

THE MECHANICS OF SWALLOWING AND THE MUSCULAR CONTROL OF DIVERSE BEHAVIOURS IN GOPHER SNAKES

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Summary

Snakes are excellent subjects for studying functional versatility and potential constraints because their movements are constrained to vertebral bending and twisting. In many snakes, swallowing is a kind of inside-out locomotion. During swallowing, vertebral bends push food from the jaws along a substantial length of the body to the stomach. In gopher snakes (*Pituophis melanoleucus*) and king snakes (*Lampropeltis getula*), swallowing often begins with lateral bending of the head and neck as the jaws advance unilaterally over the prey. Axial movement then shifts to accordion-like, concertina bending as the prey enters the oesophagus. Once the prey is completely engulfed, concertina bending shifts to undulatory bending that pushes the prey to the stomach. The shift from

concertina to undulatory bending reflects a shift from pulling the prey into the throat (or advancing the mouth over the prey) to pushing it along the oesophagus towards the stomach. Undulatory kinematics and muscular activity patterns are similar in swallowing and undulatory locomotion. However, the distinct mechanical demands of internal versus external force exertion result in different duty factors of muscle activity. Feeding and locomotor movements are thus integral functions of the snake axial system.

Key words: feeding, snake, *Pituophis melanoleucus*, *Lampropeltis getula*, muscle, functional morphology, biomechanics.

Introduction

Most organismal structures have multiple roles. Understanding the functional versatility, as well as potential constraints, of complex organismal structures requires information about how they are used in diverse environments and behaviours (e.g. Biewener and Gillis, 1999; Carrier, 1991). Snakes are particularly interesting models for this kind of integrative research because their simplified body forms constrain their movements to various axial bends and twists. However, given this constraint, snakes have a remarkably diverse behavioural repertoire, including at least five distinct types of locomotion (Gans, 1986) as well as complex axial bending, twisting and coiling movements associated with feeding and other behaviours. In particular, undulatory locomotion, constriction and specialised feeding biology are hypothesised to have been key aspects of snake evolution (Gans, 1961, 1962; Greene, 1983, 1994; Greene and Burghardt, 1978; Pough and Groves, 1983). Together, these behaviours represent a suite of integrated, and often simultaneously used, axial functions.

Lateral bending of the vertebral column is a critical component of diverse snake behaviours. In most snakes, ingestion of food begins with unilateral movements of the highly kinetic jaws (Albright and Nelson, 1959; Bolt and Ewer, 1964; Dullemeijer, 1956, 1959; Gans, 1961; Kardong,

1977, 1986), but then swallowing is completed by the axial system, which transports the prey along the body to the stomach (e.g. Cundall, 1995; Frazzetta, 1966; Gans, 1961; Janoo and Gasc, 1992; Kardong, 1977; Kardong and Berkhoudt, 1998).

At least three distinct axial bending patterns have been reported during swallowing in snakes (Cundall, 1995; Janoo and Gasc, 1992; Kardong, 1977; Kardong and Berkhoudt, 1998). During the first stage of ingestion, snakes use unilateral movements of the jaws and simple lateral bending of the head and anterior neck to ingest the prey (Albright and Nelson, 1959; Bolt and Ewer, 1964; Cundall, 1995; Frazzetta, 1966; Gans, 1961; Kardong, 1977, 1986). Accordion-like, concertina bending movements of the neck ('compression–extension cycles' of Cundall, 1995; Kardong and Berkhoudt, 1998) often occur during pauses between unilateral jaw movements. During concertina bending, the snake's body is drawn forward over the prey into several sharp bends, which are then straightened by pushing the head forwards. These concertina bends help draw the ingested part of the prey into the oesophagus.

As the prey moves from the jaws into the throat, the concertina bending shifts to undulation, in which a wave of bending is propagated along the body from the head towards

the stomach. This transition may represent a brief, but distinct, stage of swallowing (Kley and Brainerd, 1996). The shift from concertina to undulatory bending reflects a mechanical shift from pulling the prey into the mouth and throat (or advancing the snake's mouth over the prey; Cundall, 1983; Cundall and Gans, 1979; Kardong, 1977, 1986) to pushing the prey along the oesophagus towards the stomach.

Pilot studies indicated that swallowing undulations are kinematically similar to those of lateral undulatory locomotion and recruit some of the same muscles (Moon, 1997; Moon and Kley, 1997). In both lateral undulation and swallowing, waves of axial bending are propagated along the body from head to tail. In locomotion, the bends exert forces laterally against rigid surface objects (Jayne, 1988a; Moon and Gans, 1998; Mosauer, 1932), whereas in swallowing they push internally against the compliant prey. The kinematic similarity between swallowing and locomotor movements suggests that the epaxial muscles have qualitatively similar timing of activity in swallowing and locomotion. However, the different patterns of force exertion may in turn require differences in the timing of muscle activity. Comparison of feeding and locomotor movements can illustrate how muscle recruitment varies in diverse behaviours with different mechanical demands.

