

CONSTRICTION STRENGTH IN SNAKES

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ABSTRACT: Constriction was probably one of the key innovations that enabled snakes to subdue relatively large prey. It involves a snake winding or wrapping its body around a prey animal and squeezing, which restrains the prey from escaping and defending itself, and typically kills it quickly. Published observations and experiments on constriction have indicated that it is strong enough to kill prey by suffocation, circulatory arrest, or spinal fracture. However, constriction strength has been measured in very few species of snakes, and thus far only in relatively small individuals. In this study, we measured constriction pressures of 5–175 kPa in 12 species and 30 individuals, which varied in diameter from 0.85 to 12.50 cm. Constriction pressure varied significantly with snake diameter and number of loops in the coil. The measured pressures are high enough to kill many kinds of prey animals by circulatory arrest or spinal fracture, both of which are faster than killing prey by suffocation alone, and therefore are probably safer for the constrictor.

INTRODUCTION

A major trend in the evolution of snakes was an increased ability to consume large prey items (Greene, 1983; Cundall and Greene, 2000). Constriction behavior was a key innovation that enabled snakes to immobilize and subdue large prey (Greene and Burghardt, 1978; Cundall, 1987; Greene, 1994; Cundall and Greene, 2000; Mehta, 2005). Constriction involves a snake winding or wrapping its body around a prey animal and squeezing it. This restrains the prey animal from escaping and defending itself, and typically kills it quickly (McLees, 1928; Willard, 1977; Greene and Burghardt, 1978; Hardy, 1994). Variation in constriction behavior has been documented (Shrewsbury, 1969; Willard, 1977; Greene and Burghardt, 1978; Mori, 1991, 1993a, b, 1994, 1995; Mehta, 2003, 2005). However, few studies have addressed the mechanisms and performance of constriction (Hardy, 1994; Moon 2000; Lourdais et al., 2005; Mehta, 2005).

As with any muscular output, constriction strength depends on the cross-sectional area of active muscle, which is a major determinant of muscle force (Ruben, 1977; McMahon, 1984; Lourdais et al., 2005). The total cross-sectional area of axial muscle that is used in a constriction coil varies with the diameter of a snake (Moon and Candy, 1997), and with the number of loops in a coil. The force exerted by a snake's epaxial muscles is transmitted to the prey animal being constricted, resulting in increased pressure within the body of the prey. Constriction pressure is a biologically meaningful measure of performance (i.e., a snake's ability to subdue

a prey animal) because the pressure is important in immobilizing and killing the prey (McLees, 1928; Hardy, 1994). However, constriction pressure has been measured in few species of snakes, and thus far mainly in relatively small individuals (Moon, 2000; Mehta, 2005).

The major goal of this study was to analyze how constriction strength changes with snake diameter and number of loops in a coil. To this end, we measured constriction pressures in a diversity of snakes that varied widely in body size. These results help explain how constriction varies among snakes, and how it has been a key mechanism in the feeding biology and evolution of snakes.

MATERIALS AND METHODS

Experiments

We measured constriction pressures exerted on prey by 30 snakes of different sizes from 12 species (Table 1). For all snakes, we measured the constriction pressure exerted on relatively small mammalian prey (mice, rats, and hamsters) comprising 1–28% (\bar{x} = 6.13%) of the snake's mass. We chose not to analyze how relative prey mass was related to constriction pressure because we intentionally chose larger prey animals for larger snakes, and did not systematically vary prey mass. For dead prey (purchased frozen from a commercial supplier and thawed before use), we warmed the prey and shook it with long forceps while snakes constricted to simulate prey movements, which have been shown to elicit maximal responses from the snake (Moon, 2000). Whenever we recorded multiple feedings by the same snake, we analyzed only the single feeding event that involved the highest constriction pressure.

For small snakes (less than about 1.5 m SVL), we measured constriction pressure with a Harvard

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Table 1. Snakes used in this study of constriction strength.

