

## Post-cranial prey transport mechanisms in the black pinesnake, *Pituophis melanoleucus lodingi*: an x-ray videographic study

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### Summary

Most previous studies of snake feeding mechanisms have focused on the functional morphology of the highly specialized ophidian jaw apparatus. Although some of these studies have included observations of post-cranial movements during feeding, the functional roles of these movements have remained poorly understood. In this study, we used x-ray videography to examine post-cranial prey transport mechanisms in a colubrid snake, *Pituophis melanoleucus lodingi*. We found that prey transport in this species progresses through four distinct phases, three of which are characterized by either undulatory or concertina-like movements of the anterior portion of the trunk. In the first phase of transport (the oral phase), unilateral movements of the jaws are used to pull the head forward around the prey. In the second phase (the orocervical phase), unilateral jaw movements continue, but are augmented by concertina-like movements of the anterior portion of the trunk. In the third phase (the cervical phase), prey transport occurs exclusively through concertina-like movements of the neck. Finally, in the fourth phase (the thoracic phase), prey is transported to the stomach via undulatory movements of the trunk. Our observations of feeding behavior in a phylogenetically diverse sample of fourteen other snake species demonstrate that similar post-cranial transport mechanisms are used by a wide variety of alethinophidian snakes that feed on large, bulky prey.

**Key words:** snakes, feeding, prey transport, functional morphology, x-ray videography

### Introduction

During the last fifty years, the feeding mechanisms of snakes have been studied extensively by functional morphologists (e.g., Gans, 1952, 1961; Dullemeijer, 1956; Albright and Nelson, 1959a,b; Boltz and Ewer, 1964; Frazzetta, 1966; Kardong, 1977, 1986; Cundall and Gans, 1979; Cundall, 1983, 1995; Kardong and Berkhoudt, 1998; Kley, 2001). Because prey transport in snakes depends largely on movements of the jaws (gnathic transport) rather than on movements of the tongue (hyolingual transport) or head (cranioinertial transport), most of this research has focused primarily on the morphology and function of the highly specialized ophidian jaw apparatus. However, several studies have also included observations of post-cranial movements during feeding (e.g., Dullemeijer, 1956; Gans, 1961; Frazzetta, 1966; Dullemeijer and Povel, 1972;

Kardong, 1977, 1986; Kardong and Berkhoudt, 1998). These observations suggest that movements of the trunk may also play a significant role in the transport of prey, but the descriptions of these movements have generally been brief, and therefore a detailed understanding of post-cranial prey transport mechanisms in snakes has been lacking.

Although most descriptions of post-cranial movements during prey transport in snakes have been based only on external observations, two recent studies have examined these movements in greater detail through the use of cineradiography. Janoo and Gasc (1992) used this technique to study the kinematics of swallowing in *Vipera ammodytes* feeding on rats. They found that this species uses “in situ lateral undulation” of the anterior portion of the vertebral column to transport prey through the esophagus. However, a different kinematic pattern was later described by Cundall (1995), who

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studied the mechanics of prey transport in *Cylindrophis ruffus* feeding on fish. He found that *Cylindrophis* uses unilateral movements of the jaws to initiate ingestion, but that once the prey begins to enter the esophagus, this mechanism is abandoned in favor of a different mechanism involving concertina-like movements of the neck and bilaterally synchronous movements of the jaws. These studies demonstrate that movements of the trunk contribute to prey transport in at least some species of snakes, but they also show that the gross patterns of movement associated with these post-cranial transport mechanisms are variable. However, because these studies were conducted using different species of snakes and different types of prey, and because they focused on different points in the swallowing process, the source of this variability is not yet well understood.

In this study, we used x-ray videography to examine the roles of post-cranial movements throughout all stages of prey transport (i.e., ingestion, intraoral transport and swallowing) in the black pinesnake, *Pituophis melanoleucus lodingi*. Preliminary results from this study indicated that prey transport in this species progresses through four distinct phases, three of which are characterized by extensive movements of the anterior portion of the trunk (Kley and Brainerd, 1996). This four-phase model was recently adopted by Moon (2000), who used a combination of electromyography and standard videography to study the mechanics and muscular control of vertebral bending during feeding in gopher snakes (*Pituophis catenifer*) and kingsnakes (*Lampropeltis getula*). Here we provide a more detailed kinematic description of the four phases of prey transport in *Pituophis m. lodingi*, focusing particularly on the functional roles of post-cranial movements during feeding as revealed by x-ray videography. In addition, we compare the post-cranial prey transport mechanisms used by *Pituophis* to those used by other snakes, based on our observations of feeding behavior in a phylogenetically diverse sample of 14 additional alethinophidian taxa feeding on a variety of different prey types.

## Materials and methods

### Experimental animals

Three black pinesnakes (*Pituophis melanoleucus lodingi* Blanchard, 1924; Colubridae) were obtained from a commercial herpetological supplier. Small adults (300–530 g) were chosen for this study to maximize the proportion of each snake's body that could be included within the limited area of the x-ray beam during videofluoroscopy. The snakes were maintained individually in appropriately sized ABS plastic reptile cages (Neodesha Plastics; Neodesha, KS). Laminated heat pads, affixed to the underside of each cage at one

end, provided thermal gradients within the enclosures, thereby allowing the snakes to thermoregulate themselves. The snakes were maintained on a diet of pre-killed laboratory mice and rats, offered once every two to four weeks, and had free access to water at all times.

### X-ray videography

X-ray videography was conducted at the radiographic facility at the Museum of Comparative Zoology, Harvard University. The snakes were fasted for at least one week prior to feeding trials. After being transported to the radiographic facility, they were given a recovery period of approximately 24 hours before they were fed. During most feeding trials, the snakes were offered pre-killed laboratory mice (*Mus musculus*) or rats (*Rattus norvegicus*). Prey-to-predator mass ratios ranged from 0.03 to 0.23 in these trials.

