

RESEARCH ARTICLE

The king of snakes: performance and morphology of intraguild predators (*Lampropeltis*) and their prey (*Pantherophis*)

David A. Penning^{1,2,*} and Brad R. Moon¹**ABSTRACT**

Across ecosystems and trophic levels, predators are usually larger than their prey, and when trophic morphology converges, predators typically avoid predation on intraguild competitors unless the prey is notably smaller in size. However, a currently unexplained exception occurs in kingsnakes in the genus *Lampropeltis*. Kingsnakes are able to capture, constrict and consume other snakes that are not only larger than themselves but that are also powerful constrictors (such as ratsnakes in the genus *Pantherophis*). Their mechanisms of success as intraguild predators on other constrictors remain unknown. To begin addressing these mechanisms, we studied the scaling of muscle cross-sectional area, pulling force and constriction pressure across the ontogeny of six species of snakes (*Lampropeltis californiae*, *L. getula*, *L. holbrooki*, *Pantherophis alleghaniensis*, *P. guttatus* and *P. obsoletus*). Muscle cross-sectional area is an indicator of potential force production, pulling force is an indicator of escape performance, and constriction pressure is a measure of prey-handling performance. Muscle cross-sectional area scaled similarly for all snakes, and there was no significant difference in maximum pulling force among species. However, kingsnakes exerted significantly higher pressures on their prey than ratsnakes. The similar escape performance among species indicates that kingsnakes win in predatory encounters because of their superior constriction performance, not because ratsnakes have inferior escape performance. The superior constriction performance by kingsnakes results from their consistent and distinctive coil posture and perhaps from additional aspects of muscle structure and function that need to be tested in future research.

KEY WORDS: Constriction, Cross-sectional area, Force, Muscle, Pressure, Scaling

INTRODUCTION

The structure and function of an organism relate in part to predatory and anti-predator adaptations (Darwin, 1859; Wainwright, 1994). Predators are generally larger than their prey (Arnold, 1993; Radloff and Du Toit, 2004), and as prey increase in size relative to their predators, they become less vulnerable to predation (Magalhães et al., 2005). Furthermore, as trophic ranks (Holt et al., 1999) converge between predators (i.e. intraguild competitors; Polis et al., 1989), predators become less likely to attack prey greater than 25–50% of their own mass (Buskirk, 1999; Palomares and Caro, 1999; Wise, 2006). When the predator and prey are closely matched in size and have similar feeding morphology, an attack can bring

such a high risk to the predator that it might be avoided entirely, even if the benefits of successful predation would be high (Donadio and Buskirk, 2006). However, some snakes consume intraguild prey that are well matched in predatory abilities and in some cases are even larger than themselves (Jackson et al., 2004).

Modifications of the feeding apparatus have allowed many snakes, including ones that eat other snakes (ophiophagous), to incorporate massive prey into their diets (Traill, 1895; Smith, 1910; Greene, 1997; Cundall and Greene, 2000; Jackson et al., 2004; Leong and Shunari, 2010). Many ophiophagous snakes are venomous (Greene, 1997), effectively offsetting the risks associated with trophic similarity between similarly sized combatants; often only a single bite is needed to subdue prey. Non-venomous ophiophagous snakes must use other prey-handling behaviors, such as constriction. Kingsnakes (genus *Lampropeltis* Fitzinger 1843) are non-venomous, constricting snakes that are well known for the ability to consume other snakes (Ernst and Ernst, 2003), including ones that are larger than themselves (Jackson et al., 2004). Surprisingly, kingsnakes are able to capture, constrict and fully ingest other snakes (such as ratsnakes in the genus *Pantherophis* Fitzinger 1843) that seem well matched in predatory ability, in that they are effective constrictors on some of the same kinds of rodents that kingsnakes eat. Furthermore, the prey snake can be larger than the kingsnake (Ernst and Ernst, 2003; Jackson et al., 2004). There is currently no known mechanism that differentiates the abilities of these two constricting snakes, yet kingsnakes always seem to subdue ratsnakes and ‘win’ the predatory encounter (Jackson et al., 2004). Here, we sought to understand how this one-sided predation event is possible.

Morphology and physiology set the functional limitations on predator–prey dynamics (Webb, 1986). Although both morphology and physiology are important, behavior can determine the ways in which morphological elements and physiological capacities are used (Hertz et al., 1982). For snakes that use constriction behavior, predation performance can be evaluated by measuring peak constriction pressure (Moon, 2000; Moon and Mehta, 2007; Boback et al., 2015; Penning et al., 2015; Penning and Dartez, 2016). Constriction pressure is a biologically important measure of performance (Moon and Mehta, 2007) because it can determine the time needed to subdue the prey and reduces the chances of prey escaping or causing injury to the snake. Potential ways of escaping from a constriction coil include pulling out of the coil, counter-constricting to make the aggressor release its coil, and clawing or biting to gain release. Therefore, pulling force is a potentially important measure of performance in snakes because it indicates a snake’s ability to escape from the grip of a predator (Lourdais et al., 2005). Geometric scaling offers testable *a priori* expectations as to how force production scales with body size (Pennycuik, 1992). Because muscle force is proportional to muscle cross-sectional area (MacIntosh et al., 2006), we expect pulling force to scale with snake body mass^{0.66}.