Species	Number of individuals	SVL (cm)	Trunk diameter (cm) in region used for coiling
<i>Acrantophis dumerilii</i>	1	112.0	6.1
<i>Boa constrictor</i>	6	88.5–188.7	2.8–12.5
<i>Charina bottae</i>	3	29.0–35.0	0.85–1.0
<i>Lampropeltis getula</i> *	1	111.0	2.4
<i>Lichanura trivirgata</i>	2	43.5–51.2	1.3–1.7
<i>Morelia variegata</i>	2	119.0–183.0	3.8–3.9
<i>Pantherophis</i> (= <i>Elaphe</i>) <i>guttata</i>	4	60.0–66.0	1.8–2.4
<i>Pituophis catenifer</i> ¹	5	110.5–131.0	2.3–3.1
<i>Python regius</i>	3	35.2–126.0	1.6–4.7
<i>Python sebae</i>	1	178.2	9.6
<i>Sanzinia madagascariensis</i>	1	152.3	5.1
<i>Tropidophis haetianus</i>	1	37	0.92
Total	30	29.0–188.7	0.85–12.5

* Data from Moon (2000), using Harvard Apparatus transducer and same methods as in this study.

Apparatus Research Grade Blood Pressure Transducer (Harvard Apparatus, Holliston, Massachusetts; Fig. 1) or a Tycos sphygmomanometer (Welch Allyn Medical Products, Skaneateles Falls, New York). These transducers gave calibrated output to 40 kPa. The Harvard Apparatus Research Grade Blood Pressure Transducer gave progressively less calibrated output from 40 to 133 kPa, whereas the Tycos sphygmomanometer simply could not record pressures above 40 kPa. To make the recordings, we lightly taped a small (usually 2 ml) rubber pipette bulb to the fur of the prey animal (Fig. 1). The bulb was filled with water (Harvard Apparatus transducer) or air (Tycos sphygmomanometer), and was connected to the transducer via flexible tubing. To avoid bubbles in the bulb and tubing, we used hot water that had cooled slowly, and we inspected the clear tubing to ensure that no bubbles were present.

For large snakes, we measured constriction pressure with a World Precision Instruments PM100 Pressure Sensor (World Precision Instruments, Inc., Sarasota, Florida), which gave calibrated output to 690 kPa. We used the same technique as described above, except that we used a larger, air-filled rubber bulb and tubing. Changes in pressure were slow enough (on the order of seconds or more) for all transducers to show the changes accurately.

When snakes coiled around prey, we counted the number of loops formed to make the coil. We also used digital calipers to measure the diameter of each snake in one to three locations that were used in the con-

striction coil. To predict the constriction pressures of very large snakes, we extrapolated pressure based on the regression described below.

Analyses

We analyzed how constriction strength changes with snake size by computing a least-squares multiple regression with peak pressure as the dependent variable and the independent variables comprising snake diameter in the region used for coiling (usually about 40% of the anterior–posterior length of the snake) and number of loops in the coil. Because the bivariate data suggested a nonlinear relationship between constriction pressure and snake diameter, we also computed a quadratic regression.

Constriction pressure is generated by muscle force, which is proportional to muscle cross-sectional area, and hence to snake thickness. Therefore, we expected peak constriction pressures to scale with the snake diameter squared (i.e., diameter²) in a bivariate analysis of pressure and snake thickness. We obtained the scaling exponent for the relationship between peak pressure and snake diameter by computing the reduced major axis regression slope. Finally, we tested whether the expected and measured slopes were significantly different using a Student's *t*-test (Zar, 1984).

