SHORT COMMUNICATION

The big squeeze: scaling of constriction pressure in two of the world's largest snakes, *Python reticulatus* and *Python molurus bivittatus*

David A. Penning‡, Schuyler F. Dartez* and Brad R. Moon

ABSTRACT

Snakes are important predators that have radiated throughout many ecosystems, and constriction was important in their radiation. Constrictors immobilize and kill prey by using body loops to exert pressure on their prey. Despite its importance, little is known about constriction performance or its full effects on prey. We studied the scaling of constriction performance in two species of giant pythons (*Python reticulatus* and *Python molurus bivittatus*) and propose a new mechanism of prey death by constriction. In both species, peak constriction pressure increased significantly with snake diameter. These and other constrictors can exert pressures dramatically higher than their prey's blood pressure, suggesting that constriction can stop circulatory function and perhaps kill prey rapidly by over-pressurizing the brain and disrupting neural function. We propose the latter 'red-out effect' as another possible mechanism of prey death from constriction. These effects may be important to recognize and treat properly in rare cases when constrictors injure humans.

INTRODUCTION

Constriction behaviour was probably very important in the evolution and radiation of snakes, allowing for the subjugation of otherwise unobtainable prey, including large and potentially dangerous ones such as alligators, deer and, rarely, humans (Greene and Burghardt, 1978; Murphy and Henderson, 1997). Constricting snakes exert pressure by coiling around and squeezing their prey, typically killing it before swallowing (Moon and Mehta, 2007). Constriction takes energy and time, and risks injury to the snake (Murphy and Henderson, 1997; Moon and Mehta, 2007). Constriction performance is important because it can affect feeding success, and hence growth and fitness (Moon and Mehta, 2007).

Constriction pressures are generated by forces from the snake's axial musculature applied to the prey. These forces are proportional to the cross-sectional area of active muscle, and therefore to snake diameter (Moon and Mehta, 2007). Force production during constriction may also be increased by using more of the body because the segmental axial muscles act mainly in parallel (Moon and Mehta, 2007). As snakes increase in size, so should their peak

constriction pressures. However, constriction involves a dynamic interaction between predator and prey, and can have highly variable outcomes. Despite the widespread use of constriction, the cause of death during constriction has been uncertain; it may involve several non-exclusive mechanisms including suffocation, circulatory arrest or spinal injury (reviewed by Moon and Mehta, 2007). Moon (2000) first tested the possibility that constriction causes circulatory arrest and demonstrated that constriction pressure can be substantially higher than the systolic blood pressure of mice that are eaten by constrictors. Later, Moon and Mehta (2007) tested snakes of different species and sizes, and inferred that low pressures may cause suffocation, moderate pressures may cause circulatory arrest, and extremely high pressures may cause spinal injury. Boback et al. (2015) nicely extended this earlier work by directly measuring circulatory function in rats during constriction; they showed that a constriction pressure of 20 kPa can severely impede cardiac and circulatory function in rats. In the prey, heart rate decreased, cardiac electrical activity became abnormal, and blood pressure increased ca. sixfold in the vena cava near the heart and decreased by half peripherally in the femoral artery, all indicating that constriction can induce circulatory arrest (Boback et al., 2015). However, to our knowledge, no previous work has tested the effects of constriction pressure on neural tissue, one of the most immediately important tissue systems in the prey.

Giant snakes have fascinated humans for centuries (Murphy and Henderson, 1997). Despite such intense curiosity and ongoing study, we have yet to fully understand how these animals work, especially as predators. Snakes in the genus *Python* are typically highly stereotyped constrictors (Greene and Burghardt, 1978) and vary dramatically in body size. For example, both reticulated pythons (*Python reticulatus*) and Burmese pythons (*Python molurus bivittatus*) are born ca. 100–200 g in mass and 45 cm in length, and can reach maximum lengths of 8–10 m (Murphy and Henderson, 1997) and exceed 60 kg (this study). Accompanying this dramatic growth are shifts in reproductive output, energy stores, prey base, habitat use and other variables (Shine et al., 1998). However, to our knowledge, no data are available on predatory performance in either of these giant snakes, and no study has evaluated intraspecific scaling of constriction performance for any snake species. Here, we describe the ontogeny of constriction performance in reticulated and Burmese pythons and discuss how it relates to interspecific data from the literature. Lastly, we discuss the implications of our findings for the cause of prey death during constriction.

