average cross-sectional areas derived by HW and Wr were 1.5–2× higher than those by both Ro and Vo ($P < 0.05$ for all comparisons). Therefore, values likely to be closest to ingestible size are those produced by the Ro and Vo methods.

TABLE 1. Summary of untransformed means and variances for cross-sectional area (mm^2) estimates derived by four methods

Taxon	Method	\bar{x}	S^2
<i>Rattus</i>	HW	1915	159×10^4
	Wr	1728	115×10^4
	Ro	1204	57.3×10^4
	Vo	955	31.5×10^4
<i>Mus</i>	HW	454	3.61×10^4
	Wr	454	2.10×10^4
	Ro	339	0.796×10^4
	Vo	289	0.608×10^4

TABLE 2. Means and standard deviations of log-transformed cross-sectional area (mm^2) estimates derived by four methods

Taxon	Method			
	HW	Wr	Ro	Vo
<i>Rattus</i> \bar{x} (\pm SD)	3.19 (\pm 0.32)	3.14 (\pm 0.31)	2.99 (\pm 0.28)	2.90 (\pm 0.28)
<i>Mus</i> \bar{x} (\pm SD)	2.61 (\pm 0.21)	2.63 (\pm 0.17)	2.51 (\pm 0.14)	2.44 (\pm 0.14)

Lines connect methods that are not significantly different using post hoc Fisher's LSD tests for *Rattus* and Dunnett's *C* tests for *Mus*.

Linear measures of mammals are inextricably tied to volume and mass, and change in any linear dimension should result in a change in cross-sectional area. Therefore, we determined the relationship between each standard linear measure (HW method) of a rodent and its cross-sectional area measured by the Ro method. Log cross-sectional area was highly correlated to log length in both *Rattus* and *Mus* and cross-sectional area scaled to length with positive allometry in each (Table 3 and Fig. 3). Log cross-sectional area was also highly correlated to log height in *Rattus* (but not in *Mus*) and to log width in both taxa (Table 3 and Fig. 3). Cross-sectional area scaled with positive allometry to both height and width in both taxa (Table 3 and Fig. 3). Therefore, unless positive allometry is accounted for, all three standard linear measures alone overestimate ingestible prey size.

Mass is the most widely used measure of prey size, and its relationship to smallest attainable cross-sectional area is important, because, unlike linear measures, the quantity is not affected by deformation. Log cross-sectional area was highly correlated to log mass for both taxa, and cross-sectional area scaled to mass with negative allometry (Table 3 and Fig. 4). Therefore, mass alone underestimates ingestible prey size.

Anatomy

X-ray images reveal that in the resting condition, the vertebral column is strongly curved with a prominent lordosis (i.e., ventral convexity)

TABLE 3. Reduced major axis regression analysis of log-transformed single predictors on log-transformed cross-sectional area for *Rattus* and *Mus*

Taxon	Predictor	Slope (CI)	Y-int.	r^2	<i>P</i>
<i>Rattus</i>	Mass	0.69 (0.66–0.72)	1.53	0.98	<0.05
	Length	2.03 (1.86–2.21)	-1.49	0.92	<0.05
	Height	1.71 (1.55–1.89)	0.22	0.88	<0.05
	Width	1.77 (1.63–1.93)	0.018	0.92	<0.05
<i>Mus</i>	Mass	0.64 (0.59–0.70)	1.63	0.91	<0.05
	Length	1.72 (1.48–2.00)	-0.83	0.73	<0.05
	Height	1.31 (1.05–1.64)	0.80	0.40	<0.05
	Width	1.14 (1.01–1.30)	0.89	0.82	<0.05

P values indicate slopes differ significantly from 1.