RESULTS

Snakes typically formed 0.5–2.0 loops around prey. Peak constriction pressures were 5–175 kPa (which is equivalent to 14–1,313 mm Hg and 0.76–25.00 PSI) in snakes with diameters of 0.85–12.5 cm (Fig. 2). In

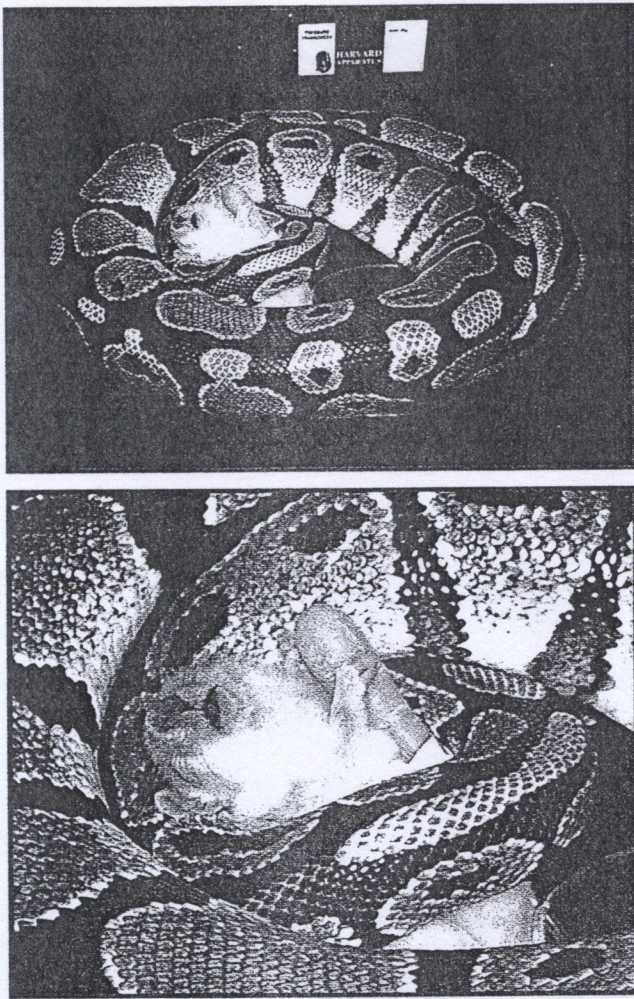


Fig. 1. A loosened coil in *Python regius* showing the snake, prey, and pressure transducer (top), and a close-up view showing the pipette bulb used as the pressure sensor for some prey and the tubing that connected it to the transducer (bottom). The rat prey shown here was purchased frozen from a commercial supplier and thawed before being offered to the snake.

general, doubling of snake diameter increased constriction pressure 2.6-fold. Because we could not be certain that snakes constricted with maximal effort, these measured pressures represent minimum constriction strengths.

Larger (thicker) snakes and snakes that used more loops exerted significantly higher pressures than other snakes (constriction pressure = $15.20 \times \text{diameter} + 16.41 \times \text{number of loops} - 29.43$; $R^2 = 0.91$, $F_{2,27} = 142$, $P < 0.001$). Because the bivariate relationship between snake diameter and peak constriction pressure suggested a nonlinear relationship (Fig. 2), we computed a quadratic regression. The equation for this relationship was $y = 30.3x - 1.1x^2 - 32.0$, where y = peak constriction pressure and x = snake diameter, but the fit was only marginally better ($R^2 = 0.92$, $F_{27} = 155$, $P < 0.001$) than that for the multiple regression. The bivariate