Both predation (constriction pressure) and escape (pulling force) performance are affected by the cross-sectional area (CSA) of

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muscle (Moon and Candy, 1997; Lourdaï et al., 2005), and in principle can use up to about half of a snake's axial musculature (e.g. all the muscles on the concave parts of a constriction coil or on the concave parts of multiple axial bends used in pulling movements). Larger snakes have more muscle CSA (Moon and Mehta, 2007); therefore, changes in body size can be expected to have significant effects on these measures of performance in snakes (Moon and Mehta, 2007; Penning et al., 2015; Penning and Dartez, 2016). Although *a priori* expectations can be generated regarding the scaling of muscle force (Pennycuik, 1992), constriction pressure is much more variable (Moon and Mehta, 2007; Penning et al., 2015; Penning and Dartez, 2016) and depends on the area of contact and force exertion. It is not clear *a priori* how the surface area of contact should change with size during the dynamic interaction between predator and prey (Penning et al., 2015). Given that the relationship between constriction pressure and the surface area of contact has not yet been quantified for snakes of any size, we do not have enough information to generate testable hypotheses about the predicted scaling of constriction pressure with body size. Although constriction pressure and pulling force are distinct variables that are typically related to different behaviors, they are appropriate indicators of predation and escape performance in snakes (Moon, 2000; Lourdaï et al., 2005; Moon and Mehta, 2007; Boback et al., 2015; Penning et al., 2015; Penning and Dartez, 2016). Therefore, they can be compared across species and sizes to understand the factors that affect the outcome of this predator–prey interaction.

To understand how one constricting snake can capture, subdue and consume another constricting snake with similar predatory and defensive mechanisms, we quantified and compared muscle CSA, and measures of predation performance and escape performance across the ontogeny of two intraguild competitors, kingsnakes and ratsnakes. We chose the study species based on previously published work on intraguild predation in snake-eating snakes, dietary records, and geographic distributions (Ernst and Ernst, 2003; Jackson et al., 2004). We used three species of kingsnakes: *Lampropeltis californiae* (Blainville 1835), *Lampropeltis getula* (Linnaeus 1766) and *Lampropeltis holbrooki* (Stejneger 1903); and three species of ratsnakes: *Pantherophis alleghaniensis* (Holbrook 1836), *Pantherophis guttatus* (Linnaeus 1766), and *Pantherophis obsoletus* (Say 1823) (Pyron et al., 2013).

We address several questions about how form and function change across ontogeny and differ between species (*Lampropeltis* spp. and *Pantherophis* spp.). How does axial muscle CSA vary and change with size in kingsnakes and ratsnakes? What constriction pressures are exerted on prey and how do they change with size? What pulling forces can these snakes produce during escape attempts, and how do they change with size? We discuss several possible mechanisms that can determine the winner of predatory interactions between two constricting snakes.

MATERIALS AND METHODS

We chose our overall sample sizes based on available specimens and previously published work for both morphological (Jayne and Riley, 2007; Herrel et al., 2011) and performance investigations (Moon and Mehta, 2007; Penning et al., 2015; Penning and Dartez, 2016). For each experiment below, we provide the sample size for that specific experiment.

Morphology and scaling

We measured the morphology of 36 preserved snakes (4 *L. holbrooki*, 9 *L. getula*, 8 *P. guttatus* and 15 *P. obsoletus*) from a teaching collection (University of Louisiana at Lafayette) or the personal

collection of D.A.P. (20 females, 16 males). We lacked specimens for measuring the morphology of *L. californiae* and *P. alleghaniensis*. We weighed each snake and measured its snout–vent length (SVL). All specimens experienced similar fixation and preservation durations. Although some tissue dehydration might have occurred, the results would be consistent across all specimens (Herrel et al., 2014). Because snakes are known to exhibit longitudinal variation in external shape and in muscular anatomy (Nicodemo, 2012), we quantified their muscle CSA along the body. Specifically, we cut each specimen into sections at 20, 40, 60, 80 and 100% of its SVL (i.e. down to the cloaca, based on our observations that the tail typically is not involved in a constriction coil), photographed each cross-section, and measured the anatomical CSA of major muscle groups (see below). For small cross-sections, we used a Canon EOS Rebel T5i digital camera attached to a Zeiss Stemi 2000-C stereoscopic microscope, with the cross-sections immersed in 70% isopropyl alcohol. For larger cross-sections, we used an Olympus Stylus Tough TG-630 digital camera. Each photograph included a scale; we confirmed that the images had square pixels, making a single scale appropriate. We measured the muscle CSA of five epaxial muscles (semispinalis–spinalis complex, multifidus, longissimus dorsi and iliocostalis; Fig. 1) in each section of the body (following Jayne and Riley, 2007; Herrel et al., 2011) using ImageJ software (NIH; <https://imagej.nih.gov/ij/>) (following Herrel et al., 2011). We chose this method of measuring muscle CSA to follow previous methods (Lourdaï et al., 2005; Jayne and Riley, 2007; Herrel et al., 2011) and because a simple measure of external body width (a dimension of length) would represent only half of the possible variation in muscle cross-sectional area (length²); furthermore, previous work has shown that although linear measures are significantly related to muscle cross-sectional areas, they miss a considerable portion of the variation in muscle cross-sectional area (Lourdaï et al., 2005, found that $R^2=0.73$ for this relationship).