I studied the muscular control and kinematics of vertebral bending during swallowing in five gopher snakes (*Pituophis melanoleucus*) and one king snake (*Lampropeltis getula*). Specifically, I tested the hypotheses that the epaxial muscles are important vertebral flexors during swallowing and that their activation patterns are similar in swallowing and locomotor undulations. I then discuss how kinematic patterns and muscular control vary in response to the distinct mechanical demands of locomotor and feeding movements. Finally, I draw on the limited available data from snakes, lizards and other reptiles to trace the evolution of some snake feeding movements.

Materials and methods

I recorded the kinematics, epaxial muscle activity and pressure exerted on prey during swallowing in five gopher

snakes (four *Pituophis melanoleucus affinis* Hallowell and one *P. m. deserticola* Stejneger) and one king snake (*Lampropeltis getula nigrita* Zweifel and Norris; Table 1). Only four of the gopher snakes were used in the statistical analyses. Although the single king snake is an insufficient sample on which to base generalisations, the limited results from this individual indicate kinematic and electromyographic (EMG) similarities to the gopher snakes.

All snakes were housed on a seasonal photoperiod and were fed laboratory mice weekly to monthly as needed; snakes were not fed for at least 1 week before use in the experiments. For the experiments, the snakes were placed in an open 300 mm×500 mm glass aquarium. The open top allowed free movement of the wiring and tubing connected to the animals. The ambient and surface temperatures under the video spotlights ranged from 23 to 28 °C over the course of the experiments. This range approximated the optimal temperatures for feeding movements in gopher snakes (Greenwald, 1974). In all experiments, mice were offered to the snakes with long forceps, and recordings were made of constriction prior to swallowing (Moon, 2000).

Videography and electromyography

The feeding trials were videotaped using a Sony S-VHS video camera placed horizontally approximately 2.5 m from the aquarium containing the snake. The aquarium was lined with a grid for scale and contained a mirror at 45 ° from the horizontal to reflect a dorsal view into the video camera. I recorded the experiments at 30 frames s⁻¹, which proved adequate for the slow movements recorded (0.04–0.63 Hz).

I used Measurement TV software (MTV; DataCrunch Software) to digitise the outlines or vertebral midline of the snakes at 5 frames s⁻¹, which was eight times the highest movement frequencies observed. I then used Fin software (DataCrunch) to calculate vertebral bending angles. To calculate bending angles, Fin uses a finite-element analysis based on the digitised vertebral midline of an animal or on a midline spline that it calculates from a digitised body outline. For some snakes, I digitised the vertebral midline directly, and for others I digitised the body outline, from which Fin

Table 1. Sizes and electrode placements for the king snake (*Lampropeltis getula*) and gopher snakes (*Pituophis melanoleucus*) from which muscle activity was recorded

| Snake | Mass (g) | SVL + TL (mm) | BV + TV | Muscles | Electrode placement |
|-------|----------|---------------|---------|-------------|--------------------------|
| L1 | 378 | 1110+150 | 226+49 | SSP, LD | Bilateral V50, V75 |
| P8 | 341 | 970+155 | 231+61 | SSP, LD | Bilateral V25, V75, V125 |
| P12 | 614 | 1255+190 | 233+57 | SSP, LD, IL | Bilateral V50, V75 |
| P13 | 596 | 1310+170 | 241+61 | SSP, LD, IL | Bilateral V25, V75 |
| P17 | 561 | 1105+130 | 243+52 | SSP, LD, IL | Bilateral V25, V75 |
| P19 | 759 | 1180+100 | 244+33 | SSP, LD, IL | Bilateral V25, V75 |

P, *Pituophis melanoleucus*; L, *Lampropeltis getula*.

SVL, snout-to-vent length; TL, tail length; BV, number of vertebrae from snout to vent; TV, number of tail vertebrae; SSP, M. semispinalis; LD, M. longissimus dorsi; IL, M. iliocostalis; V, vertebra.

computed a midline. I set the finite element length to correspond to vertebral length, measured as the distance between adjacent ventral scales (Alexander and Gans, 1966). I then used a four-point moving average to smooth small fluctuations in the vertebral bending angles.

