

## How snakes eat snakes: the biomechanical challenges of ophiophagy for the California kingsnake, *Lampropeltis getula californiae* (Serpentes: Colubridae)

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### Abstract

In this study we investigated how ophiophagous snakes are able to ingest prey snakes that equal or exceed their own length. We used X-ray video, standard video, dissection, and still X-rays to document the process of ophiophagy in kingsnakes (*Lampropeltis getula*) feeding on corn snakes (*Elaphe guttata*). Most kingsnakes readily accepted the prey snakes, subdued them by constriction, and swallowed them head first. In agreement with previous observations of ophiophagy, we found that the predator snake forces the vertebral column of the prey snake to bend into waves. These waves shorten the prey's body axis and allow it to fit inside the gastrointestinal (GI) tract and body cavity of the predator. Dissection of a kingsnake immediately following ingestion revealed extensive longitudinal stretching of the anterior portion of the GI tract (oesophagus and stomach), and no visible incursion of the prey into the intestine. X-ray video of ingestion showed that the primary mechanism of prey transport was the pterygoid walk, with some contribution from concertina-like compression and extension cycles of the predator's vertebral column in two out of three observations. Complete digestion was observed in only one individual, as others regurgitated before digestion was finished. X-ray stills taken every 4 days following ingestion revealed that the corn snakes were about half digested within the first 4 days, and digestion was complete within 15 days.

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**Keywords:** Ophiophagy; Feeding mechanism; Pterygoid walk; Swallowing; Regurgitation

### Introduction

Many genera of snakes (e.g., *Cylindrophis*, *Agkistrodon*, *Lampropeltis*, *Drymarchon*, *Ophiophagus*, *Micrurus*, *Atractaspis*, and many others) have members that include snakes or other elongate prey as part or all of their diet (Greene, 1997). A few published observations indicate that some snakes are even able to ingest other

snakes that equal or exceed their own body length (Hurter, 1893; Wall, 1921; Ditmars, 1931; Evans, 1948; Rose, 1962).

The finding that snakes can ingest snakes of equal or greater length raises several mechanical problems and questions. First, the caudal end of the stomach in snakes is located at approximately two-thirds of the distance from snout to vent (e.g., Bergman, 1953, 1955). A prey snake that is equal in total length (TL) to the predator will be at least 50% longer than the distance from the tip of the predator's snout to the end of its stomach. How is

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the prey packed into the gastrointestinal (GI) tract and body cavity (pleuroperitoneal cavity) of the predator? Does the stomach stretch longitudinally to allow the prey snake to fill the full length of the body cavity (i.e., is the pylorus displaced caudally during swallowing)? Or might part of the prey snake advance past the pylorus and into the intestine, thereby filling the full length of the predator's body cavity? Or is the final position of the prey snake limited by the resting position of the stomach, leaving the caudal one-third of the predator's body cavity empty?

Second, if the two snakes are similar in total length, then the length of the prey will exceed the length of the predator's body cavity because its TL exceeds the snout–vent length (SVL) of the predator. Therefore, the prey will have to be folded or curled in some way in order to fit inside the SVL of the predator. Is the prey bent in half, coiled up, or thrown into waves to decrease its length and pack it into the space available? Or might one end of the prey be left to protrude from the mouth of the predator while the other end is gradually digested?

Preliminary answers for some of these questions are provided by published observations of snakes consuming snakes of equal or greater length (Hurter, 1893; Wall, 1921; Ditmars, 1931; Evans, 1948; Rose, 1962). In these previous observations, the entire prey snake was ingested—one end did not protrude from the predator's mouth during digestion. Ditmars (1931) shows an X-ray image of a prey snake inside a Florida kingsnake, *Lampropeltis getula floridana*. The vertebral column of the prey snake is bent into waves, and the thin tip of the prey's tail is folded backward into a hairpin loop near the head of the predator. Rose (1962) shows an X-ray of a neonatal *Crotaphopeltis* that swallowed one of its clutch mates, and Evans (1948) shows a cleared and stained preparation of a young *Thamnophis* that consumed another snake from the same litter. In both the X-ray and the cleared and stained preparation, the vertebral column of the prey snake is bent into waves, similar to the configuration in the image published by Ditmars. These previous descriptions of ophiophagy are brief, report single instances of ophiophagy, and generally describe only the end result of the process. Our goal in the present study is to document the entire process of ophiophagy from initial strike to the completion of digestion in multiple instances of California kingsnakes feeding on corn snakes of equal or greater total length. Our primary tool is X-ray video, which allows us to observe the process of ingestion over long periods of time in multiple individuals. Our results can then be compared with results from previous studies of snakes feeding on other prey types.