Predation performance

All experimentation was approved by the University of Louisiana at Lafayette's Institutional Animal Care and Use Committee (approval no. 2016-8717-006). We tested the constriction performance of 182 snakes (21 *L. californiae*, 12 *L. holbrooki*, 56 *L. getula*; 21 *P. alleghaniensis*, 22 *P. guttatus* and 50 *P. obsoletus*),

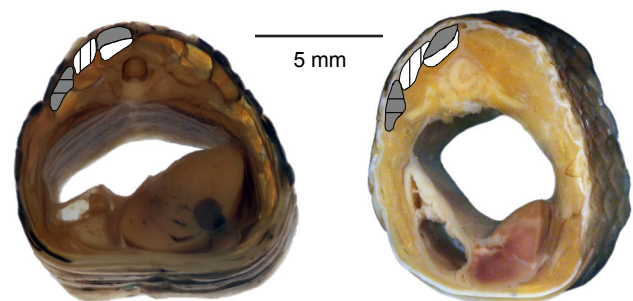


Fig. 1. Anatomical cross-sections of kingsnakes and ratsnakes.

Photograph of anatomical cross-sections taken at 40% of snout–vent length for a small kingsnake (left, *Lampropeltis getula*, 20.1 g) and ratsnake (right, *Pantherophis guttatus*, 18.8 g). Major epaxial muscles are delineated with plain gray (semispinalis–spinalis complex), plain white (multifidus), hatched white (longissimus dorsi) and hatched gray (iliocostalis). Cross-sections of the liver can be seen in the bottom right in both specimens, with the stomach to the left. Photographs of 40% SVL were chosen based on image quality.

encompassing 98 females and 84 males. Kingsnakes and ratsnakes eat a variety of prey, but all frequently consume small mammals (Ernst and Ernst, 2003). To compare constriction performance between snakes, we fed all snakes pre-killed rodents (mass ratio = $15.2 \pm 0.6\%$ snake mass, mean \pm s.e.m.) with an attached pressure sensor. The prey sizes were within the normal range reported in the literature from dietary records (Rodríguez-Robles, 2002) and previous work on constriction performance (Moon and Mehta, 2007; Penning et al., 2015; Penning and Dartez, 2016). Dead prey are commonly used to measure maximum constriction pressures (Moon and Mehta, 2007; Penning et al., 2015; Penning and Dartez, 2016), and manually simulating movements in dead prey produces similar results to those from constriction of live prey (Moon, 2000). We placed pressure sensors externally on the prey and anchored them in place with wax-coated string; this placement yielded similar sensitivities and outputs to internal placement of the sensor (Penning and Dartez, 2016). For smaller snakes (<0.5 m), we used a 0.5 ml water-filled latex balloon as the pressure sensor, and for larger snakes we used a 2 ml water-filled rubber pipette bulb as the pressure sensor. Both sensors are made of similarly compliant materials that transmitted applied force to the transducer. In pilot tests, both sensors produced accurate and repeatable results when known forces were applied.

We connected the pressure sensor to a research-grade blood pressure transducer (model 60-3002, Harvard Apparatus, Holliston, MA, USA) and offered prey to each snake with long forceps. We shook the prey to simulate movement and elicit a strong response from each snake (following Moon and Mehta, 2007; Penning and Dartez, 2016). Each snake participated in one to three constriction trials and experienced simulated struggling for 5 min with limb and body twitches approximately every 10 s. If we recorded multiple constriction events from a single snake, we analysed the single feeding event with the highest constriction pressure (Moon, 2000). During the constriction event, we recorded peak constriction pressure from the digital readout built into the transducer (which had a refresh rate of 2 Hz) and the number of loops used in the constriction coil. We report peak constriction pressure as the response variable based on previously published methods (Moon and Mehta, 2007; Penning et al., 2015; Penning and Dartez, 2016) and our current experimental design. Constricting snakes are known to respond to prey cues and will downregulate constriction performance when prey movement ceases (Moon, 2000; Boback et al., 2012). Because we offered pre-killed prey and controlled all prey movements, we did not measure pressure exertion over time. When we stopped simulating prey-struggling, all snakes responded by reducing their constriction pressures. Once peak constriction pressure began to decline, we removed the pressure sensor from the prey and the snakes completed the feeding event. While snakes were swallowing their prey, we measured their maximum diameters with digital calipers (Series 500, Mitutoyo, Aurora, IL, USA).

Escape performance

We tested maximum pulling forces of 98 snakes (7 *L. californiae*, 7 *L. holbrooki*, 32 *L. getula*; 8 *P. alleghaniensis*, 6 *P. guttatus* and 38 *P. obsoletus*) encompassing 53 females and 45 males. To measure maximum pulling force, we anchored each snake to a large flat surface using gaffer's tape placed just behind the head. We attached a Pesola scale (Rebmattli 19, CH-6340 Baar, Switzerland) to the snake just anterior to the cloaca with gaffer's tape. Pesola scales showed no signs of drift when tested repeatedly over 5 min periods with weights of approximately 50% of the total measurement capacity of the scale. We chose the scale size for each snake based

on pilot data and with the capacity to measure twice the pulling-force capacity of the snake (snake pulling force/scale force maximum = $51 \pm 3\%$). Further, Pesola scales provided similar and repeatable results when calibrated against an isometric force transducer (MLT500/A, AD Instruments, Colorado Springs, CO, USA). Once the scale was attached, we manually straightened the snake to its maximum length and anchored the spring scale with tape to the flat surface. We then gently agitated the anchored snake to elicit a pulling motion for 5 min (Lourdais et al., 2005, methodology summarized in fig. 2). As the snake attempted to pull free from linear subjugation, it pulled against the spring scale and displaced a marker on the scale. We used a GoPro Hero 4 Black camera (GoPro, Inc., San Mateo, CA, USA) to record spring scale displacements during the pulling movements (720 pixel video at 60 frames s^{-1}). Using Tracker 4.87 software (Open Source Physics, <http://www.opensourcephysics.org/index.cfm>), we advanced frame by frame and recorded the maximum pulling force for each snake during its 5 min trial, and then converted the scale values from mass (g) to pulling force (N).