The superficial epaxial muscles, the *Mm. spinalis-semispinalis*, *longissimus dorsi* and *iliocostalis*, have the largest cross-sectional areas of the axial muscles, are interconnected in the most complex way and are hypothesised to be the most important axial flexors (Gasc, 1974, 1981; Ruben, 1977a). For the electromyographic (EMG) recordings, I implanted bipolar hook electrodes into the semispinalis portion of the *M. spinalis-semispinalis* (SSP), the *M. longissimus dorsi* (LD) and the *M. iliocostalis* (IL) at two or three longitudinal positions on each snake (Table 1). To compare the muscular control of locomotor and feeding movements, I implanted electrodes in the epaxial muscles bilaterally between vertebrae 25 and 125 (as indicated by ventral scale counts; Alexander and Gans, 1966). The electrodes were made of Teflon-coated stainless-steel wire (Medwire, Sigmund Cohn Corp.) with a bipole spacing of 1.0 mm and bare recording tips of 0.5 mm. To ensure proper placement, I implanted and removed the electrodes surgically. For implantation, I anaesthetised the snakes with Halothane using an open drop method (Bennett, 1996), made a short longitudinal incision in the skin and underlying fascia, used a dissecting probe to identify the target muscle, and then inserted the electrodes into the muscle using a hypodermic needle. Incisions were sealed with small amounts of cyanoacrylate glue and a surgical spray wound dressing.

The electrode leads were fixed to the skin with cyanoacrylate glue and small patches of tape at intervals along the trunk. The leads were bound into one bundle and connected to the amplifier cabling *via* Amphenol gold mini-connector pins. The amplifier cables were hung from the laboratory ceiling so that the snake could move with minimal resistance from the cabling.

Each snake was tested over a period of up to 1 week, during which the electrodes remained in place and had a stable impedance. Upon surgical removal of each electrode, I used a dissecting probe to separate the instrumented muscle segment from its neighbours just enough to confirm that the electrode was implanted completely within the target muscle segment.

The EMG signals were amplified by Tektronix FM 122 or Tektronix 26A2 differential preamplifiers (gain 1000 or 5000; bandwidth 100 to 10 000 Hz), then by Honeywell 117 DC amplifiers (gain 1 or 5) to stabilise the signal current, and were recorded on FM tape. The signals were recorded at 19.05 cm s^{-1} on a Honeywell 101 medium-band tape recorder (bandwidth 100–2500 Hz). The EMG signals were digitised at 8000 to 10 000 Hz (real time) per channel using a Keithley 12-bit analogue-to-digital converter and DataCrunch software, and then digitally filtered below 100 Hz and above 2500 Hz. These sampling rates were sufficient to reproduce accurate EMG spike frequencies and amplitudes (Jayne et al., 1990; Moon, 1996).

Plethysmography

The forces exerted by the snakes on the prey produce elevated pressures in the body of the prey, which may be recorded using plethysmography. To record the pressures in the prey during swallowing, I implanted small pressure-transducer bulbs into the coelomic cavities of mice. For these recordings, I used both live and dead mice (maintained at body temperatures of 38–40 °C). The bulb and the tubing that connected it to the pressure transducer were swallowed by the snakes. Just before the pressure bulb reached the region of the stomach, it was gently pulled back out by the tubing, with little disturbance to the snake. The pressure signals from a Gould-Statham P23 physiological pressure transducer and a Harvard Apparatus blood pressure transducer were calibrated over the range 0–40 kPa (0–300 mmHg). Both transducers gave stable output with no measurable drift over periods of 30 min. The pressure signals were recorded on the same tape as the EMG signals.

Analyses

I recorded kinematic, electromyographic and pressure data for 25 feeding events by four gopher snakes. I analysed quantitative data for 15 of these events, which encompassed 35 bending movements and 100 bursts of muscle activity (Table 2). I qualitatively examined the kinematic and electromyographic data from the other snakes in Table 1 (P8 and L1), plus two additional uninstrumented gopher snakes.

From the digitised video and EMG signals, I used the software described above to calculate vertebral bending angles (degrees per joint), EMG burst duration (s), the rectified integrated area for each EMG burst (sV; this represents the area under the voltage/time curve, after standardising the signals for preamplifier gain) and EMG duty factor (the proportion of the undulation cycle that involves epaxial muscle activity). In the results for and discussion of relative muscle activation phases and EMG duty factors, values are expressed as a proportion of the undulatory cycle: 0 represents the straight posture at the start of a bending cycle, 0.25 is the first peak of bending, 0.5 is the inflection where the body straightens and reverses curvature, and 0.75 is the second peak of bending in the cycle. In the slow movements studied, the muscle activity times are much longer than any potential delays

Table 2. *Samples used in the statistical analyses of kinematic, electromyographic (EMG) and force data from feeding in gopher snakes (Pituophis melanoleucus)*

| Snake | Number of feedings | Number of bending movements | Number of EMG bursts | Number of pressure samples |
|-------|--------------------|-----------------------------|----------------------|----------------------------|
| P12 | 4 | 4 | 6 | 1 |
| P13 | 2 | 5 | 12 | 0 |
| P17 | 7 | 22 | 70 | 5 |
| P19 | 2 | 4 | 12 | 1 |
| Total | 15 | 35 | 100 | 7 |

in excitation–contraction coupling, times to peak tension and relaxation times. Therefore, these factors are unlikely to affect major inferences about muscle actions.