X-ray videos were recorded at 60 fields  $s^{-1}$  onto a Panasonic AG-1970 S-VHS VCR from a Siemens radiographic unit equipped with a Sirecon image intensifier. Most feedings were recorded in dorsoventral projection. In several feeding trials, small lead markers were affixed to the dorsolateral and ventrolateral skin of the snakes along the anterior portion of the trunk, thereby allowing us to visualize the movement of different regions of the integument relative to one another and also relative to the vertebral column and ribs. In addition, in some feeding trials, small steel pellets were injected subcutaneously into pre-killed rodent prey to provide clear landmarks for kinematic analyses. A total of 30 prey transport sequences were recorded from three individuals.

### Analysis of x-ray videographic data

Representative x-ray video sequences chosen for kinematic analysis were converted from analog to digital format using a Macintosh computer equipped with a Radius Video Vision Studio digitizing board. Video clips were then converted to sequentially numbered PICT files with a time resolution of 5 frames  $s^{-1}$ , a sampling rate that permitted adequate characterization of the relatively slow movements associated with prey transport in the species being studied. Individual PICT files were analyzed using NIH Image software to record the position of the snake's jaws, to note the directionality of vertebral bending, and to measure the kinematic variable "Neck Length". "Neck Length" was defined as the distance along the snake's vertebral column (exclusive of any bends) between the posterior margin of the exoccipital bones and a reference vertebra located posterior to the region of cervical compression. Thus, as the number and magnitude of bends formed along the vertebral column during cervical compression increased, "Neck Length" decreased.

### Observations of other species

In addition to *Pituophis melanoleucus lodingi*, one or two individuals of five other species of snakes were used in x-ray videographic feeding trials for purposes of comparison: 1 *Python breitensteini* Steindachner, 1880 [Pythonidae]; 2 *Eryx conicus conicus* (Schneider, 1801) [Boidae]; 1 *Elaphe alleghaniensis* (Holbrook, 1836) [Colubridae]; 2 *Lampropeltis getula floridana* Blanchard, 1919 [Colubridae]; and 2 *Nerodia fasciata pictiventris* (Cope, 1895) [Colubridae]. In these feeding trials, *Python*, *Eryx* and *Elaphe* were given rodents (*Rattus* and *Mus*), *Lampropeltis* were given both rodents and snakes (*Nerodia* and *Elaphe*), and *Nerodia* were given several different species of fishes. These types of prey were chosen in an attempt to closely approximate the natural diets of these species (e.g., Wright and Wright, 1957; Greene, 1997; Stuebing and Inger, 1999; Mahendra, 1984). Pre-killed prey were used in all of these feeding trials.

Post-cranial movements were also observed externally during feeding in adults of several additional taxa: 2 *Xenopeltis unicolor* Reinwardt, in Boie, 1827 [Xenopeltidae]; 2 *Loxocemus bicolor* Cope, 1861 [Loxocemidae]; 1 *Python regius* (Shaw, 1802) [Pythonidae]; 2 *Boa constrictor imperator* Daudin, 1803 [Boidae]; 2 *Epicrates cenchria cenchria* (Linnaeus, 1758) [Boidae]; 2 *Charina reinhardtii* (Schlegel, 1848) [Boidae]; 2 *Eryx colubrinus loveridgei* Stull, 1932 [Boidae]; 3 *Drymarchon corais corais* (Boie, 1827) [Colubridae]; and 1 *Atractaspis bibronii* Smith, 1849 [Atractaspididae]. In all of these supplementary feeding trials, laboratory rodents (*Mus* or *Rattus*) were used as food.

### Results

#### Prey transport in *Pituophis melanoleucus lodingi*

X-ray videographic recordings of *Pituophis melanoleucus* feeding on rodents revealed that prey transport in this species progresses through four functionally distinct phases, each characterized by a distinctive transport mechanism or set of transport mechanisms (Fig. 1). However, these four phases do not conveniently correspond with traditionally recognized stages of feeding (ingestion, intraoral transport, processing, and swallowing; Schwenk, 2000a). As recently emphasized by Cundall and Greene (2000), these conventional terms "...can be applied to snakes only by merciless stretching of the original definition." Therefore, we make no attempt to do so here. Instead, we introduce a new and more appropriate, snake-specific feeding terminology.

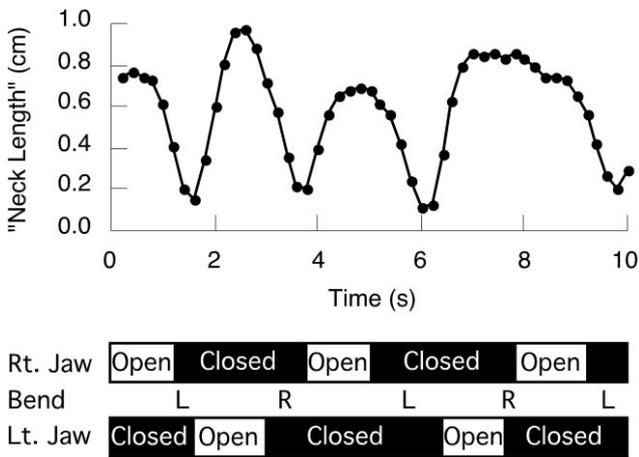
**Phase I. The oral phase:** The oral phase consisted entirely of jaw-mediated intraoral transport (Fig. 1A). During this first phase of transport, the snakes used reciprocating, unilateral cycles of protraction and retraction of the palatamaxillary arches to ratchet themselves forward over their prey. This mechanism, often referred to as the "pterygoid walk" (Boltt and Ewer, 1964), has been described in detail for several genera of alethinophidian snakes (e.g., Albright and Nelson, 1959a,b for *Elaphe*; Frazzetta, 1966 for *Python*; Kardong, 1977 for *Agkistrodon*; Cundall and Gans, 1979 for *Nerodia*), and the gross patterns of jaw movements we observed in *Pituophis* were generally consistent with these descriptions.