Statistical analyses

We used \log_{10} -transformed data for all models. To quantify the scaling of muscle CSA against body mass, we used reduced major axis (RMA) regression (Smith, 2009). To test for differences in slopes and elevations between kingsnakes and ratsnakes, we added snake species as a categorical variable to the RMA regressions; this is the RMA equivalent of ANCOVA (in the `smatr 3` code package in RStudio; Warton et al., 2012) and allows for comparisons between slopes (factor A \times factor B) and intercepts (factor A + factor B) in models with a categorical predictor. To evaluate constriction performance, we used ordinary least-squares (OLS) multiple regression with peak constriction pressure as the dependent variable, and snake species, maximum body diameter and the number of loops used in a coil as independent variables. To evaluate pulling force, we used OLS multiple regression with pulling force as the dependent variable, snake species as a categorical variable, and snake body mass as the independent variable. Following previous methods (Herrel et al., 2011; Penning, 2016) and the general recommendations for regression analyses based on regression-line symmetry (Smith, 2009), we used RMA regression for comparisons between two morphological variables and OLS regression for comparisons between one morphological and one performance variable. We retained all data in all models because the results were the same with all data retained and with outliers removed. All statistical tests were considered significant when $P < 0.05$. We performed analyses in JMP Pro 11.0.0 (SAS Institute Inc., Cary, NC, USA), RStudio (version 0.99.441; <http://www.rstudio.com/>), and Past 3.08 (Hammer et al., 2001).

RESULTS

Morphological scaling

The five major epaxial muscles were easily delineated in most cross-sections (Fig. 1). For 11 of the cross-sections, we had to confirm muscle identities and boundaries with further probing and visual inspection. Muscle cross-sectional areas varied at each position along the body (Table 1). We did not have specimens available for quantifying muscle CSA in *L. californiae* and *P. alleghaniensis*. Muscle CSA increased with body mass in all cross-sections in all species (Table 2); in most sections and species, CSA also scaled with positive allometry (slope greater than 0.67). At each position along the body, the slopes (mass \times species interaction; Table 2) and intercepts (mass + species) for muscle CSA did not differ

Table 1. Descriptive statistics of body mass and muscle cross-sectional area (CSA) in kingsnakes (*Lampropeltis* spp.) and ratsnakes (*Pantherophis* spp.)

Species	N	Body mass (g)	Muscle CSA				
			20% SVL	40% SVL	60% SVL	80% SVL	100% SVL
<i>L. getula</i>	4	32±13.8 (14–74)	0.07±0.04 (0.02–0.19)	0.065±0.02 (0.03–0.13)	0.06±0.02 (0.02–0.10)	0.04±0.008 (0.02–0.06)	0.02±0.005 (0.02–0.04)
<i>L. holbrooki</i>	9	272±91.8 (12–634)	0.37±0.11 (0.03–0.87)	0.39±0.12 (0.03–0.88)	0.36±0.12 (0.03–0.93)	0.32±0.10 (0.02–0.82)	0.15±0.05 (0.01–0.37)
<i>P. guttatus</i>	8	107±78.2 (9–652)	0.18±0.13 (0.036–1.05)	0.20±0.13 (0.04–1.12)	0.19±0.13 (0.04–1.05)	0.14±0.09 (0.03–0.77)	0.08±0.04 (0.015–0.37)
<i>P. obsoletus</i>	15	494±110 (14–1274)	0.55±0.11 (0.05–1.39)	0.66±0.13 (0.04–1.70)	0.72±0.15 (0.04–1.94)	0.69±0.16 (0.03–2.12)	0.36±0.08 (0.01–1.03)

Values are mean±s.e.m. with ranges in brackets.

Muscle CSA was measured in cm² at each position along the body (% of SVL).

significantly among species of *Lampropeltis* or *Pantherophis* (all $P>0.05$; Table 2). Across ontogeny, muscle CSA at each location increased similarly in all species (Table 2).

Predation performance

All snakes readily struck at and constricted rodent prey vigorously using one to three loops of the body in a coil. Kingsnakes typically constricted using a single posture (Fig. 2A), with multiple loops forming a tight coil like that of a spring; 91% of the 89 kingsnakes used such a coil. Peak constriction pressures were 5.3–41.6 kPa for kingsnakes and 3.2–23.7 kPa for ratsnakes (Table 3). Ratsnake constriction postures were much more variable than the typical kingsnake posture, with loops placed at different positions and angles on prey, loops that overlapped one another, and with the ratsnake's head inside or outside the coil (Fig. 2B). Of the 93 ratsnakes, only 5.4% used spring-like coils. Across all six species, there was no significant difference between the number of loops used in a coil (Kruskal–Wallis $H=6.8$, $P>0.23$; Table 3).

Starting with a full-factorial model (pressure=diameter×number of loops×species), we sequentially removed non-significant factors to arrive at the final model (pressure=diameter+number of loops+species; $F_{7,174}=61.3$, $P<0.001$, adjusted $R^2=0.70$). Diameter ($F_{1,174}=148.1$, $P<0.0001$), number of loops ($F_{1,174}=9.88$, $P<0.003$) and species ($F_{5,174}=18.65$, $P<0.0001$) were all significant factors in the final model. Within each genus, there were no significant pair-wise differences between covariate-adjusted means for peak constriction pressure (Tukey's HSD tests; Fig. 3). However, kingsnakes constricted with higher pressures than ratsnakes (Fig. 3).