To examine the relationships among these measures of muscle activity and vertebral bending, I used a multiple regression analysis. In the regression, the dependent variable was the maximum change in bending angle during muscle activity and the independent variables were EMG burst rectified integrated area, burst duration, the interaction burst area \times burst duration and individual snake, which was coded as a dummy variable following Zar (1984).

This analysis included only unilateral muscle activity associated with lateral bending. Each burst of muscle activity was included as a separate case in the analyses because variable patterns of activation showed that the three epaxial muscles can act independently. In addition, because a unit of EMG burst area can be produced by a short, large-amplitude burst or by a longer burst of lower amplitude, I included area, duration and their interaction (area \times duration) in the regression analyses. This approach is warranted because of the potential statistical problems associated with the alternative approach of scaling area by duration (Packard and Boardman, 1987). Prey size may also affect the EMG and bending patterns, but was excluded from the regression because of the small range tested: most prey animals ranged from 7.5 to 53.5 g, which encompassed 1–7% of the snake's mass, and only one prey animal was larger (122.5 g, 20% of the snake's mass). The regression was computed using centred variables, and correlations were considered significant at $P=0.05$.

Results

Anatomy

Each of the epaxial muscles, *Mm. spinalis-semispinalis* (SP-SSP), *longissimus dorsi* (LD) and *iliocostalis* (IL), consists of overlapping segments that together form a longitudinal column. These three groups of muscles are interconnected into

a complex series of muscle–tendon segments (Fig. 1). To simplify the terminology of the multiple origins and insertions of these muscle–tendon chains, I specify 'anterior' and 'posterior' tendons, and use the general term 'insertion'. The number of vertebrae spanned by muscles or tendons reflects the number of joints spanned by the muscle fibres or tendon (i.e. it includes one vertebra of insertion); this method of counting vertebrae differs from that of Jayne (1982) by not including both vertebrae of insertion. I use the terms 'cervical' or 'neck' to indicate approximately the 22 anteriormost vertebrae, whose anterior tendons are shortened by their insertion on the skull and first few vertebrae, and the terms 'axial' and 'trunk' to indicate the rest of the vertebral column.

The anterior tendon of the SP-SSP inserts on the dorsal posterior edge of a neural spine and extends posteroventrally for 10 vertebrae to the SP-SSP fibres. The SP-SSP fibres share the anterior tendon, but split posteriorly into discrete SP and SSP muscles. From the anterior SP-SSP tendon, the SP fibres span three vertebrae posterodorsally and insert on the tendons of two adjacent segments of the *M. multifidus* (which was not studied here). The SSP fibres span four vertebrae posteroventrally and insert on the anterior dorsal tendon of the LD. The SSP-LD tendon spans four vertebrae between the SSP and LD fibres. It begins as a discrete ribbon but then becomes obscured for a short distance in the fascia overlying the SSP column (Fig. 1, arrow); I could not detect an insertion on the skeleton by this tendon. The fibres of the LD extend posteriorly for four vertebrae and terminate on a vertebral prezygapophysis. Overall, the SSP-LD system spans 22 vertebral joints.

Anteriorly, the LD also gives rise to an anterior ventral tendon that spans four vertebrae anteriorly and connects to the fibres of the IL. The IL extends anteriorly for seven vertebrae to insert on an anterior tendon, which spans five more vertebrae and inserts on a rib. The IL-LD system spans 20 vertebrae. Overall, a single epaxial muscle–tendon chain spans 22 vertebrae and has four insertions on the skeleton.