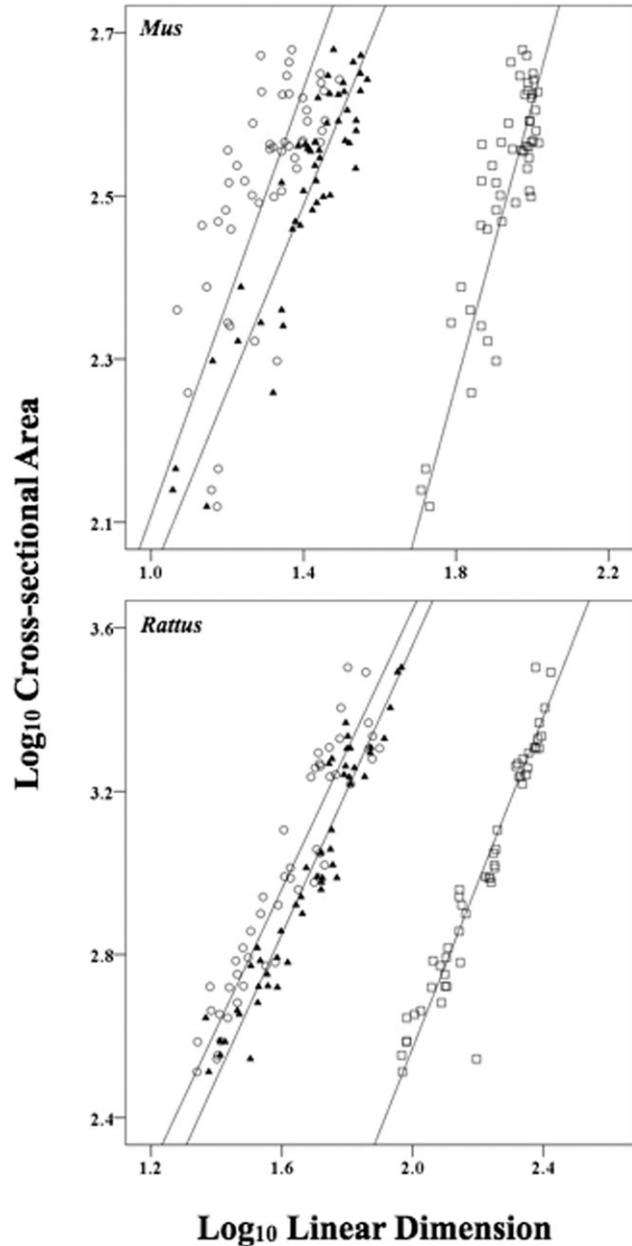


Fig. 3. Plot of log-log relationship between single linear measures and smallest attainable cross-sectional area for *Rattus* (upper) and *Mus* (lower). \square = length, \blacktriangle = width, and \circ = height.

between the sixth cervical (C6) and third thoracic (T3) vertebrae, and an even more prominent kyphosis (i.e., ventral concavity) between T9 and the first lumbar vertebrae (L1) (Fig. 5A). In addition, the skull is flexed ventrally at the atlanto-occipital joint. The Ro manipulation extends both the head and curvatures in the vertebral column, decreasing the angle of the head by $\sim 20^\circ$ and both vertebral curves by $\sim 45^\circ$. Maximal angular displacement between adjacent vertebrae was roughly 20° and occurred once at each vertebral

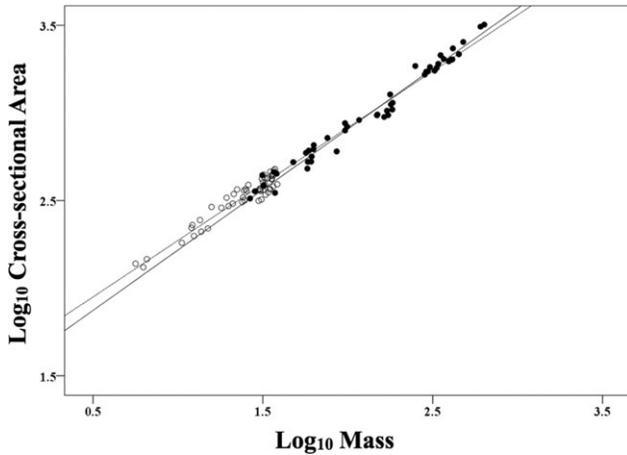


Fig. 4. Plot of log-log relationship between smallest attainable cross-sectional area and mass of rodent prey. ● = *Rattus*, ○ = *Mus*.

curve (between T2 and T3 and T11 and T12 for curves 1 and 2, respectively). The straightening of the head and spine effectively lengthens the body (measured from the rostral tip of the nasal to the caudal edge of the fourth sacral vertebrae) by ~12% (Fig. 5C), and this is coincident with the caudal movement and redistribution of the thoracic and abdominal viscera. The sternum is elevated and the costal cartilages bend, decreasing the angles between the ribs and the vertebral column and compressing the thoracic cavity (Fig. 5A,C). The distal ends of the clavicles are protracted, bringing the shoulder joints cranially, and the forelimbs are pressed against the side of the body (Fig. 5B,D). The hind limbs are adducted and extended caudally (Fig. 5A–D). These changes are similar to those seen in the rat inside the python (Fig. 5E,F), a consequence of shaping done by the snake.