**Fig. 1.** X-ray video fields of *Pituophis m. lodingi* swallowing a mouse, recorded in dorsoventral projection, illustrating the four stages of prey transport observed in this study: (A) oral phase; (B) orocervical phase; (C) cervical phase; (D) thoracic phase.

Throughout the oral phase of transport, movements of the upper jaws were closely coordinated with complex, three-dimensional rotations of the skull. During jaw opening, depression of the advancing mandibular ramus was accompanied by a rotation of the braincase about its longitudinal axis toward the contralateral side. This rolling movement served to further disengage the teeth of the advancing palatamaxillary arch from the surface of the prey and was particularly evident in snakes feeding on relatively bulky prey. Immediately after the initiation of jaw opening, the braincase was also rotated dorsally and laterally (toward the contralateral side) about the cranio-vertebral joint as the advancing upper jaw arch was protracted. These rotations augmented jaw protraction by moving the toothed elements of the advancing upper jaw further forward than would be possible through protraction of the palatamaxillary arch alone.

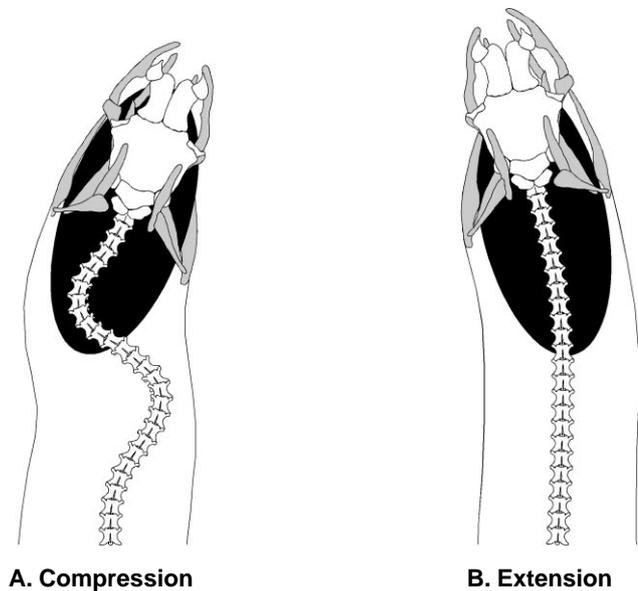
**Phase II. The orocervical phase:** As prey transport continued, lateral rotations of the skull about the cranio-vertebral joint became increasingly attenuated due to the presence of the prey in the snake's mouth and anterior esophagus. At this point, concertina-like movements of the vertebral column began to appear in the cervical region, marking the beginning of the second phase of transport, the orocervical phase (Fig. 1B). During this phase, unilateral ratcheting movements of the upper jaws continued, but these were closely coordinated



**Fig. 2.** Kinematic summary of a representative sequence of orocervical phase prey transport in *Pituophis m. lodingi* swallowing a mouse. During cervical compression (decreasing “neck length”), both left and right jaws are closed. Then, during cervical extension (increasing “neck length”), the advancing jaw is opened and the vertebral column is straightened, resulting in protraction and rotation of the skull about the fixed contralateral jaw. Note that the orientation (left or right) of the anteriormost bend in the vertebral column (“bend”) during cervical compression corresponds to the jaw that is advanced during the following jaw protraction.

with cyclical, concertina-like extensions and compressions of the neck region. Cervical compression was achieved by drawing the vertebral column and ribs forward over the prey and by pulling the head backward. Cervical extension was more variable, involving either concertina-like straightening of the vertebral column or the propagation of an undulatory wave caudally along the anterior portion of the trunk.

Throughout the orocervical phase, extension of the vertebral column occurred simultaneously with jaw advance (Fig. 2). Consequently, during jaw protraction, the braincase was forced anteriorly relative to the fixed jaw. Furthermore, the directional pattern of vertebral bending during cervical compression varied according to whether the left or right jaw was about to advance. The anteriormost bend in the neck was formed in such a way as to induce a rotation of the braincase about the fixed jaw upon cervical extension and jaw protraction. For instance, following protraction and subsequent closure of the left jaw, the vertebral column in the cervical region was drawn into concertina-like bends, with the anteriormost bend directed toward the right (Fig. 3A). Subsequently, during opening and protraction of the right jaw, these bends in the vertebral column were straightened, thereby inducing a rotation of the braincase about the fixed left jaw (Fig. 3B).



**Fig. 3.** Mechanics of orocervical phase prey transport in *Pituophis m. lodingi*. The prey is represented by the black oval. The snout complex (premaxilla, nasals, septomaxillae and vomers) has been omitted to provide an unobstructed view of the jaws (shaded). Following closure of the left jaw and subsequent cervical compression (A), the right jaw is opened and the vertebral column is straightened (B). This extension of the neck protracts and rotates the braincase about the fixed jaw during jaw protraction, thereby maximizing the anterior displacement of the advancing jaw.

Because rodents were nearly always ingested head-first, the snake encountered increasingly wider portions of its prey as transport continued. Furthermore, compression of the rodent's thorax within the snake's mouth and esophagus resulted in a ballooning of the rodent's abdominal region remaining outside of the snake's mouth. Once the snake reached this wider, "bunched up" portion of the rodent, prey transport appeared to become more difficult, and the distance advanced with each jaw protraction decreased. Cervical compression was generally greatest at this point. In addition, a different kinematic pattern of cervical extension and jaw protraction was often seen as the snake reached the widest portion of its prey. Instead of executing a single jaw protraction with each cervical extension, the snake would frequently perform two jaw protractions per extension. In such instances, one jaw was protracted simultaneously with cervical extension, but immediately following closure of that jaw and prior to subsequent cervical compression, the other jaw was also advanced. Lateral rotation of the head during this second jaw protraction was typically of a lesser magnitude than that which was associated with the initial cervical extension and jaw advance.