To analyse the scaling of constriction performance across body size the same way as in previous work (Moon and Mehta, 2007; Penning et al., 2015; Penning and Dartz, 2016), we regressed peak constriction pressure against snake diameter. Diameter ($F_{1,175}=300.1$, $P<0.0001$) and species ($F_{5,175}=18.4$, $P<0.0001$) were significant factors. The interaction (diameter×species) was not significant ($F_{5,170}=0.38$, $P>0.8$), resulting in a similar scaling relationship between pressure and snake diameter for all six species (overall $\beta=0.88$). As with the full model, there were no significant differences between species in covariate-adjusted means within each genus (Tukey's HSD tests, all $P>0.05$). However, all kingsnake means were significantly higher than all ratsnake means (Tukey's HSD tests, all $P<0.05$; Fig. 4).

Escape performance

In the tests of escape performance, snakes bent their bodies into S-shaped curves and pulled against the Pesola scale in attempts to free themselves. Restrained snakes typically exerted their maximum pulling forces <1.5 min into the 5 min trial. Maximum pulling forces ranged from 0.9 to 24.5 N (Table 3). In a full model (pulling force=mass×species), the interaction ($F_{5,86}=0.25$, $P>0.9$) and species factor ($F_{5,86}=2.1$, $P>0.068$) were not significant. Removing the interaction term did not result in a significant species effect, producing a final model that included only pulling force and mass. Larger snakes pulled with significantly higher forces than smaller individuals, regardless of species (pulling force=0.69×mass–0.68; $F_{1,96}=1967$, $R^2=0.95$, $P<0.0001$; Fig. 5). Maximum pulling force scaled isometrically with body size ($\beta=0.69$; 95% CI=0.65–0.72).

DISCUSSION

Morphology and scaling

At every position sampled along the body, muscle CSA scaled positively with body mass in both kingsnakes and ratsnakes, and

Table 2. Species comparisons of the scaling relationships for muscle cross-sectional area (CSA) relative to body mass for kingsnake species (*Lampropeltis* spp.) and ratsnake species (*Pantherophis* spp.)

Position (% of SVL)	Species	Slope	Intercept	R ²	Species×mass	Species+mass
20	<i>L. getula</i>	1.25 (0.80, 1.94)	−3.34 (−3.86, −2.22)	0.98	<i>P</i> >0.23 (4.3)	<i>P</i> >0.53 (2.2)
	<i>L. holbrooki</i>	0.80 (0.74, 0.86)	−2.64 (−2.47, −2.21)	0.99	–	–
	<i>P. guttatus</i>	0.85 (0.69, 1.06)	−2.76 (−2.76, −2.16)	0.95	–	–
	<i>P. obsoletus</i>	0.79 (0.73, 0.85)	−2.64 (−2.49, −2.19)	0.98	–	–
40	<i>L. getula</i>	0.95 (0.35, 2.53)	−2.60 (−4.17, −1.02)	0.86	<i>P</i> >0.91 (0.52)	<i>P</i> >0.63 (1.78)
	<i>L. holbrooki</i>	0.79 (0.72, 0.85)	−2.27 (−2.41, −2.13)	0.99	–	–
	<i>P. guttatus</i>	0.82 (0.64, 1.05)	−2.32 (−2.67, −1.98)	0.94	–	–
	<i>P. obsoletus</i>	0.80 (0.73, 0.89)	−2.31 (−2.51, −2.12)	0.97	–	–
60	<i>L. getula</i>	0.83 (0.68, 0.98)	−2.48 (−3.96, −1.00)	0.84	<i>P</i> >0.95 (0.31)	<i>P</i> >0.18 (4.90)
	<i>L. holbrooki</i>	0.87 (0.73, 1.03)	−2.53 (−2.85, −2.20)	0.96	–	–
	<i>P. guttatus</i>	0.82 (0.68, 0.99)	−2.35 (−2.60, −2.10)	0.97	–	–
	<i>P. obsoletus</i>	0.83 (0.76, 0.91)	−2.36 (−2.54, −2.19)	0.98	–	–
80	<i>L. getula</i>	0.63 (0.19, 2.07)	−2.33 (−3.68, −0.97)	0.76	<i>P</i> >0.48 (2.47)	<i>P</i> >0.39 (2.96)
	<i>L. holbrooki</i>	0.88 (0.72, 1.09)	−2.61 (−3.01, −2.22)	0.95	–	–
	<i>P. guttatus</i>	0.79 (0.62, 1.01)	−2.41 (−2.72, −2.10)	0.94	–	–
	<i>P. obsoletus</i>	0.92 (0.86, 0.98)	−2.63 (−2.77, −2.49)	0.99	–	–
100	<i>L. getula</i>	0.55 (0.34, 0.88)	−2.41 (−2.80, −2.02)	0.97	<i>P</i> >0.16 (5.12)	<i>P</i> >0.39 (2.99)
	<i>L. holbrooki</i>	0.85 (0.68, 1.07)	−2.85 (−3.27, −2.43)	0.93	–	–
	<i>P. guttatus</i>	0.82 (0.68, 0.99)	−2.76 (−3.01, −2.51)	0.97	–	–
	<i>P. obsoletus</i>	0.91 (0.85, 0.97)	−2.88 (−3.28, −2.73)	0.99	–	–

Values are based on reduced major axis regressions on log₁₀ data with snake species as a categorical variable (muscle CSA=species×mass). Slope and intercept confidence limits (95%) are in parentheses. Comparisons between species for each section of the body are for differences between slopes (species×mass) and elevations (species+mass), and are given by *P* at each SVL site with test statistics in parentheses. Muscle CSA was measured in cm² and mass in g.

in most sections and species, muscle CSA scaled with positive allometry (Table 2). The lack of significant differences between species in muscle CSA and its scaling means that similarly sized kingsnakes and ratsnakes have the same amount of muscle that can be used in constriction or escape movements. However, there might be differences in muscle physiological cross-sectional area (the area

of a muscle perpendicular to the muscle fibers), and hence maximum force production, that we have not yet detected.