MATERIALS AND METHODS

This research was approved by the University of Louisiana at Lafayette's Institutional Animal Care and Use Committee. We tested 65 snakes in the collections of private breeders. *Python reticulatus* Schneider 1801 (*N*=48)

Department of Biology, University of Louisiana at Lafayette, Lafayette, LA 70504-43602, USA.
*Present address: Louisiana Department of Wildlife and Fisheries, White Lake Wetlands Conservation Area, Gueydan, LA 70542, USA.

‡Author for correspondence (davidapenning@gmail.com)

were 0.84–5.5 m long (snout–vent length, SVL) and 1.2–18.0 cm maximum diameter. *Python molurus bivittatus* Kuhl 1820 (*N*=17) were 0.83–3.7 m in SVL and 3.6–15.5 cm diameter. All snakes were fed live or recently killed prey (*Rattus norvegicus* and *Oryctolagus cuniculus*) with an attached pressure sensor. Prey type and size depended upon the owner's feeding regimen. Whenever we fed snakes pre-killed prey, we shook the prey with forceps or tongs to simulate activity and elicit maximal constriction performance (following Moon and Mehta, 2007).

For smaller snakes, we used a 2 ml water-filled rubber pipette bulb attached to the prey as a pressure sensor, connected to a Research Grade Blood Pressure Transducer (Model 60-3002, Harvard Apparatus, Holliston, MA, USA). For larger snakes, we used either a Pressure Manometer (Model SYS-PM100R, World Precision Instruments, Sarasota, FL, USA) with a water-filled 100 ml rubber pipette bulb as the sensor, or an Omega Instrument Remote Sensor attached to a DPI 705 Digital Pressure Indicator (Omega Engineering, Inc., Stamford, CT, USA) with an air-filled Inflatable Dent Remover Pad (Model LT-800, 20.32×20.32 cm, Lock Technology, Inc., Naperville, IL, USA) as the sensor. We loosely attached sensors to the prey's thoracic region with string, hook-and-loop straps, or tape. Once we instrumented the prey, we placed it in proximity to the snake. Snakes readily struck at, constricted and consumed their prey. We recorded peak constriction pressure (kPa), the number of loops used during constriction, and maximum snake diameter. We removed the pressure sensor when the snake began to swallow.

To assess constriction performance, we analysed the scaling of peak constriction pressure using least-squares multiple linear regression with peak pressure as the dependent variable and snake diameter and number of loops in a coil as independent variables (all non-transformed data). We also log-transformed our data and used *t*-tests to compare our regression coefficients to interspecific values from Moon and Mehta (2007). We performed analyses in R Studio and Past 3, and removed non-significant factors to arrive at the final models (considered significant at *P*<0.05).

RESULTS AND DISCUSSION

Reticulated and Burmese pythons both constricted the prey vigorously using coils of 1–4 loops (Fig. 1). Reticulated pythons exerted maximum pressures of 8.27–53.77 kPa, with larger individuals exerting significantly higher peak pressures than smaller individuals (constriction pressure=15.17+diameter×1.39; R^2=0.29, $F_{1,46}$=19.06, *P*<0.0001; Fig. 1). Burmese pythons constricted with maximum pressures of 18.0–42.93 kPa, with larger individuals exerting significantly higher peak pressures than smaller individuals (constriction pressure=17.7+diameter×1.42; R^2=0.61, $F_{1,15}$=26.56, *P*<0.0002; Fig. 1). In a multiple linear regression with a species×diameter interaction (overall $F_{3,61}$=9.325, *P*<0.0001), the slopes (interaction *t*=0.04, *P*>0.96) and intercepts (*t*=0.43, *P*>0.66) did not differ significantly between these species. The number of loops in a coil did not significantly affect peak pressure in either species (reticulated *t*=0.42, *P*>0.6; Burmese *t*=0.32, *P*>0.7), in contrast to the results of Moon and Mehta (2007). Reticulated and Burmese pythons used a broader range of loops than other species (1–2 loops were reported by Moon and Mehta, 2007), and it seems likely that the pattern observed across multiple species is not a reliable predictor of behaviour within any one of the species. It is also possible that different loops within a coil exert different forces, and hence contribute differently to the overall pressure experienced by the prey. For example, one loop may exert maximum force while others hold the prey in place, preventing escape but not exerting maximum force.