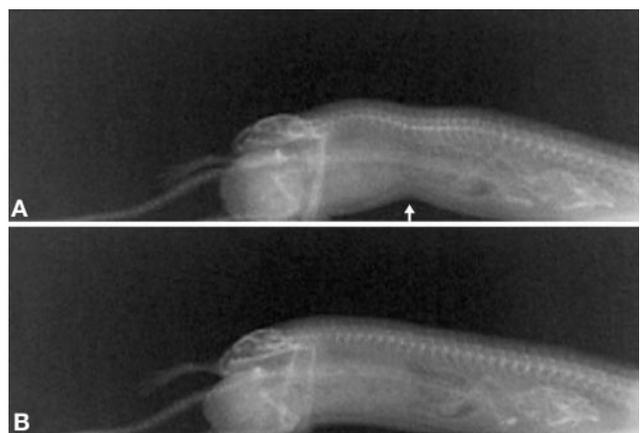
As transport continued and the proportion of the prey contained within the snake's esophagus increased, the concertina-like movements of the vertebral column in the cervical region began to occur increasingly independently of the integument. As the vertebral column and ribs were drawn forward over the prey during cervical compression, the ventrolateral integument in the region around the prey remained largely stationary. Following compression, but prior to subsequent extension, the integument was drawn forward over the prey. Anterior translation of individual vertebrae relative to lead markers affixed to the ventrolateral skin of the snakes generally ranged between one and three body segments during compression. As noted previously by Cundall (1995), this independent movement of the axial skeleton relative to the integument bears a striking resemblance to that which is seen during internal concertina locomotion in uropeltid snakes (Gans, 1976) and some caecilians (Gaymer, 1971; Summers and O'Reilly, 1997). However, in *Pituophis* (and in most other snakes), a relatively tight ligamentous connection exists between the neural arches of the vertebrae and the mid-dorsal portion of the integument. Therefore, the independence that occurs between the axial skeleton and the skin during the orocervical phase of prey transport in *Pituophis* is limited to the ventral portion of the body.

Throughout the orocervical phase, neck compression was often accompanied by a slight ventral flexion of the head. Cranial ventroflexion became more pronounced, however, near the end of the orocervical phase. This behavior appeared to compress the pharynx, thereby mini-

mizing retrograde movement of the prey during cervical compression. In addition, as orocervical transport continued and the proportion of the prey contained within the esophagus increased, a zone of constriction encircling the prey became evident immediately prior to each cervical extension (Fig. 4). This constriction seemed to result both from adduction of the ribs and from a slight sagittal flexion of the trunk in the region surrounding the prey. Thus, the snake appeared to be anchoring itself to its prey during neck extension and jaw protraction.

**Phase III. The cervical phase:** The third phase of prey transport, the cervical phase, began once the snake had progressed forward over the prey to a point at which the posteriormost teeth of the upper jaws could no longer engage the surface of the prey. At this point, the unilateral jaw ratcheting mechanism characteristic of the first two phases of transport became ineffectual, and cycles of concertina-like cervical compression and extension became the sole means of prey transport (Fig. 1C). The general pattern of vertebral bending during the cervical phase of transport was identical to that observed during the orocervical phase. However, neck extension during this phase of transport functioned to push the entire head forward over the prey rather than to pivot the braincase around a fixed point of contact between the jaws and the prey.

Throughout the cervical phase of transport, concertina-like movements of the vertebral column in the neck region were accompanied by extensive movements of the head. As during the orocervical phase, the head was flexed strongly ventrally during cervical compression.



**Fig. 4.** X-ray video fields of orocervical phase prey transport in *Pituophis m. lodingi*, recorded in lateral projection. Immediately prior to cervical extension (A), a region of constriction appears surrounding the prey (arrow). This constriction in the anterior portion of the trunk persists throughout jaw protraction, and disappears only after the neck is fully extended (B).

Then, during cervical extension, the head was rotated laterally about the cranio-vertebral joint, and upper jaw protraction continued in a manner similar to that observed during earlier stages of transport. However, movements of the jaws had no direct effect on the prey during this phase of transport because the prey was positioned behind the head. Instead, lateral rotation of the head and protraction of the jaws appeared to function in stretching the ventrolateral integument forward over the prey during neck extension.

Occasionally during the cervical phase the snake would raise its head and neck up off of the substrate. This behavior occurred more frequently with relatively small prey items, and the vertical angle of the snake's head and neck relative to the substrate was highly variable. In addition, as during orocervical transport (Fig. 4), an area of constriction in the region of the trunk surrounding the prey was often seen prior to and during cervical extension, suggesting that the snake was attempting to grip the prey with its trunk during neck extension and jaw protraction.

The cervical phase was relatively brief in duration, generally consisting of fewer than five compression-extension cycles. However, more cervical compression-extension cycles were sometimes observed in feeding trials involving exceptionally bulky prey.