DISCUSSION

Previous attempts to measure mammals as prey have used size categories determined by pushing rodents through holes of specific sizes (Loop and Bailey, 1972; Shine, 1991). From our perspective, this method generates two problems. The first is that this method does not actually measure the rodent, but simply generates size classes. The second is that pushing a rodent through a hole with “a modest amount of pressure” (Loop and Bailey, 1972) produces an estimate of cross-sectional area approximately 1.2–1.4× the value obtained by pulling the same rodent through holes with modest force. Mass is distributed caudally in both cases, as the anterior trunk is compressed (Fig. 2, as for our *Wr* method), but our radiographs show that a rodent prey’s mass is redistributed as it elongates during swallowing events (Fig. 5). Previous measures of smallest attainable prey diameter

may have actually been closer to that of our *Wr* method, thereby overestimating ingestible size.

Shine (1991), although claiming to have used cross-sectional diameter as a measure of “effective size,” actually used mass in all analyses, because he found mass to be highly correlated with cross-sectional diameter. Mass is the most commonly used measure of size in the laboratory setting, because it is highly correlated to linear dimensions, but it provides little information on the size of prey relative to the size of the predator’s gape (Greene, 1983). Our data show that the smallest attainable cross-sectional area scales negatively to mass, and the allometric relationship is slightly different for rats and mice. Therefore, in order for mass to be used as a measure of ingestible size, the scaling relationship has to be determined prior to the analysis.

Estimates of body size are obviously subject to methods of measurement and our data suggest that, for the same animal, different methods can generate significantly different average cross-sectional areas with variances that are also orders of magnitude different (Tables 1 and 2). However, our data also show that if good measures of length (Jewell and Fullagar, 1966) are combined with volume (as for our *Vo* method), cross-sectional area measures will be similar to those obtained by compressing a rodent into the smallest cylindrical mass possible (*Ro*) with similar repeatability (Table 1). Radiographs of rodents both rolled into cylinders and ingested by snakes indicate that *Ro* and, subsequently, *Vo* methods provide reasonable estimates of ingestible prey size, and we suggest that, when possible, either method be used when measuring rodents as prey.

Measuring intact small mammals recovered from stomach contents of snakes provides the smallest attainable size of prey (Rodríguez-Robles et al., 1999a,b; Rodríguez-Robles, 2002; Glaudas et al., 2008), because ingested prey have been formed into cylinders during ingestion (see Fig. 6, Rodríguez-Robles, 2002). Our anatomical data suggest that if cross-sectional area was derived from height or width of prey from stomach contents, it should approximate the same values generated by our *Ro* method. Unfortunately, stomach contents are often not measureable, and if species can be identified, measuring preserved conspecifics is commonly done (Rodríguez-Robles et al., 1999a,b; Rodríguez-Robles and Greene, 1999; Rodríguez-Robles, 2002; Fabien et al., 2004). Our results show that this practice is problematic, because all linear measures of conspecifics potentially generate cross-sectional area estimates that are larger than ingestible size. While our *Vo* method would be convenient to use under these conditions, it is also a source of error, because the length measurement required is dependent on the condition of the animal at time of preservation, how it was pre-