Log-transformed constriction pressure in both species scaled with significantly lower slopes ($\beta_{reticulated}$=0.25, $\beta_{Burmese}$=0.33) than the interspecific data reported by Moon and Mehta (2007; β=1.39; t_{46}=13.21, *P*<0.0001 and t_{15}=11.24, *P*<0.0001, respectively; Fig. 2). The lower slopes within species than
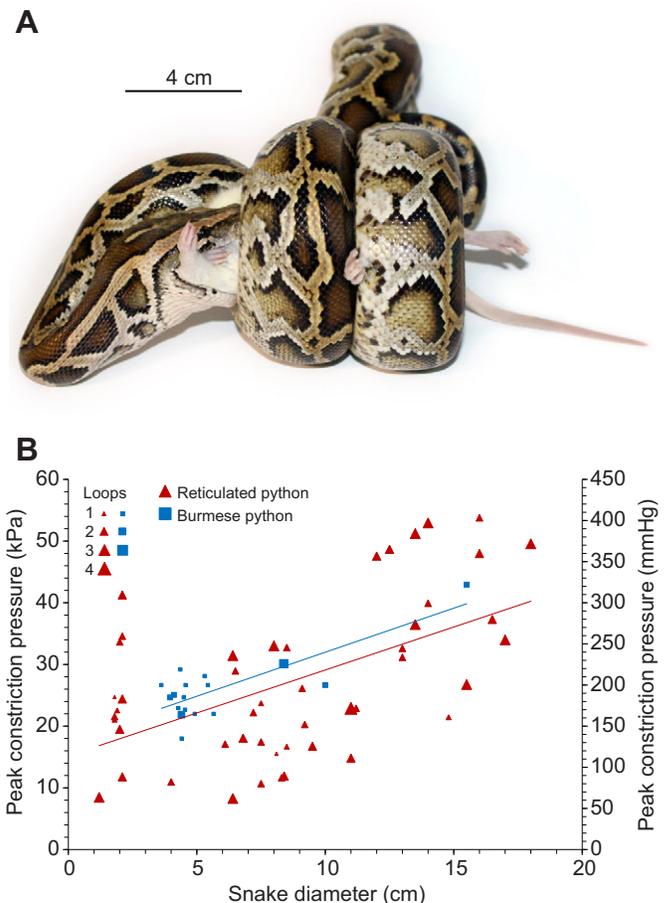

Fig. 1. Constricting pythons coil around and squeeze prey animals, which exerts pressure on the prey that scales positively with snake diameter. (A) A 1081 g juvenile Burmese python (*Python molurus bivittatus*) constricting a lab rat (*Rattus norvegicus*) weighing 99 g. (B) The scaling relationship between peak constriction pressure and snake diameter. See Results and Discussion for description of the regression model.

between species could result from several factors. Constriction requires muscle exertion, and therefore energy; so snakes may modulate their effort and use submaximal but fully sufficient performance, conserving energy in the process. For example, one of our smallest snakes was capable of generating pressures comparable to those of some of the largest pythons tested (Fig. 1), suggesting that the larger pythons were not using their maximum capacities to subdue prey. However, a large snake has a large diameter, and therefore a larger surface area over which it exerts force, although the relationships among force, surface area and pressure are not yet well quantified in snakes. It is possible that larger snakes exert maximum force during constriction, but the area over which it is exerted on the prey results in lower overall pressure. Reticulated and Burmese pythons were not available for the interspecific study by Moon and Mehta (2007), and the species they used were not available in sufficient numbers for this study. When comparing individual performance, the pressures generated by small reticulated and Burmese pythons (<6 cm in diameter) are similar to those of small pythons reported by Moon and Mehta (2007). Moon and Mehta (2007) reported constriction pressures of four snakes with diameters >7 cm; we recorded pressures from 34 snakes with diameter >7 cm. The incorporation of more large snakes from additional species would result in a different interspecific scaling
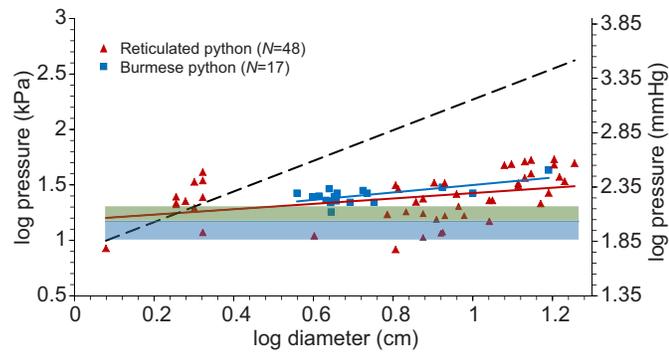
Fig. 2. Constriction pressure scales differently in *Python reticulatus* and *P. molurus bivittatus* than in other species. The interspecific slope (dashed line) from Moon and Mehta (2007) represents 30 snakes from 12 species, ranging in size from 0.85 to 12.5 cm in diameter. Blood pressure values (top green bar, systolic; bottom blue bar, diastolic) are from mice, rats, rabbits, sheep and humans (Flindt, 2003).