**Phase IV. The thoracic phase:** Once the prey was well behind the head, the cycles of concertina-like cervical compression and extension that characterized the previous two phases of transport ceased. These cyclical movements of the neck were replaced by a continuous wave of lateral undulation that was propagated caudally along the trunk. The appearance of this continuous undulatory wave marked the beginning of the final phase of transport, the thoracic phase (Fig. 1D). During this terminal phase, a bend was formed in the trunk immediately anterior to the prey. If the prey was relatively large, this bend in the body would maintain the static position of the prey (relative to the substrate) as the snake locomoted over and around it. If the prey was relatively small, however, the bend would be propagated caudally relative to the substrate, pushing the prey through the esophagus and toward the stomach. In both cases, propulsion of the prey through the esophagus was often aided by the propagation of a caudally directed "wave" of bilateral rib adduction. This adduction of the ribs produced a region of constriction in the trunk immediately anterior to the trailing edge of the prey, and as this region of constriction was propagated caudally, it assisted in pushing the prey toward the stomach. In feeding trials involving exceptionally small prey, bilateral rib adduction appeared to be the primary propulsive mechanism during the thoracic phase, with little undulatory movement observed.

### Prey transport in other species

X-ray videographic recordings of *Python breitensteini*, *Eryx conicus*, *Elaphe alleghaniensis* and *Lampropeltis getula* feeding on rodents revealed that these species use four-phase prey transport systems similar to that of *Pituophis melanoleucus*. However, movements of the vertebral column during the orocervical phase of transport in *Lampropeltis* differed slightly from those observed in the other genera. Specifically, the neck in *Lampropeltis* was straightened almost entirely through the propagation of a posteriorly directed wave of lateral undulation rather than through concertina-like extension.

Prey transport in *Lampropeltis getula* proceeded differently when snakes instead of rodents were eaten. In both the oral and orocervical phases of transport, the jaws were ratcheted over the prey at a rapid rate, with little or no pause between successive jaw protractions. In addition, lateral rotation of the head during jaw protraction was of a greater magnitude than that which was seen in this species when feeding on rodents, and these head rotations continued unimpeded throughout both the oral and orocervical phases of transport. In all feeding trials in which snakes were offered as food, *Lampropeltis* continued to use a unilateral jaw ratcheting mechanism well after the prey had entered the esophagus, and abandoned this mechanism only after the prey's tail began to enter the mouth. From this point on, prey transport occurred exclusively through post-cranial movements.

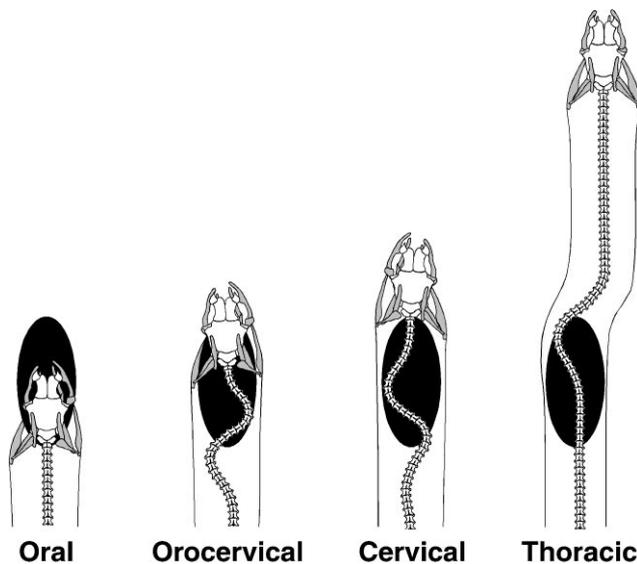
Prey transport in the piscivorous *Nerodia fasciata* was unusual among the species that we studied. In particular, vertebral bending in the cervical region was less pronounced than that observed in other species; ingestion and intraoral transport appeared to be mediated almost entirely by the jaws. However, once the prey had been transported almost entirely into the esophagus, cycles of cervical compression and extension became slightly more conspicuous. Also peculiar among the snakes that we studied was the manner in which *Nerodia* propelled prey through the esophagus. Instead of propagating a continuous propulsive wave caudally along the body, *Nerodia* exhibited intermittent lateral bending during swallowing. As a result, transport of the prey through the esophagus and into the stomach was relatively slow and irregular.

Finally, our external observations of feeding behavior in *Xenopeltis unicolor*, *Loxocemus bicolor*, *Python regius*, *Boa constrictor*, *Epicrates cenchria*, *Charina reinhardtii*, *Eryx colubrinus*, *Drymarchon corais*, and *Atractaspis bibronii* indicate that the post-cranial contribution to intraoral transport and swallowing is extensive in all of these species. In all cases, concertina-like neck movements were observed during intraoral trans-

port, and swallowing was achieved mainly through undulatory movements of the trunk. Cervical compression-extension cycles were especially pronounced in *Atractaspis*, *Xenopeltis* and *Loxocemus*. Although we were not able to visualize directly precise movements of the vertebral column and ribs during these feeding trials, it appeared that all of these taxa used a four-phase transport system similar to that of *Pituophis*.

## Discussion

Our results demonstrate that the role of the post-cranial musculoskeletal system during prey transport in *Pituophis melanoleucus* is both extensive and dynamic. Prey transport in this species progresses through four functionally discrete phases, three of which involve concertina-like or undulatory movements of the anterior portions of the vertebral column (Fig. 5). Furthermore, in each of the three phases of transport during which post-cranial movements occur, the functions of these movements are different.



**Fig. 5.** Four-phase model of prey transport in alethinophidian snakes. The prey is represented by the black oval. During the oral phase, prey is transported into the mouth exclusively by unilateral, ratchet-like movements of the jaws. During the orocervical phase, these jaw movements are augmented by concertina-like movements of the anterior portion of the trunk. In this phase of transport, cervical extension is synchronized with jaw protraction so that extension of the neck functions to protract and rotate the braincase relative to the fixed jaw. During the brief cervical phase, the jaws are no longer in contact with the prey, and the snake advances over the prey in a concertina-like fashion. Finally, during the thoracic phase, the prey is propelled through the esophagus and into the stomach by a continuous, caudally directed wave of lateral undulation. Note that throughout all phases of transport, the prey remains in a relatively constant position as the snake advances over it.