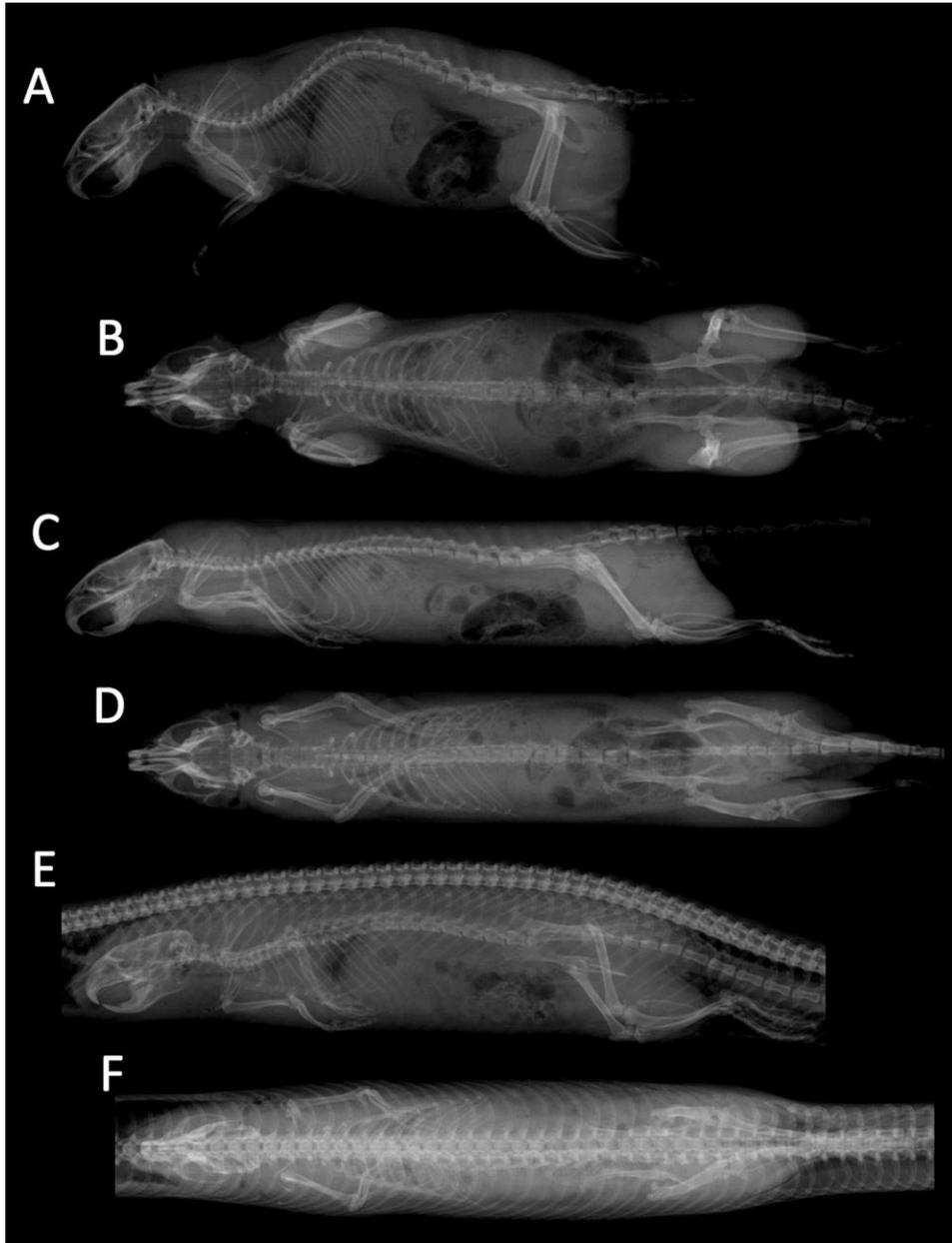


Fig. 5. Lateral and ventral X-ray images of an adult Norway rat in both the HW (A,B) and Ro (C,D) conditions. Images (E) and (F) are lateral and ventral X-rays of an adult Norway rat showing the musculoskeletal changes that occur 30 min after engulfment by a reticulated python (*B. reticulatus*, shown).

served, and the researcher's choice of landmarks (Jewell and Fullagar, 1966). However, if the scaling relationship between a mammal's linear dimension and its smallest attainable cross-sectional area is known (or determined as a part of the study), a single linear measure could accurately estimate ingestible size. We suggest using either Ro or Vo methods to derive smallest attainable cross-section areas of freshly killed conspecifics and then determining the allometric relationship between the desired linear predictor and

smallest attainable cross-sectional area as a part of the study.

Prey width/diameter (Loop and Bailey, 1972; Pough and Groves, 1983; Shine, 1991) and height (Cundall and Deufel, 2006) can be used in conjunction with snake head dimensions to generate estimates of relative prey size. Snout-vent length is also used, when prey type varies across vertebrate taxa (Vincent et al., 2005). Our data show that cross-sectional area estimates from height and width measurements of unmanipulated prey (HW)

are higher and more variable than those of prey rolled into cylinders (Ro), and smallest attainable cross-sectional area (using the Ro method) scales positively to resting linear dimensions (from the HW method). Therefore, to use any linear dimension as a measure of ingestible prey size, both the correlation coefficient and scaling relationship to smallest attainable cross-sectional area should be obtained for prey prior to the analysis. Fortunately, the laboratory setting is ideal for rolling prey into cylinders (Ro) or measuring length and volume (Vo), and our data provide the necessary information for two commonly used mammal species.