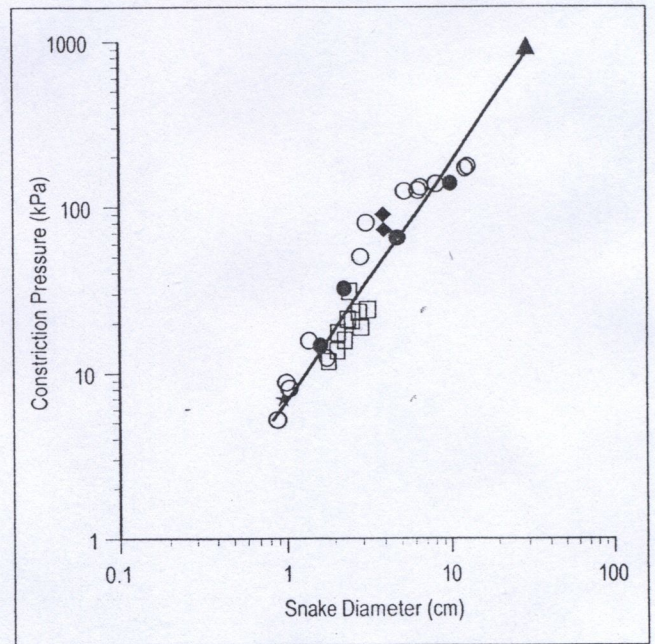


Fig. 2. Peak constriction pressures measured for snakes of different sizes ($N = 12$ species and 30 individuals). The line indicates a bivariate least-squares linear regression ($y = 7.72x^{1.39}$, $R^2 = 0.88$); the multiple regression that included both snake diameter in the region of coiling and number of loops is described in the text. Hollow circles indicate species of *Acrantophis*, *Boa*, *Charina*, *Lichanura*, and *Sanzinia*; diamonds indicate species of *Morelia*; solid circles indicate species of *Python*; squares indicate species of *Lampropeltis*, *Pantherophis* (= *Elaphe*), and *Pituophis*; the star indicates *Tropidophis haetianus*; and the triangle indicates the predicted pressure for a giant (30 cm in diameter) constrictor.

relationship between the number of loops in a coil and constriction pressure was much less clear ($R^2 = 0.25$) than that between snake diameter and pressure ($R^2 = 0.88$), perhaps because some parts of the coil pressed against the pressure transducer bulb only indirectly by pushing the prey against it from another direction.

Peak pressure scaled in proportion to snake diameter^{1.46} in the reduced major axis regression, which was significantly different from the predicted scaling with diameter². Peak constriction pressures varied somewhat among species. Species of *Acrantophis*, *Boa*, *Morelia*, and *Sanzinia* typically exerted above-average pressures, as indicated by the regression line (Fig. 2). Species of *Charina*, *Lichanura*, and *Python* exerted approximately average pressures. In contrast, colubrid snakes exerted pressures that were lower than average. Extrapolation based on the regression indicated that very large constrictors, such as Green Anacondas (*Eunectes murinus*) and Reticulated Pythons (*P. reticulatus*), may be able to constrict with pressures approaching 900 kPa (Fig. 2).

DISCUSSION

Constriction strength depends significantly on both size (diameter) and behavior (number of loops used in a coil). Thicker snakes and snakes that use more loops can immobilize and subdue larger prey animals than other snakes. The range of constriction pressures is impressive: the pressure exerted by living snakes increased as much as 33-fold (to 175 kPa) as snake diameter increased 15-fold (Fig. 2). This trend of greater constriction strength with increasing snake sizes and numbers of loops in a coil was clear, even though considerable variation existed among individuals of similar sizes. The lower than expected scaling exponent (pressure is proportional to diameter^{1.46} rather than diameter²) suggests that the scaling of constriction pressure reflects a compromise between pressure being proportional to the number of loops in a coil (i.e., to length¹) and to muscle cross-sectional area (length²).

The remarkable strengths of constrictors derive in part from the complex arrangement of the axial muscles, which overlap extensively along the body and act in parallel to generate the high forces used in constriction and other behaviors. Constriction behavior and strength are likely to vary with several factors, such as the size and anatomy of the musculature, type and activity level of prey, relative sizes of snakes and prey, conditions of snakes, number of loops used in a coil, position of a coil around the prey animal, age or experience, and snake body temperature. Each of these factors is known to vary, and some studies have demonstrated their effects on constriction behaviors used by snakes (Loop and Bailey, 1972; Willard, 1977; Greene and Burghardt, 1978; Greenwald, 1978; Shine and Schwaner, 1985; Jones, 1988; Mori, 1991, 1993a, 1996; de Queiroz, 1984; Moon, 2000; Lourdaïs et al., 2005; Mehta, 2005). Factors such as these probably contributed to the variation in pressure that we observed among similarly sized individuals of the same species.