The four phases of prey transport that we recognize here correspond roughly to the four stages of “swallowing” recently outlined by Moon (2000). However, the terminology that we use is based on anatomical landmarks (oral, orocervical, cervical, and thoracic phases) rather than on specific mechanisms (the snout shifting, concertina bending, ventral flexion, and undulatory bending stages of Moon). We prefer this anatomically based terminology for three reasons. First, snakes often use more than one transport mechanism at a time. In particular, the snout shifting, concertina bending and ventral flexion mechanisms described by Moon are frequently used simultaneously. Second, the specific mechanisms used by snakes to transport their prey often vary according to the characteristics of the prey itself (i.e., size, shape, consistency). For example, although “undulatory bending” is commonly used to transport large, bulky prey through the esophagus, smaller prey are sometimes swallowed without the aid of such movements. Finally, we believe that Moon’s use of the term “snout shifting” is potentially confusing because this term was coined previously by Cundall (1995) to describe the specific feeding mechanism used by *Cylindrophis ruffus*. Because the snout shifting mechanism used by *Cylindrophis* differs in many significant ways from the pterygoid walk mechanism used by the majority of alethinophidian snakes, the broad application of the term “snout shifting” to all alethinophidians should be avoided.

### The functional roles of post-cranial prey transport movements

Throughout the oral phase of transport, prey is moved into and through the mouth almost entirely via unilateral, ratchet-like movements of the upper jaws. During this phase, the anterior portion of the trunk remains relatively still, and no undulatory or concertina-like movements are seen. However, extensive lateral bending occurs at, or slightly posterior to, the cranio-vertebral joint. These bending movements are coordinated with translational movements of the jaws so that as the left jaw is being protracted, the head is rotated laterally to the right, and vice versa. Such synchronized lateral rotations of the head function to move the toothed elements of the advancing upper jaw farther along the surface of the prey than would be possible through protraction of the jaws alone (Albright and Nelson, 1959b; Frazzetta, 1966; Kardong, 1977, 1986; Cundall and Gans, 1979; Cundall, 1983; Kardong and Berkhoudt, 1998).

As noted by Kardong (1986), lateral rotation of the head about the cranio-vertebral joint becomes increasingly attenuated as the snake advances further over the prey, especially in the case of rodent prey. This attenua-

tion appears to result from two factors. First, as the prey is forced into the relatively narrow esophagus, it is compressed. As a result of this compression, the prey becomes stiffer, thereby making rotation at the overlying cranio-vertebral joint more difficult. Second, as the snake advances to wider regions of the prey, the portion of the prey remaining outside of the oral cavity often bulges laterally beyond the angle of the mouth, and therefore comes to act as a mechanical barrier to head rotation. Once one or both of these factors become an impediment to head rotation, cycles of concertina-like compression and extension are initiated in the neck region, marking the beginning of the orocervical phase of prey transport.

Our x-ray videographic data suggest that the concertina-like movements that characterize the orocervical phase of prey transport function primarily to maximize forward displacement of the upper jaws during jaw protraction. As emphasized by Dullemeijer (1956), forward extension of the neck during unilateral jaw protraction forces the braincase and advancing upper jaw anteriorly relative to the fixed contralateral jaw. However, we also found that neck extension induces a rotation of the braincase about the fixed jaw (although the magnitude of this rotation is less than that which occurs during the oral phase of ingestion), and that the directionality of bending during cervical compression alternates according to whether the left or right jaws are about to be protracted (Fig. 3). Thus, concertina-like movements in the anterior portion of the trunk during orocervical prey transport appear to represent an alternative mechanism for augmenting upper jaw protraction. Once the resistance to rotation at the cranio-vertebral joint increases to a point at which the relatively short neck abductors (cervical portions of the *M. retractor costae biceps* and *M. longissimus dorsi*; Pregill, 1977; Albright and Nelson, 1959b) can no longer rotate the head effectively, the longer and more powerful epaxial muscles of the trunk (e.g., *Mm. spinalis et semispinalis*, *M. longissimus dorsi*, *M. iliocostalis*; Mosauer, 1935; Gasc, 1974) are recruited to protract and rotate the braincase during jaw advance.

Cervical compression and extension during the orocervical phase of transport may also function to stretch bulky, compliant prey, thereby reducing its diameter and making it easier to swallow (Gans, 1961; Cundall and Greene, 2000). However, in feeding trials involving exceptionally large rodent prey, and in the few instances in which snakes ingested rodents tail-first rather than head-first, cervical compression-extension cycles were initiated before the prey entered the esophagus. These observations lend further support to the hypothesis that the main function of concertina-like trunk movements during orocervical prey transport is to augment movements of the jaws rather than to act directly

on the prey itself. Furthermore, they suggest that increased resistance to rotation at the cranio-vertebral joint (occurring when the snake reaches wider portions of the prey), rather than entry of the prey into the esophagus *per se*, is the primary stimulus for the initiation of cervical bending during prey transport.

The cervical phase of prey transport begins once the snake has advanced to the point at which the posterior-most pterygoid teeth can no longer engage the prey. The concertina-like neck movements that characterize this phase are identical to those seen earlier during orocervical transport, but their function is entirely different. As explained above, during orocervical transport extension of the neck functions to augment the unilateral pterygoid walk mechanism by protracting and rotating the braincase relative to the fixed jaw. During the cervical phase, however, the jaws are no longer contributing to prey movement. Therefore cervical compression and extension are no longer used to augment jaw movements, but instead become the primary mechanism of prey transport. Specifically, during neck compression, the head is flexed ventrally and drawn posteriorly, thereby forcing the prey further into the esophagus. At the same time, the trunk is drawn forward, creating slack in the part of the body surrounding the prey. Then, during subsequent extension of the neck, this area of slack is straightened, resulting in the head being pushed forward relative to the prey. These cervical compression-extension cycles are repeated until the snake has progressed far enough forward to be able to form a bend in its neck anterior to the prey bolus, at which point the thoracic phase begins.