A few recent studies have investigated the mechanisms by which snakes ingest small prey (type I, *sensu* Greene, 1983), such as insects and snails (e.g., Sazima, 1989; Kley and Brainerd, 1999; Kley, 2001, Götz, 2002), but most

previous studies have focused on the mechanics of feeding on relatively massive, bulky prey (type III, *sensu* Greene, 1983), such as mammals (e.g., Albright and Nelson, 1959a, b; Frazzetta, 1966; Cundall, 1983; Kardong and Berkhoudt, 1998; Moon, 2000; Kley and Brainerd, 2002). Our study will provide new data on the mechanisms by which snakes ingest massive, elongate prey (type II, *sensu* Greene, 1983), particularly massive, elongate vertebrate prey (type IIb, Cundall and Greene, 2000).

Our X-ray video results will be particularly interesting to compare with Kley and Brainerd's (2002) X-ray video study of alethinophidian snakes feeding on rodents. In this study, four distinct phases of prey transport were identified: oral, orocervical, cervical, and thoracic. Our X-ray video observations of ophiophagy will allow us to determine whether these same four phases occur when kingsnakes ingest corn snakes, and whether the relative contributions of each phase to prey transport are similar when snakes feed on these two very different prey types—rodents and snakes.

## Materials and methods

Kingsnakes (*L. getula*) were used as the predator snakes ( $n = 4$ ; Table 1) because this species is known to include snakes in its natural diet (Wright and Wright, 1957; Van Denburgh, 1922) and because captive-bred individuals were readily available commercially. Corn snakes (*Elaphe guttata*) were used as prey snakes ( $n = 6$ ; Table 1). This species was chosen because they were snakes of appropriate size that were available commercially at the time of the experiments. All measurements of SVL and TL were made to the nearest 0.5 cm, using a flexible measuring tape. Juvenile snakes were used in this study because of the size constraints of the X-ray machine.

All snakes were maintained individually in clear plastic cages, at a temperature of 32 °C, and a light cycle of 12 h light, 12 h dark. Prior to purchase and

**Table 1.** Sizes of predator (*L. getula*) and prey (*E. guttata*) snakes used in this study (SVL = snout-to-vent length, TL = total length)<sup>a</sup>

Individual	Mass (g)	SVL (cm)	TL (cm)
<i>L. getula</i> A	11.3	28.0	31.5
<i>L. getula</i> B	14.3	35.0	40.0
<i>L. getula</i> C	13.7	32.0	36.0
<i>L. getula</i> D	17.1	35.0	40.0
<i>E. guttata</i> A	7.4	26.5	32.5
<i>E. guttata</i> B	9.7	34.0	40.0
<i>E. guttata</i> C	15.3	33.5	39.0
<i>E. guttata</i> D	13.7	35.0	37.5
<i>E. guttata</i> E	18.1	41.5	45.0
<i>E. guttata</i> F	20.0	36.5	42.5

<sup>a</sup>SVL and TL measured to the nearest 0.5 cm.

**Table 2.** Prey snake offered to predator snake in each of nine feeding trials (refer to Table 1 for sizes of predator and prey snakes)

Feeding trial	Predator snake	Prey snake	Weight ratio	Length ratio
1	<i>L. getula</i> C	<i>E. guttata</i> B	0.71	1.25
2	<i>L. getula</i> D	<i>E. guttata</i> F	1.17	1.21
3	<i>L. getula</i> A	<i>E. guttata</i> A	0.65	1.16
4	<i>L. getula</i> B	<i>E. guttata</i> C	1.07	1.11
5	<i>L. getula</i> B	<i>E. guttata</i> A	0.52	0.93
6	<i>L. getula</i> A	<i>E. guttata</i> C	1.35	1.39
7	<i>L. getula</i> A	<i>E. guttata</i> A	0.65	1.16
8	<i>L. getula</i> B	<i>E. guttata</i> D	0.96	1.07
9	<i>L. getula</i> D	<i>E. guttata</i> E	1.06	1.29

Weight ratio = prey mass/predator mass; length ratio = prey TL/predator SVL.

between experiments, all snakes were maintained on a diet of pre-killed juvenile mice.

A total of nine trials were conducted in which a live prey snake, approximately equal to or greater than the predator snake in length, was introduced into the cage of a predator snake (Table 2). Predator snakes were fasted for at least 2 weeks prior to feeding trials. Some refused to eat the prey snake offered to them and some were fed snakes more than once.

The process of ingestion was documented three times, using both standard and X-ray videography (trials 1, 2 and 6; the remaining trials were conducted to document digestion, not ingestion). One kingsnake was euthanised immediately following ingestion to document the position of the ingested snake within the GI tract of the predator. Another kingsnake was euthanised after its gut had been empty for 3 weeks, in order to document the normal topography of the GI tract for comparison. Complete digestion was documented only once, as most of the snakes regurgitated their prey before digestion was complete. Partial digestion was documented in three other snakes that retained the prey for periods of 4–7 days before regurgitating. The process of digestion was observed by still X-rays taken on days 1, 4, 8, 11, and 15 following ingestion.

X-ray videography was performed using a Siemens cineradiographic unit. X-ray and standard video were recorded using Sony miniDV camcorders at a rate of 30 frames/s. Still X-rays were taken using a Bennet X-ray unit, with an exposure time of 16 s, at 45 kV, using standard X-ray film.