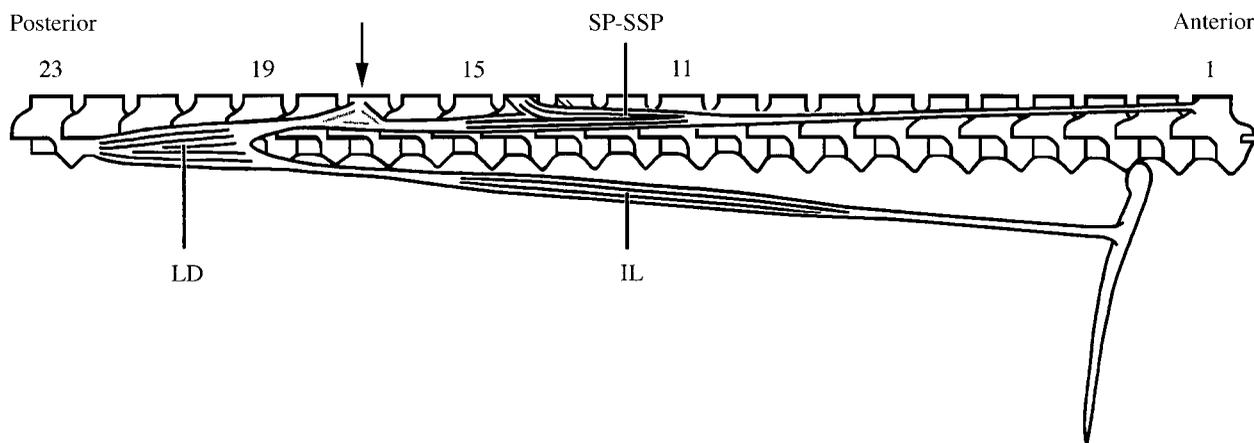


Fig. 1. Epaxial muscular anatomy of the mid trunk of the gopher snake *Pituophis melanoleucus*. IL, *M. iliocostalis*; LD, *M. longissimus dorsi*; SP-SSP, *M. spinalis-semispinalis*. The numbers indicate vertebral position from the anterior origin of the muscle–tendon chain. The arrow indicates the diffuse portion of the SSP-LD tendon in the surrounding connective tissue, which is not an insertion on the vertebra.

The limited data available indicate that the musculature of king snakes is similar to that of gopher snakes (Mosauer, 1935, unspecified sample size of *Lampropeltis getula* and *Pituophis melanoleucus*; Pregill, 1977, four *L. getula*, one *P. melanoleucus*; Jayne, 1982, one *L. getula*, five *P. melanoleucus*). Therefore, the general conclusions about anatomy/function relationships made here for gopher snakes should also apply to king snakes.

Intraoral transport

The snakes showed four kinematically and mechanically distinct stages of swallowing. Three of these stages were associated with intraoral transport and one was associated with oesophageal transport. Prey were ultimately ingested head-first, although occasionally a snake started ingesting the prey at mid-body but then released it and started swallowing it again head-first. In the first stage of ingestion, snakes always used unilateral jaw movements, usually with simultaneous lateral bending of the head and anterior neck (Fig. 2). The jaws were always protracted on the convex side of each cranial-cervical bend. In snake P17, pronounced lateral bending of the head and anterior neck involved activity of the epaxial muscles as far posterior as vertebra 25 (Fig. 3); these muscles insert *via* long anterior tendons on vertebrae 3–20.

In the second stage of swallowing, once the leading edge of the prey had moved into the anterior oesophagus, the anterior neck began bending in an accordion-like, concertina pattern over the ingested part of the prey. The concertina bending usually started during the period of unilateral jaw movements and simple lateral swinging of the head. The most common sequence of movement involved first bending of the head towards one side (simultaneous with jaw retraction on the concave side and protraction on the convex side), followed by bending towards the other side, and then pausing the lateral bending to form concertina bends. Concertina bending usually

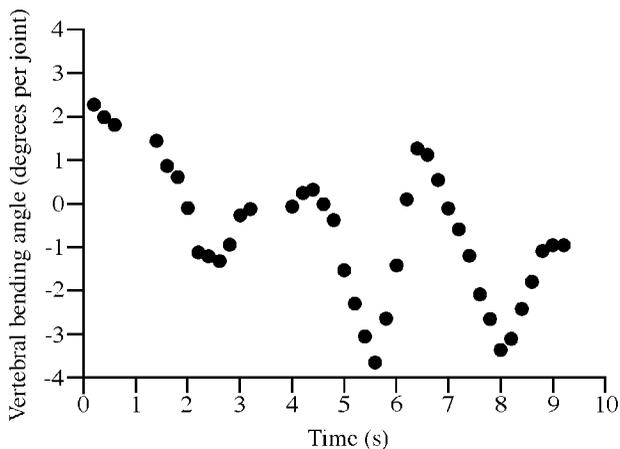


Fig. 2. Vertebral bending angles of cervical vertebra 3 during ingestion of prey in the gopher snake *Pituophis melanoleucus* (individual P17). Positive bending angles represent bending (concave) towards the right, and negative angles represent bending towards the left.

involved half- to a full-wavelength bend encompassing 10–20 vertebrae. Straightening of the concertina bends usually involved advance of the head; however, the bends were straightened occasionally by their propagation (undulation) posteriorly along the neck.

Once part of the prey had been drawn into the mouth and throat, it was often lifted up and the remainder swallowed off the substratum. Lifting involved approximately 10–40 vertebrae and varied between nearly horizontal and nearly vertical. Most of the mice (approximately 1–6% of the snake's mass) were swallowed in this way. Therefore, the jaws and axial bends, with the help of gravity, must have actively pulled the prey into the mouth and anterior oesophagus. However, a large mouse and a rat (7% and 20% of the snake's mass respectively) were swallowed while lying on the substratum. For such large prey, the snake moved its jaws and head forwards over the prey.