The post-cranial movements that characterize the thoracic phase of transport differ both functionally and kinematically from those seen earlier during orocervical and cervical transport. Most notably, this terminal phase of transport involves the propagation of a continuous wave of lateral undulation along the trunk, rather than cyclical bending and straightening of the neck. It begins with the formation of a bend in the neck immediately anterior to the prey bolus. This bend is then propagated caudally along the body, thereby propelling the prey through the esophagus. In most instances, this travelling wave of lateral undulation does not move significantly relative to the substrate. Rather, the bend in the snake's body keeps the prey stationary relative to the substrate as the snake moves forward over it. In such instances, the snake effectively uses the prey as a *point d'appui* for undulatory locomotion, advancing in this manner until the stomach has enveloped the prey. However, when relatively small prey items are being consumed, this may not be the case, and the prey may actually be pushed posteriorly toward the stomach.

Once the mechanical roles of post-cranial movements during intraoral transport and swallowing are fully un-

derstood, the functional significance of the cervical phase of prey transport becomes more clearly evident. This phase of transport occurs after the jaws have advanced beyond the prey. Therefore the jaws are no longer able to contribute to prey transport. However, the presence of the prey immediately behind the head also prevents the snake from forming a bend in its neck anterior to the prey, a necessary first step for the initiation of the thoracic phase of transport. Thus, although the cervical phase is generally brief in duration, it represents an important functional transition between jaw-mediated intraoral transport (oral and orocervical phases) and swallowing (thoracic phase).

### Post-cranial prey transport mechanisms in other snakes

Our observations of feeding behavior in a phylogenetically diverse sample of 15 species of snakes demonstrate that movements of the trunk contribute significantly to prey transport in representatives of at least six alethinophidian families (Xenopeltidae, Loxocemidae, Pythonidae, Boidae, Colubridae and Atractaspididae). These findings, when considered together with previous observations of neck bending during swallowing in viperids (Dullemeijer, 1956; Klauber, 1956; Kardong, 1977; Janoo and Gasc, 1992) and in the anilioid *Cylindrophis* (Cundall, 1995), suggest that post-cranial prey transport mechanisms may be present universally throughout Alethinophidia. However, a recent study of the feeding mechanisms of blindsnakes (Kley, 2001) showed that such mechanisms are absent or highly modified in Scolecophidia. In Typhlopidae, movements of the trunk do not contribute to prey transport. Prey are transported into and through the mouth via rapid movements of the maxillae and are then propelled through the esophagus by peristalsis. In Leptotyphlopidae, movements of the trunk do contribute to intraoral transport, but these movements differ greatly from those seen in alethinophidians. Most notably, the cervical bending associated with the leptotyphlopoid mandibular raking mechanism is executed exclusively in the sagittal plane, and neck extension occurs during jaw retraction rather than during jaw protraction. Despite these differences, the function of these neck movements in leptotyphlopids appears to be analogous to the function of the concertina-like movements that characterize the orocervical phase of transport in alethinophidians. In both cases, extension of the neck results in the braincase being pushed forward relative to either the lower (Leptotyphlopidae) or upper (Alethinophidia) jaws. As in typhlopids, propulsion of prey through the esophagus in leptotyphlopids occurs via peristalsis rather than through undulatory movements of the trunk as in alethinophidians. Although post-cranial prey transport mechanisms appear to be present in most, if not all, alethinophidian

snakes, the descriptions presented in this study, together with those from previous published accounts (Dullemeijer, 1956; Gans, 1961; Frazzetta, 1966; Kardong, 1977, 1986; Janoo and Gasc, 1992; Cundall, 1995; Kardong and Berkhoudt, 1998; Moon, 2000), demonstrate that these mechanisms are somewhat variable within Alethinophidia. For example, in most of the taxa that we examined in this study, extension of the neck during the orocervical and cervical phases occurred in a concertina-like fashion. In some species (e.g., *Lampropeltis getula*), however, the neck was straightened mainly through the propagation of a caudally directed wave of lateral undulation along the anterior portion of the trunk. Lateral undulatory movements also appear to characterize the orocervical phase of transport in at least some viperids (Kardong, 1977). The limited data currently available support few conclusions regarding the potential phylogenetic or functional significance of these differences. It is possible, however, that undulatory movements have a greater direct effect on the prey itself, and may serve to stretch bulky prey into a more elongate shape, thereby making such prey easier to swallow.

The magnitude of the neck movements seen during intraoral transport also varies considerably among taxa. Cervical compression is especially great in species that have limited upper jaw mobility (e.g., *Xenopeltis unicolor*, *Loxocemus bicolor*) or that lack palatopterygoid teeth (e.g., *Charina reinhardtii*, *Atractaspis bibronii*). This suggests that alethinophidian taxa having relatively inefficient jaw mechanisms may compensate for this inefficiency by relying more heavily on post-cranial transport mechanisms. This hypothesis is further supported by a recent study of feeding behavior in *Cylindrophis ruffus* (Cundall, 1995), a basal alethinophidian that has limited upper jaw mobility and that relies heavily on cyclical compression and extension of the neck to transport prey. In contrast, neck movements may be relatively slight in other taxa such as *Nerodia*, a genus which has an extraordinarily well-developed jaw mechanism (Cundall and Gans, 1979; Cundall and Shardo, 1995). However, given that neck movements are relatively pronounced in other colubrids that have similar jaw mechanisms, their reduced role during intraoral transport in *Nerodia* is probably due largely to the physical characteristics of the fish on which these snakes feed (see "Effects of prey type" below).