Predation and escape performance

In constriction, if we assume that the muscles on the concave side of the coil contribute to force exertion, then up to half of the total musculature can be used and contribute to the constriction pressure. In a pulling-force test, if we assume that a snake bends into sinusoidal curves and the musculature on the concave part of each curve contributes to the pulling force, then up to half of the total musculature can be used and contribute to the pulling force. So although constriction pressure and pulling force are distinct variables used in different behaviors, they are appropriate indicators of predation and escape performance, and can be compared across species and sizes to understand the factors that affect the outcome of the predator–prey interaction that we studied.

Across ontogeny, all species increased constriction performance in a similar manner (i.e. with similar slopes; Fig. 4). However, at every body size, kingsnakes produced significantly higher constriction pressures than identically sized ratsnakes. The similar escape performance among species indicates that kingsnakes win in predatory encounters because of their superior constriction performance, not because ratsnakes have inferior escape performance. What are some possible mechanisms of the superior performance by kingsnakes?

With all snakes using a similar number of loops, the orientation of loops in the coil might optimize muscle fiber orientations and force transmission. Kingsnakes produced higher constriction pressures for a given number of loops in a coil (Fig. 3), and had a more uniform coil posture than ratsnakes (Fig. 2). It is possible that the kingsnake coil posture might maximize the force applied (and therefore pressure) to the prey by reducing the need for coil adjustments and movements. Reducing the need for movements might enable both isometric and tetanic contractions that maximize force output, and could reduce periods of loosening that could allow prey to struggle more or escape. It is also possible that kingsnake

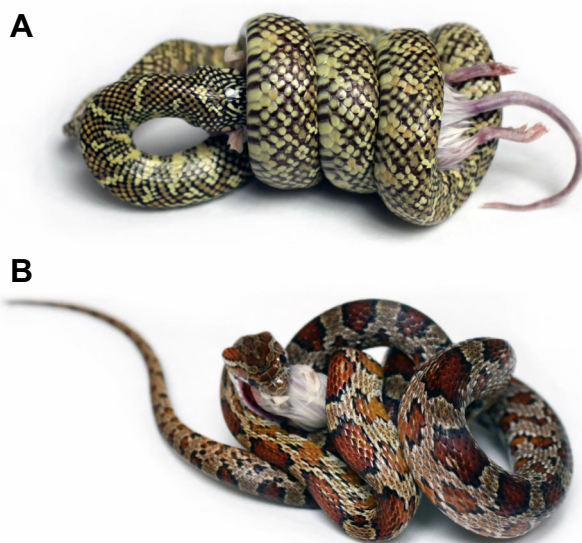


Fig. 2. Constriction coil postures of kingsnakes and ratsnakes. Typical constriction coil postures in a kingsnake, *Lampropeltis getula* (92 g; A), and a ratsnake, *Pantherophis guttatus* (86 g; B). Both snakes were constricting similarly sized mice, *Mus musculus* (12 g). The relative prey mass was 13% for the kingsnake and 13.9% for the ratsnake.

Table 3. Descriptive statistics of body mass, diameter, SVL maximum pulling force, number of loops in a coil and peak constriction pressure in kingsnakes (*Lampropeltis* spp.) and ratsnakes (*Pantherophis* spp.)

Species	N	Mass (g)	Diameter (cm)	SVL (cm)	Pulling force (N)	Number of loops	Constriction pressure (kPa)
Escape performance							
<i>L. californiae</i>	7	258±88.0 (35–592)	2.1±0.33 (1.1–3.2)	72.3±10.9 (41–102)	9.2±2.7 (2.5–19.0)	–	–
<i>L. getula</i>	32	193±49.2 (17–1010)	1.8±0.14 (0.9–4.0)	61.5±4.4 (36–124)	6.3±1.1 (0.9–23.7)	–	–
<i>L. holbrooki</i>	7	159±41.4 (16–292)	1.75±0.18 (1.0–2.2)	67.0±9.6 (31–91)	7.4±1.8 (1.0–12.7)	–	–
<i>P. alleghaniensis</i>	8	77±43.9 (15–376)	1.4±0.23 (1.0–2.9)	49.1±7.7 (33–97)	3.9±1.6 (1.5–14.3)	–	–
<i>P. guttatus</i>	6	55±21.2 (19–125)	1.2±0.13 (0.9–1.8)	45.0±4.7 (34–61)	3.3±0.9 (1.8–6.6)	–	–
<i>P. obsoletus</i>	38	129±32.3 (10–778)	1.7±0.12 (0.8–3.6)	59.1±4.5 (30–136)	5.0±0.9 (0.8–24.5)	–	–
Constriction performance							
<i>L. californiae</i>	21	189±30.1 (14–470)	1.8±0.14 (0.9–3.1)	73.1±5.9 (31–131)	–	2.1±0.2 (1–3)	22.5±1.9 (7.7–41.7)
<i>L. getula</i>	56	118±32.8 (11–1240)	1.4±0.09 (0.7–4.5)	50.8±3.5 (26–140)	–	2.0±0.1 (1–3)	17.1±1.1 (5.3–41.6)
<i>L. holbrooki</i>	12	168.3±33.1 (13–379)	1.8±0.19 (0.9–2.9)	72.7±7.3 (33–108)	–	2.3±0.2 (1–3)	20.8±1.7 (9.9–26.8)
<i>P. alleghaniensis</i>	21	37.2±17.3 (10–381)	1.1±0.09 (0.7–2.6)	40.5±3.5 (25–103)	–	1.8±0.1 (1–3)	8.9±0.6 (3.2–19.7)
<i>P. guttatus</i>	22	240.8±66.9 (6–980)	1.7±0.20 (0.8–3.5)	62.6±8.0 (22–114)	–	1.7±0.1 (1–3)	11.9±1.5 (3.2–23.7)
<i>P. obsoletus</i>	50	42.9±12.1 (7–562)	1.1±0.06 (0.7–2.9)	42.1±2.6 (23–112)	–	2.0±0.2 (1–3)	8.5±0.7 (3.2–17.3)