How snakes measure prey is currently unknown, and there appear to be no published studies devoted to this problem (but see Weaver, 2010). That snakes can measure prey is assumed by most people who keep snakes. Discussions with numerous zoo keepers and curators and uncontrolled presentations of rodent prey of different sizes suggest that many snakes can detect relatively small differences in size, but whether snake responses are due solely to prey size differences remains unclear (Mori and Vincent, 2008). Owings and Cross (2008) showed that *Crotalus oreganus* selectively avoids large ground squirrels (*Spermophilus beecheyi*) even if they are capable of swallowing them. Direction of ingestion of mammals is highly correlated to prey size (Diefenbach and Emslie, 1971), and field experiments have shown that prey too large to ingest are usually avoided (Forsman and Lindell, 1993).

Multiple, interdependent modes of sensory input are used by snakes to orient their strikes and relocate prey after their strikes, but it has not been determined which modes are used to assess prey size (Kardong and Berkhoudt, 1999). Visual stimuli (particularly movement) are important in initiating foraging in numerous snake species (for review see Shine et al., 2004). Snakes appear capable of measuring relative distance to prey prior to initiating their strikes (Cundall and Deufel, 1999), and limited field observations of *Crotalus horridus* suggest that relatively large prey species are eaten during the day as opposed to at night (Clark, 2006). Our data suggest that snakes using vision alone to assess prey would overestimate ingestible size. This might partly account for why snakes rarely attempt to capture mammals too large to swallow, though mistakes do occur (e.g., Rodríguez-Robles, 2002).

Two features of rodents that contribute to reducing cross-sectional area of the largest part of the body are the mobility of the clavicles and the potential for redistributing mass in the thoracic and abdominal cavities (Fig. 5). For snake predators, both features become relevant only when smallest attainable cross-sectional area of the rodent body approaches the maximal gape of the snake. At that point, rodents are invariably swallowed head-first and passing the rodent's should-

ers through the angle of the jaw is possibly made easier by passing each shoulder sequentially. Rodent body mass is initially displaced caudally (Fig. 2), and continued engulfment by a snake gradually shifts rodent mass back toward the rodent's head. At the same time, snake gape and gut lumen cross-sectional area are gradually increased, providing ample time for snake gape and rodent cross-sectional area to equilibrate. Whereas the effects of shaping done by the snake on rodent prey are passive, the malleability of rodent bodies and the ability of mass to be shifted also provide the potential for increasing their apparent cross-sectional area as a defensive mechanism and for reducing it when burrowing. In studies of feeding performance of gape-limited predators that eat rodents, measurements of rodent size need to take malleability into account.

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LITERATURE CITED

- Arnold SJ. 1983. Morphology, performance and fitness. *Am Zool* 23:347–361.
- Arnold SJ. 1993. Foraging theory and prey-size–predator-size relations in snakes. In: Seigel RA, Collins JT, editors. *Snakes: Ecology and Behavior*. New York: McGraw Hill, Inc. pp 87–15.
- Clark RW. 2006. Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. *Copeia* 2006:181–187.
- Cundall D, Deufel A. 1999. Striking patterns in booid snakes. *Copeia* 1999:868–883.
- Cundall D, Deufel A. 2006. Influence of the venom delivery system on intraoral prey transport in snakes. *Zool Anz* 245: 193–210.
- Cundall D, Greene HW. 2000. Feeding in snakes. In: Schwenk K, editor. *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*. San Diego: Academic Press. pp 293–333.
- Dewsbury DA. 1992. Body mass and size in female deer mice, *Peromyscus maniculatus*, as a function of time since breeding. *J Mammal* 73:794–796.
- Diefenbach CO, Emslie SG. 1971. Cues influencing the direction of prey ingestion of the Japanese snake, *Elaphe climacophora* (Colubridae, Serpentes). *Herpetologica* 27:461–466.
- Dobson S. 1992. Body mass, structural size and life history patterns of the Colombian ground squirrel. *Am Nat* 140:109–125.
- Fabien A, Bonnet X, Maumelat S, Bradshaw D, Schwaner T. 2004. Diet divergence, jaw size and scale counts in two neighboring populations of tiger snakes (*Notechis scutatus*). *Amphibia-Reptilia* 25:9–17.
- Forsman A, Lindell LE. 1993. The advantage of a big head: Swallowing performance in adders, *Vipera berus*. *Funct Ecol* 7:183–189.