Although the post-cranial contribution to prey transport in *Cylindrophis ruffus* is extensive, the coordination of neck movements and jaw movements in this basal alethinophidian species differs significantly from that of more derived macrostomatans. With the exception of *Nerodia*, all of the macrostomatatan taxa observed in this study exhibited a distinct orocervical phase of prey

transport, during which cycles of cervical compression and extension were coupled with unilateral movements of the jaws. In *Cylindrophis*, however, unilateral jaw movements are terminated soon after the leading edge of the prey begins to enter the esophagus. At this point, concertina-like movements become more pronounced in the cervical region and a pattern of bilaterally synchronous jaw opening and closing is established (Cundall, 1995). Therefore, in *Cylindrophis*, extension of the neck results in the entire head being pushed forward over the prey. In this respect, the post-cranial transport mechanism used by *Cylindrophis* during the early stages of intraoral transport is functionally equivalent to that which is used by macrostomatans during the cervical phase of transport. However, in macrostomatans this mechanism is initiated only after the jaws have advanced beyond the prey. The early onset of this mechanism in *Cylindrophis* may be due to the relative inefficiency of the jaw mechanism which it uses during the early stages of transport (Cundall, 1995).

### Effects of prey type

Our results demonstrate that post-cranial prey transport mechanisms in snakes are strongly influenced by the physical characteristics of the prey being consumed. The most important of these characteristics appears to be prey diameter. In general, cervical compression is greatest during the transport of relatively large, bulky prey. In contrast, in rare instances in which extraordinarily small prey is being consumed, the neck may remain nearly straight throughout intraoral transport. In addition, the mechanisms used during the thoracic phase of transport also vary according to prey size. When a relatively large prey item is swallowed, it is propelled through the esophagus mainly through undulatory movements of the trunk. In contrast, small prey items are often transported toward the stomach exclusively by a caudally directed wave of bilateral rib aduction.

The mechanical properties of the prey have strong effects on post-cranial transport mechanisms as well. During the transport of soft prey, such as rodents, the prey becomes increasingly compressed in the esophagus and mouth as transport continues, resulting in the posterior portion of the prey ballooning outward from the mouth. Consequently, lateral rotation of the head about the cranio-vertebral joint becomes increasingly difficult as the snake advances over the prey. In such instances, repeated cycles of cervical compression and extension assist the snake in overcoming this mechanical barrier. However, during the transport of firmer prey, such as fishes and snakes, no such mechanical barrier develops, and post-cranial movements are relatively slight or even absent throughout intraoral transport.

Finally, the shape of the prey is an important factor in determining the extent to which post-cranial movements can contribute to prey transport. As seen in *Cylindrophis* (Cundall, 1995), some snakes may abandon jaw-mediated transport soon after the prey begins to enter the esophagus, thereafter relying exclusively on post-cranial transport mechanisms. In such taxa, the relative contribution of these post-cranial mechanisms depends on what proportion of the prey remains outside of the mouth when the leading edge of the prey first enters the esophagus. In the case of elongate prey (e.g., eels, caecilians, amphisbaenians, snakes), the transition from cranial to post-cranial transport mechanisms would occur early in prey transport, and therefore the role of the latter would be relatively extensive. In the case of more spherical prey (e.g., rodents, birds, eggs), however, this transition would occur after much of the prey had already been ingested, and thus the role of post-cranial transport mechanisms would be less extensive. This effect of prey shape is probably most significant among basal alethinophidians, such as *Anilius*, *Cylindrophis* and uropeltids, which feed almost exclusively on elongate prey (Greene, 1983, 1997; Rajendran, 1985) and which have relatively inefficient jaw mechanisms (Haas, 1930; Rieppel, 1980; Cundall and Rossman, 1993; Cundall, 1995).

### The evolution of post-cranial prey transport mechanisms

Alethinophidian snakes are unusual among tetrapods in that they generally feed on relatively large vertebrate prey which they swallow whole. In addition, the ophidian *Bauplan* imposes several important biomechanical constraints on the feeding systems of snakes: the tongue is highly modified for its role in chemoreception (tongue flicking), and is no longer useful for prey transport (McDowell, 1972; Schwenk, 2000b); the hyoid is greatly reduced (Langebartel, 1968), and therefore cannot be used for pharyngeal packing (Smith, 1984, 1986); the forelimbs are lost, thus reducing the potential efficiency of cranioinertial feeding mechanisms (Gans, 1961); and elongation of the body has resulted in a wide separation between the mouth and the stomach. Furthermore, snakes generally swallow their prey without the aid of gravitational forces (prey are most commonly transported parallel to the surface of the ground), and they lack the explosive peristaltic swallowing mechanisms present in mammals. Given these facts, it is perhaps not surprising that snakes rely heavily on movements of the trunk to transport their prey. However, it is not yet clear whether the post-cranial transport mechanisms described in this paper are unique to alethinophidian snakes or if they represent the retention and elaboration of mechanisms that were already present in the ancestor of snakes (and that were

subsequently lost in the microphagous scolecophidian snakes; Kley, 2001). Sinuous neck movements are occasionally seen during intraoral transport and swallowing in a variety of non-ophidian squamates (e.g., Bellairs, 1970; Smith, 1984, 1986; Kardong *et al.*, 1997; Elias *et al.*, 2000; Moon, 2000; Schwenk, 2000b), and in some instances these movements strongly resemble those which characterize the orocervical and cervical phases of transport in snakes (Kley and Brainerd, unpublished data). However, these movements have never been described in detail, and it remains unclear how they contribute to prey transport. A better understanding of the evolution of post-cranial prey transport mechanisms in squamates will therefore depend on future research addressing the function(s) and the phylogenetic distribution of these mechanisms in lizards.

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