The range of constriction pressures that we measured suggested that constriction can kill prey by suffocation, circulatory arrest, or spinal injury. Relatively low pressures sustained for a few minutes could cause suffocation (McLees, 1928; Hardy, 1994; Moon 2000). Higher pressures exerted for relatively brief periods could cause circulatory arrest, in which blood flow is stopped and death is rapid (Hardy, 1994; Moon 2000). In circulatory arrest, the pressure exerted on the animal disrupts or completely stops blood flow in the vessels, particularly low-pressure venous flow. Constriction pressure may also compress the pericardial space and

coronary vessels, which could lead to rapid and severe interference with cardiac function (Fessler et al., 1990; Hardy, 1994; Kaplan et al., 1995). Very high pressures exerted for relatively brief periods could cause cervical or spinal dislocation that would paralyze or kill even a large prey animal very rapidly, and hence safely for the snake. Cervical and spinal dislocations have been observed in caimans, capybaras, and deer constricted by anacondas (Rivas, 2004).

In the smallest snakes (~ 1 cm in diameter), constriction pressures were substantially lower than typical mammalian systolic blood pressures (i.e., in the major arteries). This suggests that small snakes kill small mammalian prey by suffocation rather than circulatory arrest. The irregular and seemingly uncoordinated constriction of some juvenile snakes (Mori, 1993a, b, 1994, 1995, 1996; Mehta, 2003, 2005) may contribute to the low constriction pressures exerted by small individuals. However, very small (nestling) mammals probably have lower blood pressures than adults, and thus may be killed by circulatory arrest even with low constriction pressures. Additional data on constriction pressures in small snakes and blood pressures in small rodents are needed to assess how constriction kills small prey.

In snakes approximately 2.00–2.25 cm in diameter, constriction pressures were equal to or slightly higher than the arterial systolic blood pressures of their mammalian prey (approximately 10–17 kPa in mice; Turney and Lockwood, 1986). Therefore, constrictors thicker than about 2 cm are probably capable of killing small mammals mainly by circulatory arrest. All that is required for circulatory arrest to occur is for constriction to close off several major veins, all of which have blood pressures only slightly above zero (Hardy, 1994). Pressures that are several fold higher than arterial blood pressures are likely to be an order of magnitude or more higher than venous pressures. Continued heartbeats would not be able to pump any blood because none would be returning to the heart. As a result, widespread tissue death and cardiac arrest would be very rapid. Suffocation would begin during constriction, but cessation of blood flow would cause death faster than suffocation (Hardy, 1994).

The high pressures exerted during constriction suggest that localized circulatory arrest may also occur in the muscles of a snake. This seems especially likely because of the low arterial blood pressures of snakes (5–10 kPa; Lillywhite, 1987a). However, adverse effects to the snake seem unlikely because snakes are tolerant of anoxia and can support activity using anaerobic metabolism (Bennett, 1982; Lillywhite, 1987b).

In the large snakes we measured (to 12.5 cm in diameter), constriction pressures were much higher (to 11-fold) than mammalian arterial blood pressures. These pressures are certainly high enough to kill many prey animals by circulatory arrest. With the right coil placement, these pressures are probably high enough to dislocate the neck or spine of a prey animal and damage its spinal cord (Rivas, 2004).

The broken necks and spines observed by Rivas (2004) in prey animals constricted by large *Eunectes murinus* probably involved torn ligaments and dislocated vertebral joints. The ultimate loads required to tear vertebral ligaments, and hence dislocate the vertebral column in mammals the size of humans, are probably on the order of 200 N (Iida et al., 2002). This is consistent with the maximum tendon strengths of approximately 200 MPa (or 200 N/mm²) in many animals (Summers and Koob, 2002), because, in small to medium-sized mammals, the ligaments in each vertebral joint probably have a total cross-sectional area of less than one to only a few mm². These values indicate that large constrictors are capable of dislocating the vertebral columns enough to damage the spinal cord in many prey animals.