A transitional third stage of swallowing involved transport of the prey past the jaws and fully into the oesophagus. Unilateral jaw movements ceased, but concertina bending continued, often together with sharp downward bending of the head. Depression of the head appeared to push the palate against the trailing edge of the prey as it moved past the jaws and completely into the oesophagus. Concertina bending of the anteriormost (approximately 10–20) vertebrae must have involved anterior muscles, but did not involve activity of the epaxial muscles as far posterior as vertebra 25.

Oesophageal transport

Once the prey had been drawn fully into the oesophagus, the

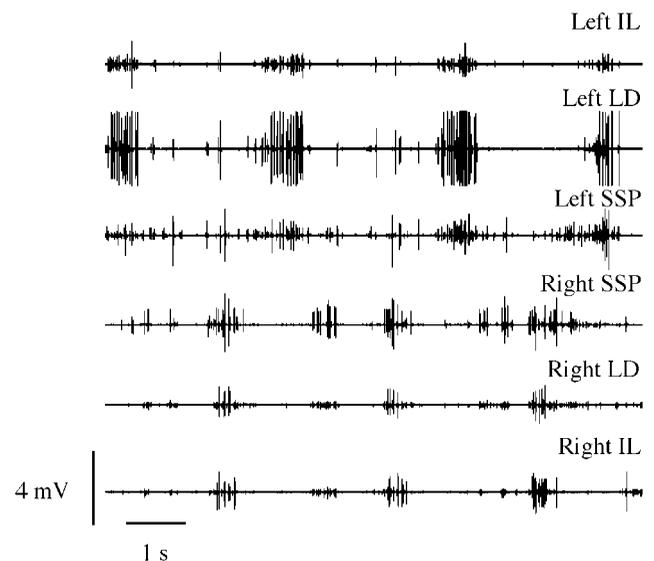


Fig. 3. Epaxial muscle activity at vertebra 25 during alternating left and right cervical bending and ingestion of prey in the gopher snake *Pituophis melanoleucus* (individual P17). IL, *M. iliocostalis*; LD, *M. longissimus dorsi*; SSP, *M. semispinalis*. Note that this muscle activity corresponds with alternating left and right bending of both vertebra 3, at which the muscles insert, and vertebra 25, the position of the LD muscle tissue and recording electrodes.

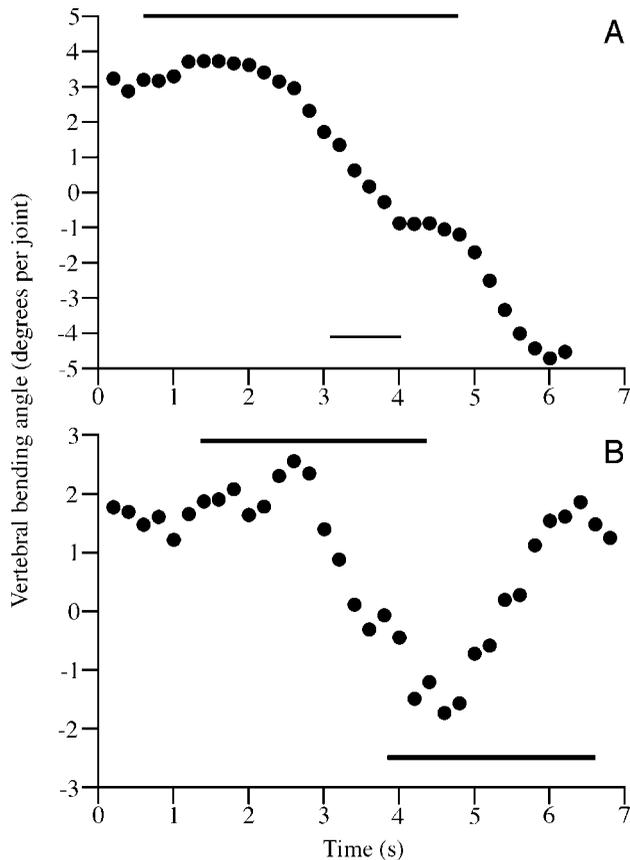


Fig. 4. Bending angles and epaxial muscle activity of vertebra 25 during swallowing undulation in the gopher snake *Pituophis melanoleucus* (individual P17). (A) A swallowing event from snake P17 in which the epaxial muscles were active from the convex to the straight regions of an axial bend. (B) Another swallowing event in which the epaxial muscles were active from the convex to concave regions of bending. Bending angles are plotted as in Fig. 2. Epaxial muscle activity at vertebra 25 is indicated by the bars above (left-side activity) and below (right-side activity) the data points; the thin bar indicates low-level muscle activity in which the electromyographic amplitude was approximately 10% or less of the larger-amplitude bursts, whereas the thick bars indicate pronounced activity.