## Results

Our observations led us to divide the process of a snake eating another snake into four distinct stages:

(1) capture; (2) constriction; (3) ingestion; and (4) digestion. The results of our nine trials are summarised in Table 3.

In six of the nine trials, the kingsnake attacked the prey snake as soon as the prey was introduced into the predator snake's cage. In one trial there was a waiting period of approximately 0.3 h before the kingsnake attacked the prey snake, and in two trials the predator snake showed no interest in eating the prey snake, even after 1.5 h. When presented with a prey snake, the kingsnake typically grabbed the prey snake in its jaws and immediately threw its body into tight coils around the prey snake. In most cases this initial grab occurred mid-body on the prey snake, but in one trial (trial 6), the initial strike was near the head of the prey snake.

The constriction phase was a struggle between the two snakes in which the prey snake attempted to escape from the coils of the kingsnake and the kingsnake attempted to subdue the prey snake (Fig. 1a). In the first three trials in which the predator successfully captured and subdued the prey (trials 1, 2, and 6), the duration of this constriction phase was between 7.0 and 7.8 h (we defined the prey as “subdued” when it ceased to struggle). However, in subsequent trials, when the kingsnakes had at least one previous experience of constricting and eating a snake, they subdued the prey snakes more quickly, reducing the time from capture to the beginning of ingestion to between 1.5 and 2.0 h in trials 7, 8, and 9.

Throughout most of the lengthy constriction phase, the kingsnake maintained a constant grip on one area of the body of the prey snake with both jaws and body coils. Occasionally, the kingsnake would relinquish its jaw-hold long enough to reposition its jaws closer to the prey snake's head. During this time the kingsnake's body coils remained tightly wrapped around the prey snake's trunk. Once the jaws were repositioned and clamped firmly on the prey, the body coils were released, and re-coiled at a new position. This sequence was repeated until the kingsnake achieved a tight hold with its coils around the neck of the prey snake and was able to grab the head of the prey snake with its jaws and begin ingestion.

In all six trials that proceeded past constriction, the process of ingestion began at the head of the prey snake. We recorded the entire process of ingestion with X-ray video in three trials (1, 2, and 6). In all three trials, prey transport began with unilateral jaw ratcheting (the “pterygoid walk”; Bolt and Ewer, 1964). The vertebral columns of both the predator and prey snakes remained fairly straight (no waves), and the predator advanced its jaws and body over and around the prey snake (Figs. 1b and 2a, b). In trial 6, after the prey snake was approximately half ingested, the kingsnake began to use concertina-like movements of its vertebral column in addition to the pterygoid walk (Fig. 2c and d). The vertebral column of the predator was thrown into waves

**Table 3.** Outcomes of feeding and digestion trials

Trial	Capture (h)	Constriction (h)	Ingestion (h)	Digestion	Notes
1	0	7.8	0.8	N/A	Euthanised and dissected immediately following ingestion
2	0	7.5	1.5	Regurgitated after 4 days	
3	Never				
4	0.3	0.3 <sup>a</sup>			
5	Never				
6	0	7.0	Not complete <sup>b</sup>	Regurgitated immediately	
7	0	1.5	0.3	Regurgitated after 7 days	
8	0	2.0	0.3	Regurgitated after 6 days	Euthanised and dissected 18 days following regurgitation
9	0	2.0	0.5	Complete after 15 days	

<sup>a</sup>Unsuccessful attempt.

<sup>b</sup>Ingestion stopped with about 4 cm of prey snake remaining.



**Fig. 1.** Kingsnakes (*L. getula*) feeding on prey snakes (*E. guttata*) of equal or greater body length. (a) Predator and prey snake tightly coiled together as the predator attempts to subdue the prey, and the prey struggles to escape (see supplemental video clip, [www.elsevier.de/zoology](http://www.elsevier.de/zoology) videoclip1). (b) Intra-oral transport (see supplemental video clip, [www.elsevier.de/zoology](http://www.elsevier.de/zoology) videoclip 2). (c) The predator snake immediately following completion of ingestion. Note its lumpy external appearance due to the waves on the body of the prey snake inside it.