This study concurs with many others in indicating that the evolutionary success of constrictors involved diverse yet highly integrated structures, physiological and biomechanical functions, and behaviors (see reviews by Cundall, 1987; Cundall and Greene, 2000). The incredible strength of constrictors is crucial to their ability to subdue prey of varying sizes, and was probably one of the key features associated with the evolution and adaptive radiation of snakes.

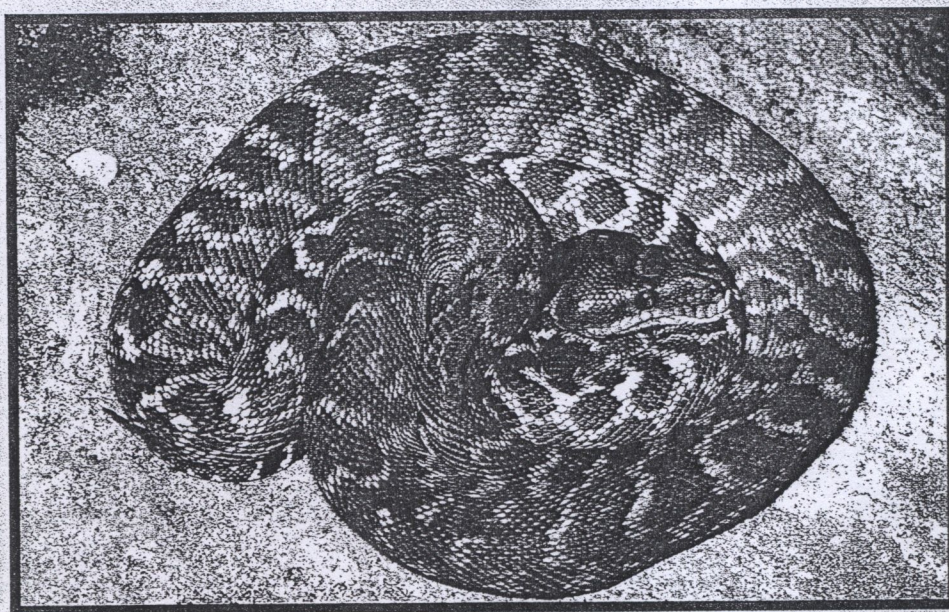
Acknowledgments.—For allowing us to measure their animals, we thank Stephen Secor and Brian Ott at the University of Alabama, Owen Maercks at the East Bay Vivarium, Jeremy Epstein at Upscale Reptiles, James Beck and the Zoo of Acadiana, and Jim O'Reilly. Specimens of *Lampropeltis getula* and *Pituophis catenifer* were collected under permits from the Arizona Game and Fish Department, and those of *Charina bottae* were collected under permits from the Washington Department of Fish and Wildlife. We are grateful to Joey Bennett, Bill Cefalu, Jr., Ben Dantzer, Craig Denesha, Gail Dodge, Carrie Duffek, Chris Fontenot, Michael Potter, Ali Rabatsky, Upscale Reptiles, and Katherine Wadsworth for help at various stages of this project. This work was conducted with IACUC approval, and was supported by American Psychological Association, the University of Louisiana at Lafayette, The University of Michigan, the

Department of Psychology at the University of Tennessee, Knoxville, and the Scholarly Activities Research Incentive Fund (SARIF) at the University of Tennessee.

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Morelia carinata has a very limited distribution in northwestern Western Australia, just inland from the coast. Because of the prominent keels on most of the dorsal scales, it is known as the Rough-scaled Python. This snake is from Hunter River, Kimberley, Western Australia.