stationary concertina bending gradually shifted to propagated undulatory bending. Depression of the head ceased during oesophageal transport. During this fourth stage of swallowing, a half- or occasionally full-wavelength bend formed in the neck anterior to the prey and pushed the prey along the oesophagus towards the stomach (Fig. 4). This bend encompassed 7–19 vertebrae and maximal angles of $2.9\text{--}19.3^\circ$ per vertebral joint ($7.11 \pm 4.20^\circ$, mean \pm s.d., $N=22$), and was propagated along the trunk at $0.04\text{--}0.63$ Hz (0.21 ± 0.13 Hz, mean \pm s.d., $N=35$). The anterior neck was usually bent most sharply, whereas the rest of the trunk was bent less sharply (e.g. Fig. 4). Immediately anterior to the prey, constriction of the trunk diameter appeared to help push the prey along the oesophagus. The swallowing undulations were often intermittent, particularly when a snake moved around the cage before swallowing was completed.

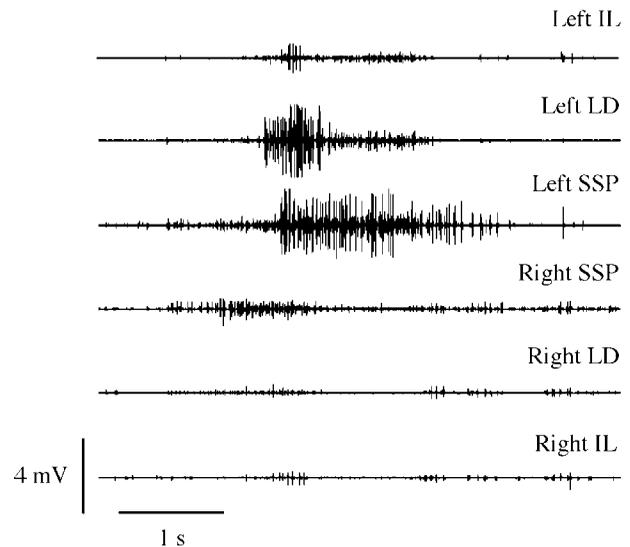


Fig. 5. Epaxial muscle activity at vertebra 25 during swallowing undulation in the gopher snake *Pituophis melanoleucus* (individual P17). IL, *M. iliocostalis*; LD, *M. longissimus dorsi*; SSP, *M. semispinalis*. In this example, muscle activity on the left side corresponds to the bend pushing directly against the prey.

As axial bending shifted from concertina to undulatory bending, epaxial muscle activity shifted from stationary unilateral activity to propagated unilateral activity (Fig. 5). The epaxial muscles were active in the axial bend immediately anterior to and overlying the internal prey (Figs 4–6; Table 3). The epaxial muscles were usually activated before maximal convexity and deactivated after maximal concavity, and therefore had large duty factors (Figs 4, 5; Table 3). However, there was substantial variation in the timing of muscular activity (e.g. Fig. 4). In one common variant, after a brief pause in a relatively straight position, the muscles were activated in

Table 3. *Timing and duty factor of epaxial muscle activity during swallowing undulations in four gopher snakes (Pituophis melanoleucus)*

| Muscle | Onset phase | Offset phase | Duty factor |
|----------------|----------------------|----------------------|-----------------------|
| IL | 0.22 ± 0.16 (27) | 0.90 ± 0.45 (26) | 0.69 ± 0.54 (27) |
| LD | 0.24 ± 0.19 (35) | 0.73 ± 0.44 (34) | 0.53 ± 0.47 (35) |
| SSP | 0.19 ± 0.20 (37) | 0.79 ± 0.45 (35) | 0.64 ± 0.46 (38) |
| IL, LD and SSP | 0.22 ± 0.19 (99) | 0.80 ± 0.45 (95) | 0.61 ± 0.49 (100) |

IL, *M. iliocostalis*; LD, *M. longissimus dorsi*; SSP, *M. semispinalis*.

Electromyographic (EMG) onset and offset timing are expressed as phase of locomotor cycle, where 0 indicates straight, 0.25 indicates maximal convexity and 0.50 indicates the subsequent straight posture.

Duty factor indicates EMG burst duration as a proportion of a single undulatory cycle.

Values shown are means \pm s.d. (N) and were calculated only for unilateral EMG bursts associated with axial bending.