exponent. Furthermore, relative meal size decreased in larger snakes because larger prey were not available, although previous work had the same limitation. Lastly, these differences may arise from as yet unidentified factors. Despite the different scaling results between studies, the constriction pressures generated by all snakes were effective in killing their prey quite rapidly. Although the constriction pressures exerted by reticulated and Burmese pythons scale differently from those of other snakes, many of the highest pressures (ca. 52 of the 65 data points) were probably high enough to force blood into the brain at high pressure in mammalian prey (Fig. 2).

In addition to suffocation, circulatory arrest and spinal dislocation, we propose the 'red-out effect' (Balldin, 2002) as a fourth possible mechanism of prey death by constriction. The red-out effect describes the effect of negative gravity on jet pilots during extreme flight manoeuvres, in which vision becomes reddened by uncontrollable blood flow to the brain and eyes (Balldin, 2002). When fighter pilots experience negative gravitational accelerations (G-forces), they incur a rush of blood to the brain that causes rapid loss of consciousness (Balldin, 2002). Constriction pressures above the venous blood pressure of the prey will impede blood flow and oxygen delivery to tissues (reviewed by Moon and Mehta, 2007; Boback et al., 2015). Constriction pressures dramatically higher than the prey's blood pressure could force blood away from the site of constriction and into the extremities, including the head and brain. We recorded maximum pressures of ca. 55 kPa from reticulated and Burmese pythons, and previous work has recorded pressures as high as 175 kPa (Moon and Mehta, 2007). Both of these values are well above the normal blood pressures of mammals (Flindt, 2003). Blood being pushed into the brain during peak constriction exertion could cause the same red-out effect described above for pilots, and could cause extensive ruptures in cranial blood vessels.

Accompanying forced haemorrhaging caused by high constriction pressures is the potential for immediate neural disruption and damage. Interfering with the nervous system of prey hinders their defensive capabilities, further reducing the risk of injury to the snake. Neural tissue is sensitive to pressure and can deform, tear and cease function entirely (Toth et al., 1997; Courtney and Courtney, 2009). Shockwave and concussive-impact pressure effects on the brain cause neural damage and failure when in the range of 55–300 kPa during transient exposures (Courtney and Courtney, 2009). Directed

pressures of ca. 140 kPa for only 20 ms on the dura of rats causes immediate incapacitation for 120–200 s (Toth et al., 1997), although lower pressures comparable to those we recorded during constriction were not tested. Pressure is probably not a localized phenomenon that dissipates near impact sites, but can travel through tissues and structures from the site of impact (e.g. constriction coil) to the neural tissue, damaging it and perhaps immediately stopping function (Courtney and Courtney, 2009).

Most pythons in this study exerted lower pressures than those reported in the literature on brain impacts, although several reached the lower range of damagingly high pressures, and other snakes can exert pressures up to ca. 175 kPa (Moon and Mehta, 2007). Pressure-wave impacts occur over milliseconds, whereas snakes constrict for orders of magnitude longer. Based on our current knowledge of how pressure affects tissues, it is likely that high constriction pressures are capable of interfering with, or completely disabling, both circulatory and neural function (Toth et al., 1997; Moon, 2000; Moon and Mehta, 2007; Courtney and Courtney, 2009; Boback et al., 2015). The world's largest snakes are capable of quickly incapacitating large and potentially dangerous prey by causing multiple kinds of injuries. The dynamic interactions, movements and resulting postures that occur during predation probably determine which kinds of injury occur, are most severe, and subdue the prey most rapidly. Furthermore, these diverse effects may be important to recognize and treat properly in those rare cases when large constrictors injure humans.

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