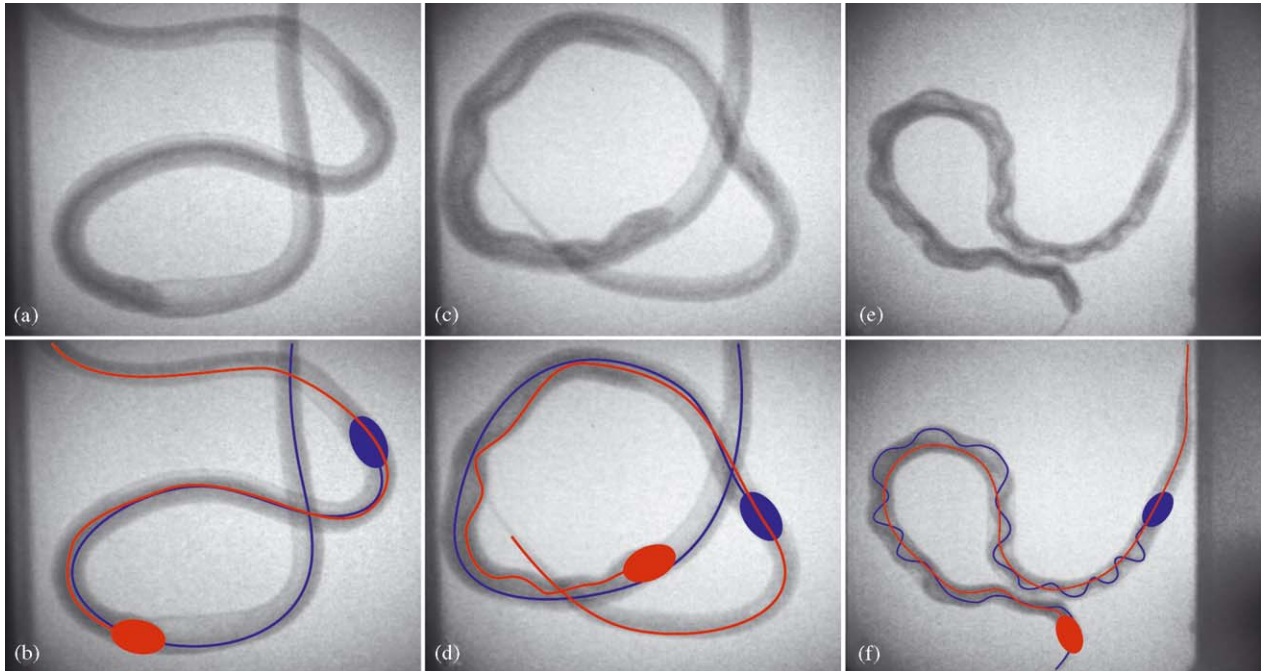
(red in Fig. 2d) and the vertebral column of the prey remained relatively straight (blue in Fig. 2d). Each time the predator shortened its own body axis, by throwing its vertebral column into waves, the head of the prey snake was forced a bit further inside the predator. Then the predator advanced its jaws as it straightened itself out. The waves were always standing waves rather than traveling waves, making them more similar to those seen in concertina locomotion than in lateral undulatory locomotion (sensu Gans, 1974).

The concertina-like movements in trial 6 were pronounced throughout the entire second half of ingestion. In trial 2, concertina-like movements were also observed in the second half of the ingestion process, but they were less pronounced. In trial 1, prey transport was accomplished almost entirely by the pterygoid walk mechanism; almost no concertina-like movements were observed.

In all six cases of ingestion (trials 1, 2, 6, 7, 8, and 9), the TL of the prey snake exceeded the SVL of the predator snake (Table 2, length ratio >1). In X-ray

video we observed that the head of the prey snake was always transported to the caudal end of the predator snake's body cavity, almost to the level of the cloaca. Once the head of the prey snake reached the end of the kingsnake's body cavity, the kingsnake continued to force the prey down until the vertebral column of the prey snake was bent into waves (prey snake blue in Fig. 2f). As the kingsnake continued ingestion, these waves became more and more pronounced, thereby shortening the body axis of the prey and permitting it to fit inside the predator. At the end of ingestion, when the body of the prey snake was completely inside the body cavity of the predator, the waves on the body of the prey snake caused the external appearance of the kingsnake to be distinctly lumpy (Fig. 1d).

As the predator snake reached the last few centimeters of the tail of the prey snake, transport slowed down, and the kingsnake appeared to experience difficulty ingesting the narrow tail tip. The kingsnake was observed waving its head laterally in an effort to ingest a part of the prey that was too narrow to be engaged simultaneously by