Values are mean±s.e.m. with data ranges in brackets. Number of loops was measured in decimal values of the number of complete loops (1/2 loop intervals).

muscle might be able to exert higher forces than ratsnake muscle by using different types of muscle contractions or by having different muscle fiber angles and therefore higher physiological cross-sectional areas. Furthermore, in seeking to escape, a ratsnake must use shortening contractions, which exert lower forces than isometric and tetanic contractions (MacIntosh et al., 2006). Additionally, constriction bouts between kingsnakes and ratsnakes can last for hours (Jackson et al., 2004), suggesting that muscle endurance might be important. Measures of total pressure (the integral of pressure versus time; Boback et al., 2015) delivered to both living and dead prey could also reveal differences in whole-body performance that have gone undetected here because we artificially controlled prey movements. Further work is needed in order to test these hypotheses. For example, experimental tests of muscle contractile force and endurance would help identify potential muscle-level differences between kingsnakes and ratsnakes. Lastly, our measures of predation performance derive from all snakes feeding on rodent prey. This was done because ratsnakes are not known to commonly feed on other snakes. Therefore, it is possible that other emergent factors might contribute to the success of intraguild predation by kingsnakes that have gone

undetected in our comparisons of performance when all snakes were fed rodent prey. There might be other ways in which ratsnakes are poor competitors (or kingsnakes superior competitors) in this ophiophagous context.

The effects of constriction pressure on prey animals

Constriction can disrupt breathing (McLees, 1928; Hardy, 1994) and circulation (McLees, 1928; Hardy, 1994; Moon, 2000; Moon and Mehta, 2007; Boback et al., 2015), cause structural damage to the spine (Rivas, 2004; Moon and Mehta, 2007), cause internal bleeding (Greene, 1983; Penning and Darte, 2016), and potentially disrupt brain function (Penning et al., 2015; Penning and Darte, 2016). Although endotherms die quickly (within 10–78 s; McLees, 1928; Hardy, 1994) from constriction, ectothermic prey might be only fatigued by constriction and swallowed alive (Hardy, 1994; Boback et al., 2015). We have observed both escape by *Anolis* lizards after extended constriction, and their death from constriction in the same time taken to kill endothermic prey (~1 min). Hence, the effects of constriction on ectotherms are variable and potentially complex; they might include harmful fluid movements, tissue distortions or damage, and neurological disruptions (Greene, 1983;