- Glaudas X, Jezkova T, Rodríguez-Robles JA. 2008. Feeding ecology of the Great Basin Rattlesnake (*Crotalus lutosus*, Viperidae). *Can J Zool* 86:723–724.
- Greene H. 1983. Dietary correlates of the origin and radiation of snakes. *Am Zool* 23:431–441.
- Iskjaer C, Slade N, Childs JE, Glass GE, Korch GW. 1989. Body mass as a measure of body size in small mammals. *J Mammal* 70:662–667.
- Jewell PA, Fullagar PJ. 1966. Body measurements of small mammals: Sources of error and anatomical changes. *J Zool* 150:501–509.
- Kardong KV, Berkhoudt H. 1999. Rattlesnake hunting behavior: Correlations between plasticity of predatory performance and neuroanatomy. *Brain Behav Evol* 53:20–28.
- Kley NJ, Brainerd EL. 2002. Post-cranial prey transport mechanisms in the black pinesnake, *Pituophis melanoleucus lodingi*: An X-ray videographic study. *Zoology* 105:153–164.
- Loop MS, Bailey LG. 1972. The effect of relative prey size on the ingestion behaviour of rodent-eating snakes. *Psychon Sci* 28:167–169.
- McArdle BH. 1987. The structural relationship: Regression in biology. *Can J Zool* 66:2329–2339.
- Mehta R. 2009. Early experience shapes the behavioral repertoires of hatchling snakes. *J Ethol* 27:143–151.
- Mori A. 1991. The effect of prey size and type on prey-handling behavior in *Elaphe quadrivittata*. *J Herpetol* 25:160–166.
- Mori A, Vincent S. 2008. Determinants of feeding performance in free-ranging pit-vipers (Viperidae: *Ovophis okinavensis*): Key roles for head size and body temperature. *Biol J Linn Soc* 93:53–62.
- Owings DH, Cross RG. 2008. Hunting California ground squirrels: Constraints and opportunities for Northern Pacific Rattlesnakes. In: Hayes, WK, Beaman KR, Cardwell MD, Bush SP, editors. *Biology of the Rattlesnakes*. Loma Linda: Loma Linda University Press. pp 155–168.
- Pough FH, Groves JD. 1983. Specializations of the body form and food habits of snakes. *Am Zool* 23:443–454.
- Rodríguez-Robles JA. 2002. Feeding ecology of the North American gopher snakes (*Pituophis catenifer*, Colubridae). *Biol J Linn Soc* 77:165–183.
- Rodríguez-Robles JA, Greene HW. 1999. Food habits of the long-nosed snake (*Rhinocheilus lecontei*), a 'specialist' predator? *J Zool* 248:489–499.
- Rodríguez-Robles JA, Bell CB, Greene HW. 1999a. Gape size and the evolution of diet in snakes: Feeding ecology of erycine boas. *J Zool* 248:49–58.
- Rodríguez-Robles JA, Bell CB, Greene HW. 1999b. Food habits of the glossy snake, *Arizona elegans*, with comparisons of the diet of sympatric long-nosed snakes, *Rhinocheilus lecontei*. *J Herpetol* 33:87–92.
- Shine R. 1991. Why do larger snakes eat larger prey items? *Funct Ecol* 5:493–502.
- Shine R, Brown GP, Elphick MJ. 2004. Field experiments on foraging in free-ranging water snakes, *Enhydryis polylepis* (Homalopsinae). *Anim Behav* 68:1313–1324.
- Silva M. 1998. Allometric scaling of body length: Elastic or geometric similarity in mammalian design. *J Mammal* 79:20–32.
- Sokal R, Rohlf FJ. 1995. *Biometry*, 3rd ed. New York: W.H. Freeman. 880 p.
- Vezina A. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. *Oecologia* 67:555–565.
- Vincent SE, Herrel A, Irschick D. 2005. Comparisons of aquatic versus terrestrial predatory strikes in the pitviper, *Agkistrodon piscivorus*. *J Exp Zool A: Ecol Genet Physiol* 303:476–488.
- Weaver RE. 2010. Chemosensory and behavioral ecology of the dipsadid snakes: *Contia tenuis*, *Diadophis punctatus*, and *Hypsiglena chlorophaea* [dissertation]. Pullman (WA): Washington State University. 137 p. Available from: Washington State University Libraries, Pullman, WA; WSU B37 2010 W43.