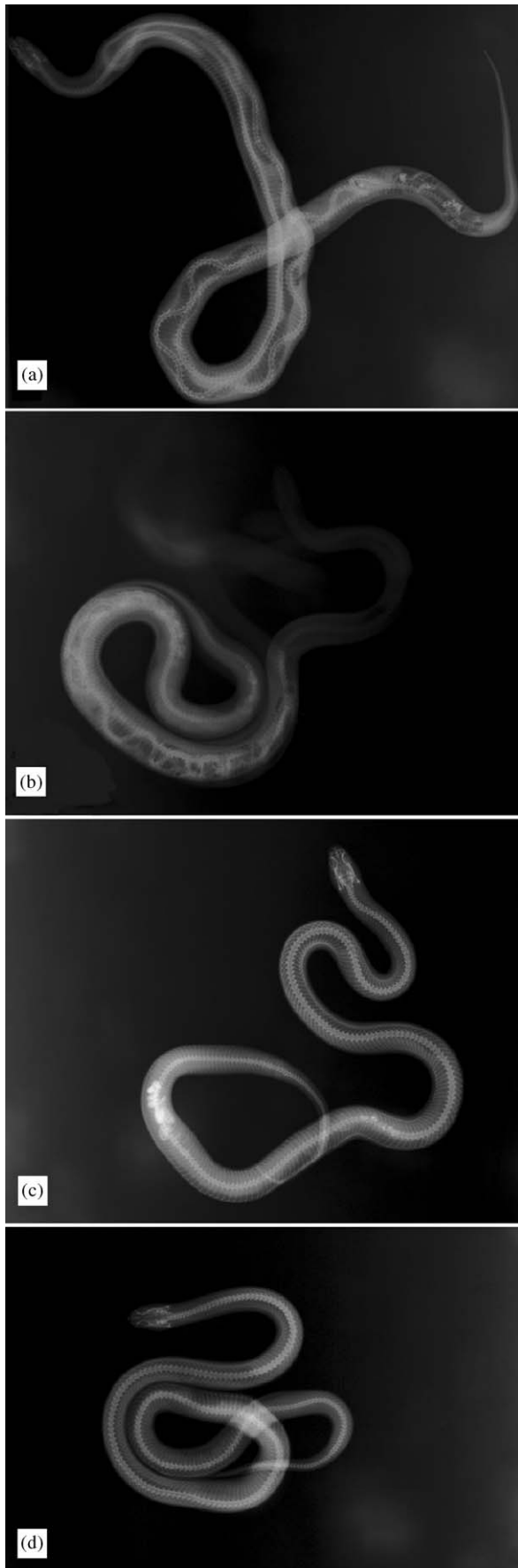
**Fig. 2.** Mechanics of ophiophagy. In the upper panels, the original images from X-ray video are shown. These are X-ray-positive images in which bones appear darker than the surrounding tissues. In the lower panels, our interpretations of the position of the two vertebral columns are shown. Panels a and b show the prey snake deep inside the predator's GI tract, with no waves on either vertebral column. Prey transport at this stage is entirely by the pterygoid walk mechanism (see supplemental video clip, [www.elsevier.de/zoology](http://www.elsevier.de/zoology) videoclip2). Panels c and d show the predator throwing its own vertebral column into concertina waves to push the head of the prey deeper into its GI tract (see supplemental video clip, [www.elsevier.de/zoology](http://www.elsevier.de/zoology) videoclip 3). In Panels e and f, the prey's vertebral column has been forced into waves. Without these waves, the prey would not fit into the length of the predator's body cavity (TL of the prey is longer than SVL of the predator). Key: red is the predator snake's vertebral column and blue is the prey snake's vertebral column.

both of the relatively widely spaced palatopterygoid tooth rows. When the tail tip did finally disappear, it was pointing toward the rostrum of the predator. Curiously, however, in four snakes examined by X-ray video or still X-rays 12 h after feeding (trials 2, 7, 8, and 9), the tail of the prey snake appeared as a hairpin-like loop in the cervical region of the predator, with the tail tip bent caudally (Fig. 3a, at top of image).

Dissection of a kingsnake euthanised immediately following ingestion revealed that the stomach and oesophagus of the predator were stretched and displaced caudally. The position of the gall bladder is a reliable marker of the end of the stomach and the beginning of the small intestine (e.g., Bergman, 1955; Guibé, 1970; Moscona, 1990). The head of the prey snake did not extend beyond the gall bladder, indicating that it did not go into the intestine. Measurement of the 32 cm SVL kingsnake dissected immediately following ingestion showed the gall bladder positioned 29 cm caudal to the snout, at a position that was 91% of the distance from the tip of the snout to the caudal end of the body cavity. The gall bladder, spleen, and pancreas were positioned together alongside the caudally displaced pylorus. In an unfed 35 cm SVL kingsnake dissected for comparison,

the gall bladder, spleen, and pancreas were positioned 25 cm caudal to the snout, or 71% of the distance from snout to vent.

In four of the six feeding trials in which ingestion was completed or nearly completed, the kingsnakes regurgitated their prey, either immediately or after 4 to 7 days (Table 3). We observed and videotaped regurgitation in two kingsnakes that failed to ingest their prey completely (in trial 6 and in one pilot observation). In each instance, the kingsnake ejected its prey by propagating vigorous, intermittent, high-amplitude, lateral undulatory waves in a cranial direction along the anterior half of its trunk. In most respects, this undulatory ejection mechanism resembled an exaggerated form of the thoracic transport mechanism described by Kley and Brainerd (2002), but executed in reverse. One of the two kingsnakes maintained a tight S-curve in its body just posterior to the head of the prey snake, but such persistent, regionalised body curvature was less evident in the other kingsnake. Both kingsnakes also exhibited occasional head retraction at irregular intervals throughout regurgitation; with the jaws held widely open, the snake pulled its head posteriorly, thereby drawing the mouth backward over the prey snake. One



of the two kingsnakes augmented this head retraction behaviour by using one or more loops of its body to pinion the prey snake against the floor and walls of the feeding enclosure (see supplemental video clip at [www.elsevier.de/zoology](http://www.elsevier.de/zoology) videoclip 4).