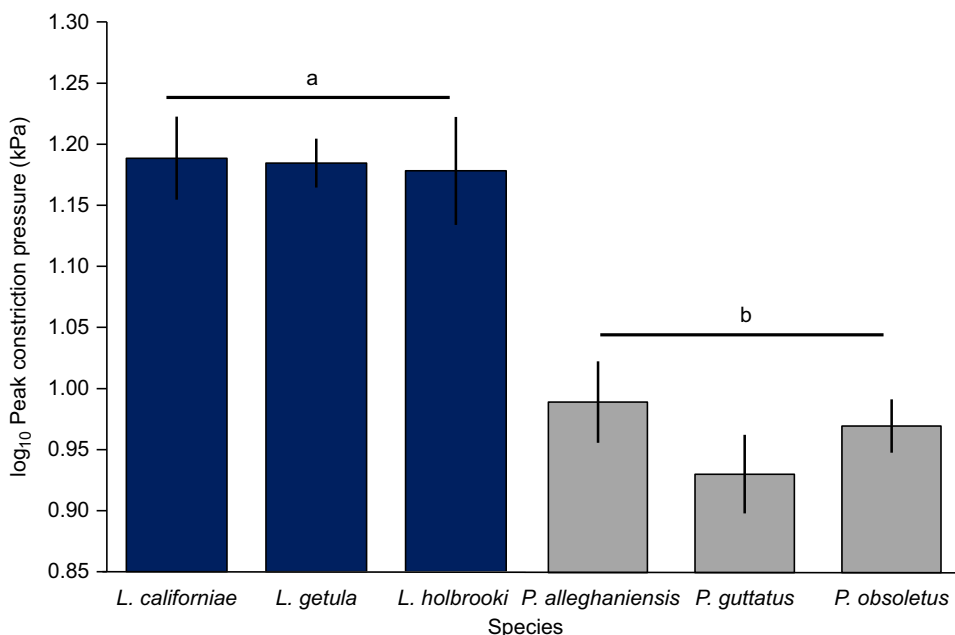


Fig. 3. Peak constriction pressures of kingsnakes and ratsnakes. Peak constriction pressures (kPa) for six species of snakes (kingsnakes, *Lampropeltis* spp., are black and ratsnakes, *Pantherophis* spp., are grey). Bars and lines indicate log-transformed covariate-adjusted means± s.e.m. for each species from a full model (pressure=diameter+species+number of loops). Significant differences (Tukey HSD, all $P < 0.05$) are denoted with different letters (a,b). Sample sizes are as follows: *L. californiae* $N=21$, *L. getula* $N=56$, *L. holbrooki* $N=12$, *P. alleghaniensis* $N=21$, *P. guttatus* $N=22$ and *P. obsoletus* $N=50$. The total sample consists of 98 females and 84 males.

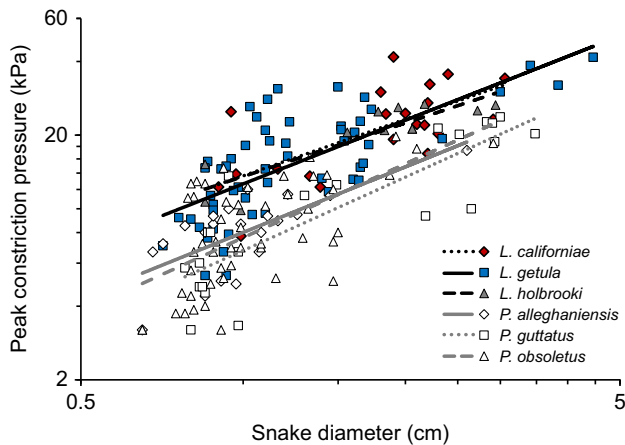


Fig. 4. Peak constriction pressure versus snake diameter. Peak constriction pressure (kPa) regressed against snake diameter (cm) for kingsnakes (*Lampropeltis californiae* $N=21$, *L. getula* $N=56$ and *L. holbrooki* $N=12$) and ratsnakes (*Pantherophis alleghaniensis* $N=21$, *P. guttatus* $N=22$ and *P. obsoletus* $N=50$). All slopes (denoted with species regression lines) are not significantly different from one another (see ‘Predation performance’ in Results). However, all kingsnake means are significantly higher than all ratsnake means (Tukey’s HSD, $P<0.05$ for all comparisons).

Rivas, 2004; Moon, 2000; Moon and Mehta, 2007; Boback et al., 2015; Penning et al., 2015; Penning and Dartez, 2016). This variation and complexity indicate that we do not yet fully understand the effects of constriction, particularly on ectothermic prey. The constricting snakes probably also experience internal pressures from the forces they exert on prey. However, blood pressures rise only slightly during constriction in boas, and less than during other behaviors such as hissing and swallowing (Wang et al., 2001). Changes in a snake’s blood pressure during constriction are not yet well known and might affect circulation to parts of their musculature, but are clearly well tolerated by the constrictors. When prey are constricted, they experience circumferential pressure that could result in high internal pressures (Halperin et al., 1993; Boback et al., 2015; Penning, 2016) that have different effects on internal

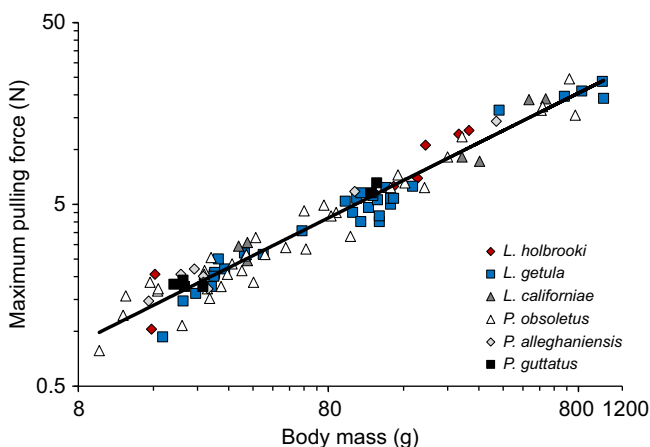


Fig. 5. Maximum pulling force versus snake mass. Maximum pulling force (N) regressed against snake mass (g) for kingsnakes (*Lampropeltis californiae* $N=7$, *L. getula* $N=32$ and *L. holbrooki* $N=7$) and ratsnakes (*Pantherophis alleghaniensis* $N=8$, *P. guttatus* $N=6$ and *P. obsoletus* $N=38$). There were no significant differences in slopes and intercepts between species, resulting in a single slope (black line) and intercept for all snakes (see ‘Escape performance’ in Results).

fluids than pressure applied at a specific point and that might be different from what the constricting snake itself experiences.

When kingsnakes and their prey snakes are well matched in size, our results show that the kingsnakes succeed in predation because they have superior constriction performance. Our study also shows that kingsnakes and their intraguild prey, ratsnakes, are comparable in total muscular cross-sectional area and escape performance. Although other aspects of the physiology of constriction still need to be examined, we presume that superior constriction performance results from their consistent and distinctive coil posture that we have shown here. These constriction abilities allow kingsnakes to succeed as intraguild predators on other snakes, including constrictors larger than themselves.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

D.A.P. collected and analysed all data, drafted the manuscript and provided funding. B.R.M. helped design the project, edit the manuscript, provide several specimens and provide funding. Both approved the final manuscript.

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