Digestion was difficult to observe because complete digestion occurred in only one of the six successful feeding trials (Table 3). In addition to the four trials in which the kingsnakes regurgitated their prey, one snake was euthanised immediately following ingestion. Fig. 3 shows still X-rays taken over a series of several days of the one kingsnake that successfully completed digestion of a prey snake. On the day following ingestion (Fig. 3a), the vertebral column of the prey snake could be seen to extend nearly the entire length of the kingsnake's body cavity, bent into waves so as to fit within the body cavity of the predator. Four days after ingestion (Fig. 3b), the vertebral column of the prey snake was confined more to the middle portion of the predator's body cavity. This was accomplished by a decrease in wavelength and increase in amplitude of the waves on the prey snake's vertebral column. On the 11th day following ingestion (Fig. 3c), the prey snake was visible only as a radiopaque mass in the caudal region of the predator snake's body cavity. Distinct bones were not visible in this mass. An X-ray taken on day 8 looked similar to the day 11 X-ray, so day 8 is not shown in Fig. 3. By 15 days following ingestion (Fig. 3d), no radiopaque remains of the prey are visible in the GI tract of the snake. Three other snakes completed between 4 and 7 days of digestion before regurgitation. Results from still X-rays of these three snakes are in agreement with the above descriptions.

## Discussion

Our results are in general agreement with previously published reports of snakes feeding on snakes of equal or greater length than themselves (Hurter, 1893; Wall,

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**Fig. 3.** A series of still X-rays taken over 15 days to document digestion of a prey snake. These are X-ray-negative images in which bones appear lighter than the surrounding tissues. (a) One day following ingestion. The vertebral column of the prey snake extends the length of the kingsnake's body cavity, and is thrown into waves to accommodate its greater length. (b) Four days following ingestion. The vertebral column of the prey snake is more tightly kinked than in (a), and confined to the middle portion of the kingsnake's body cavity. The anterior portion of the kingsnake is blurry because it moved during the 16s exposure time. (c) Eleven days following ingestion. The skeleton of the prey snake is visible only as a radiopaque mass in the gut of the kingsnake. (d) Fifteen days following ingestion. No radiopaque material is visible in the gut of the kingsnake.

1921; Ditmars, 1931; Evans, 1948; Rose, 1962). We found that after a kingsnake ingested a corn snake of equal or greater length, the corn snake filled most of the length of the kingsnake's body cavity (Figs. 2e and 3a). The prey snake was not restricted to the anterior two-thirds of the predator's body cavity, as might be predicted by the resting position of the predator's stomach. In agreement with X-ray images in Ditmars (1931) and Rose (1962), the vertebral column of the prey snake was bent into waves, which shorten the prey's body axis and allow it to fit inside the body cavity of the predator (Figs. 2e and 3a).

Previous studies have not addressed the configuration of the GI tract after a predator snake has ingested a prey snake longer than itself. Dissection of a kingsnake immediately following ingestion revealed extensive longitudinal stretching of the anterior portion of the GI tract (oesophagus and stomach), and no visible incursion of the prey into the intestine. Our measurements of GI tract configuration in an unfed kingsnake are in agreement with published reports of GI tract topography in juvenile snakes. In an extensive series of papers on the visceral anatomy of snakes, Bergman documented the position of the gall bladder (and thus the caudal end of the stomach) in six families of snakes (e.g., Bergman, 1952, 1953, 1955, 1958, 1960, 1961, 1962). The range of positions for adults is 55–75% of SVL, with most species falling within 60–70%. In juveniles, Bergman reports that the position of the gall bladder is more posterior than in adults, indicating that our measurement of 71% in a juvenile kingsnake is within the expected range. However, in our dissection of a kingsnake that had just eaten a snake longer than itself, the gall bladder was located at 91% of SVL, indicating that the oesophagus and stomach stretched longitudinally to accommodate the prey.

Most snakes typically ingest their prey head first, presumably to facilitate ingestion by swallowing in the direction of hair, feathers, or scales (Greene, 1976). However, tail-first ingestion is common in at least one genus of ophiophagous snakes, *Erythrolamprus* (Marques and Puerto, 1994; Greene, 1997; Rivas Fuenmayor, 2002). We observed head-first ingestion in all nine trials of kingsnakes ingesting corn snakes (the six documented here plus three pilot observations).

### Comparison with feeding on rodents

Kley and Brainerd (2002) found that alethinophidian snakes feeding on rodents generally exhibit four functionally distinct phases of prey transport: oral, orocervical, cervical, and thoracic. In contrast, we found that kingsnakes feeding on corn snakes exhibited just the oral and orocervical phases, with possibly some small contribution from the cervical phase. Due to the

elongate and relatively uniform shape of their snake prey, the kingsnakes were able to use the pterygoid walk mechanism throughout much or all of ingestion. Thus, the oral phase of prey transport (Phase I) was prolonged when feeding on snakes relative to feeding on rodents. In one of three feeding trials that we recorded with X-ray video, orocervical transport (Phase II) was not observed; the prey was ingested entirely with the pterygoid walk mechanism. In two other X-ray video observations, the predator initiated orocervical transport after the prey snake was about half ingested.

In each case that an X-ray was taken on the day following feeding ( $n = 4$ ), the last few centimeters of the prey snake's tail were folded back, with the tail tip pointing caudally (Fig. 3a, at the top of the image). A similar hairpin loop can be seen in a radiograph published by Ditmars (1931). Ditmars explained this hairpin loop by suggesting that the predator may have started to swallow the tip of the tail as it was ingesting the last 20% of the prey. Our observations are at odds with this explanation because in every case, the tail of the prey was pointing toward the rostrum of the predator as it disappeared into the mouth. We do not know for certain how the hairpin loop formed, because it happened some time between the end of our X-ray video recordings on the day of ingestion and the beginning of our still X-ray observations on the next day, but we hypothesise that after ingestion, the waves on the prey's body relaxed a bit, forcing the tail into a hairpin loop in the cervical region of the predator.

In some cases, the tail swallowing phase included cycles of cervical concertina compression, which may be similar to cervical (Phase III) transport of rodents (Kley and Brainerd, 2002). Prey transport during ophiophagy never advanced to the thoracic phase (Phase IV), which may be explained by the difference in shape between snake and rodent prey. In the last stage of feeding on rodents, the predator forms a kink in its neck just anterior to the prey and uses lateral undulatory movements of its trunk to transport the prey through the oesophagus and into the stomach (Kley and Brainerd, 2002). With elongate prey, such as snakes, it is not possible to form a kink anterior to the prey, so thoracic phase swallowing does not occur. We conclude that kingsnakes swallow snakes using the same basic mechanisms as for rodent prey, but with a prolonged oral phase, variable use of the orocervical phase, a variable and small contribution from the cervical phase, and no use of the thoracic phase.

### Digestion and regurgitation

Our results from X-ray stills taken 1, 4, 8, 11, and 15 days after feeding are in general agreement with previous studies of digestion in snakes (e.g., Blain and

Campbell, 1942; Skoczylas, 1970; Secor, 2003), but there appear to be differences in digestion time. Digestion was slower in our study of kingsnakes digesting corn snakes at 32 °C than in Secor's, 2003 study of Burmese pythons (*Python molurus*) digesting rats at 27–30 °C. In Secor's study, approximately half of the rat had been digested by day 2 and three-quarters by day 4. In our study, we estimate that the corn snake was only about half digested after 4 days, based on four kingsnakes that did not regurgitate before day 4 (Fig. 3b). In a study of grass snakes (*Natrix natrix*) digesting frogs at 25 °C, Skoczylas (1970) found complete digestion within 3 days. These differences in digestion time could result partially from differences in the relative sizes of the meals: 20% of the predator's body weight for *N. natrix* digesting frogs, 25% for *P. molurus* digesting rats and up to 117% for kingsnakes digesting corn snakes in our study (Tables 2 and 3). Differences in digestion time could also result from differences in how quickly these different species of snakes can up-regulate their digestive functions (Jackson and Perry, 2000; Starck and Beese, 2001, 2002; Secor, 2003), and from the characteristics of the prey, such as the thickness of the skin (Secor, 2003).

Complete digestion occurred in only one of our feeding trials. More often, the kingsnakes regurgitated their ophidian prey, either immediately or after several days of digestion. The prey items that were regurgitated after 4 to 7 days were at least half digested, indicating that the kingsnakes' digestive systems were active and that they derived some nutritional benefit from the prey. Regurgitation in snakes may result from a variety of different factors, including suboptimal environmental temperatures, physical disturbances, diseases, lesions or obstructions within the GI tract, and parasite infestations (Frye, 1991). Regurgitation may also result from simple gorging, especially among macrostomatan snakes, which are renowned for their ability to ingest enormous prey. Our kingsnakes were maintained at a constant temperature of 32 °C, and care was taken following feeding trials not to disturb them more than necessary for the X-ray imaging (this was accomplished by building cages that allowed the snakes to be X-rayed without removing them from the cage). Moreover, while on their maintenance diet of smaller mammalian prey (i.e., mice), the kingsnakes digested their meals completely with no instances of regurgitation, indicating that the snakes were generally healthy and not burdened with heavy parasite loads. Thus, we believe that the high frequency of regurgitation that we observed among the kingsnakes in this study was due primarily to the extremely large relative size of the prey snakes that they consumed.

In the two cases of regurgitation that we observed directly (trial 6 and one pilot observation), the kingsnakes appeared to eject their ophidian prey primarily via a reverse lateral undulatory mechanism, in which

high-amplitude undulatory waves were propagated cranially along the anterior portion of the trunk, thereby forcing the prey through the oesophagus and back into the mouth. In this respect, the reverse lateral undulatory mechanism by which *Lampropeltis* regurgitates snake prey resembles that which is used by other snakes to regurgitate other types of prey, such as rodents and bird eggs (Kley, pers. obs.; Gans, 1952). However, the head retraction and pinioning behaviours that we observed during the regurgitation of ophidian prey are not known to be exhibited by snakes during the regurgitation of non-elongate prey.

Considered in the context of previous studies of emetic (vomiting) behaviour in non-ophidian vertebrates, our observations in this study suggest that regurgitation in snakes differs from the emetic mechanisms of other vertebrates in two fundamental ways. In most vertebrates, expulsion of vomitus from the stomach is believed to occur primarily through an increase in intra-abdominal pressure, brought about through a variety of different muscular mechanisms in different taxa (e.g., Hatcher, 1924; Naitoh et al., 1989; Naitoh and Wassersug, 1992; Andrews et al., 2000; Sims et al., 2000). In contrast, regurgitation in snakes appears to occur mainly through the propagation of undulatory waves along the trunk, which act directly on the prey itself, physically pushing it through the oesophagus. In addition, snakes appear not to exhibit any conspicuous, stereotypical preparatory behaviours (e.g., retching, head shaking, jaw snapping, chin rubbing, etc.) prior to regurgitation, whereas such behaviours appear to be universal among other vertebrates (Andrews et al., 2000). These differences suggest that the functional morphology of regurgitation in snakes merits further, more detailed study.

### Weight ratio, ingestion ratio, and length ratio

Greene (1983) explored the maximum limits of prey size in a variety of snakes. He quantified the difference in mass between predator and prey as weight ratio (WR = prey mass/predator mass). The maximum WR he reported for a non-venomous snake is 0.6 for *Python sebae* ingesting an unidentified prey item (Pitman, 1974, cited in Greene, 1983). Greene reported that the highest WRs achieved by snakes are those of venomous elapids and especially viperids, which occasionally exceed 1.0. The maximum WR reported by Greene is 1.56 for a juvenile specimen of the viperid *Bothrops atrox* that swallowed a teiid lizard. A similar WR of 1.57 was reported by Branch et al. (2002) for a juvenile *Bitis caudalis* that swallowed a gecko. Mulcahy et al. (2003) recently reported a WR of 1.72 for a sidewinder (*Crotalus cerastes*) that they found dead. They suggested that it might have been the ingestion of such a large meal



that led to the snake's death. Pough and Groves (1983) proposed that viperids are capable of achieving high WRs through the possession of a suite of morphological specialisations, such as stout bodies and a wide gape, relative to other snakes.

In our study, the highest WR for a snake that completed ingestion was 1.17 (trial 2). The kingsnake in trial 6 almost accomplished a WR of 1.35, but gave up and regurgitated with approximately 4 cm of the prey snake's tail still not ingested. The WR of the one snake that completed digestion (trial 9) was 1.06. Our findings of high WRs (>1.0) in a non-venomous colubroid suggest that venomousness is not the key factor in determining WR limits between non-venomous kingsnakes versus venomous elapids and viperids.

The other parameter that Greene (1983) quantified was the ingestion ratio (IR = prey diameter/predator's head diameter). A small-headed snake swallowing an egg or a bulky rat, for example, would have a high IR. The relationship between WR and IR may provide an answer to the question of why ophiophagous snakes would invest so much energy in ingesting prey items that appear to involve so much effort. The advantage to a snake eating another snake is that since their heads may be approximately equal in width, and the shape of the prey does not at any point become wide, the IR is low, and they are able to achieve a high WR in the absence of specialised gape capacities such as those of viperids.

If the stomachs of snakes are capable of longitudinal stretching to accommodate high WR, low IR prey, it seems possible that the same mechanism of gastric packing could be used to accommodate large numbers of low WR, low IR prey, such as a litter of baby mice. It would be interesting to investigate whether snakes would voluntarily allow their stomachs to be stretched to the degree that we observed, or whether, given the opportunity, they would stop after just a few prey items, possibly lessening the likelihood of regurgitation. We do not know whether, under natural conditions, kingsnakes would eat snakes longer than themselves if smaller prey were available.

The parameter of greatest interest in our study was the relationship between the lengths of predator and prey, so we introduce here another ratio, the length ratio (LR = TL of prey/SVL of predator; Table 2). The reason for using TL for prey and SVL for predator is that the length from mouth to cloaca (SVL) of the predator is the space into which the entire length (TL) of the prey snake must fit, so the tail length of the predator is not relevant. The highest LR recorded in our study was 1.29, and happened to be trial 9, the only snake that completed digestion. There are few data from other studies to put our LRs into context, but we hope that our LRs may be useful as a starting point for subsequent studies of elongate prey ingestion.

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## Appendix A. Supplementary data

The online version of this article contains additional supplementary data. Please search for doi:10.1016/j.zool.2004.06.001 at <http://dx.doi.org>.

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