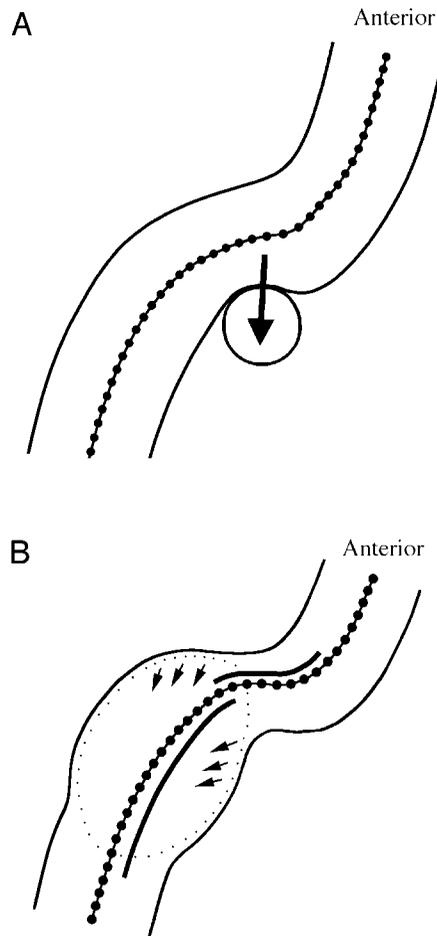


Fig. 6. Diagram of the trunk of a gopher snake (*Pituophis melanoleucus*) during terrestrial lateral undulatory locomotion (A) and undulatory swallowing (B). Epaxial muscle activity in B is indicated by the filled bars, and the areas of presumed force exertion are indicated by the arrows.

the straight region and deactivated once the bend became maximally concave (two examples of this variability are shown in Figs 4, 6); this pattern is similar to the bending produced during epaxial muscle stimulation in anaesthetised snakes (B. R. Moon, unpublished observations).

The epaxial muscles were active unilaterally in snakes that rested on the substratum, but bilaterally (Fig. 7) in snakes that

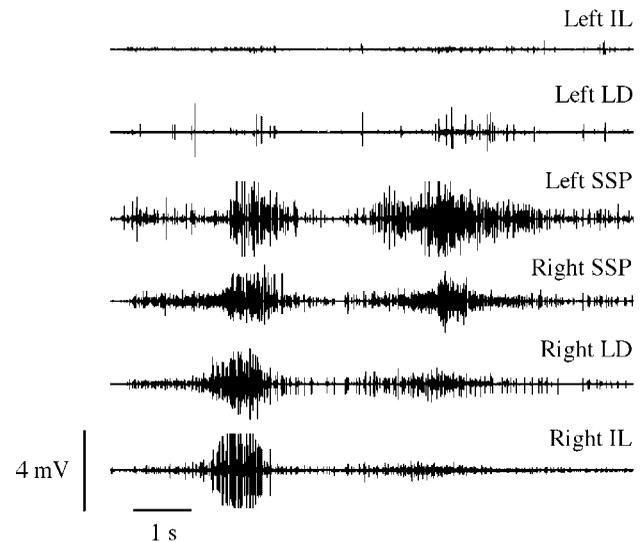


Fig. 7. Bilateral epaxial muscle activity associated with lifting in the gopher snake *Pituophis melanoleucus* (individual P17). IL, M. iliocostalis; LD, M. longissimus dorsi; SSP, M. semispinalis. Note that mainly the SSP is active bilaterally.

lifted their head and anterior trunk during swallowing. However, bilateral epaxial muscle activity was not significantly correlated with lifting ($r=0.25$, $P=0.29$, $N=20$). A preliminary analysis of the data for both gopher and king snake showed a significant correlation, which indicated that the lack of significance in gopher snakes alone was due to the small sample tested.

Epaxial muscle burst rectified integrated area was significantly correlated with burst duration ($r=0.75$, $P<0.001$, $N=100$). This correlation warranted the inclusion of burst area, duration and the interaction area \times duration in the regression analysis. During muscle activity, the electrode-bearing segment often changes from a bend towards one side to a bend towards the other side. Therefore, the change in bending angle of that segment during a burst of muscle activity is often larger than the angles reported above for a single half-wavelength bend. The change in bending angle during muscle activity was significantly correlated with EMG burst duration, but not with burst area (Fig. 8; Table 4). This was the case even when outliers (cases with studentized residuals less than -2 or greater

Table 4. Regression results for maximum change in vertebral bending angle during epaxial muscle activity during swallowing by gopher snakes (*Pituophis melanoleucus*)

| Dependent variable | Overall adjusted r^2 | Overall F_{df} | Standardised partial regression coefficients for independent variables | | | | | |
|--------------------------|------------------------|-------------------------|--|------------------|------------------------------------|---------------|---------------|---------------|
| | | | EMG area (s V) | EMG duration (s) | Area \times duration interaction | Individual d1 | Individual d2 | Individual d3 |
| Bending angle ($N=95$) | 0.46 | 14.75 _{6,89} * | 0.20 | 0.82* | -0.04 | 0.10 | 0.002 | -0.07 |

* indicates $P<0.001$.

The F value from the regression ANOVA is subscripted with regression and residual degrees of freedom.

Electromyographic (EMG) burst area, duration and the interaction area \times duration are described in the text; d1–d3 indicate the dummy variables that represent individual snakes.

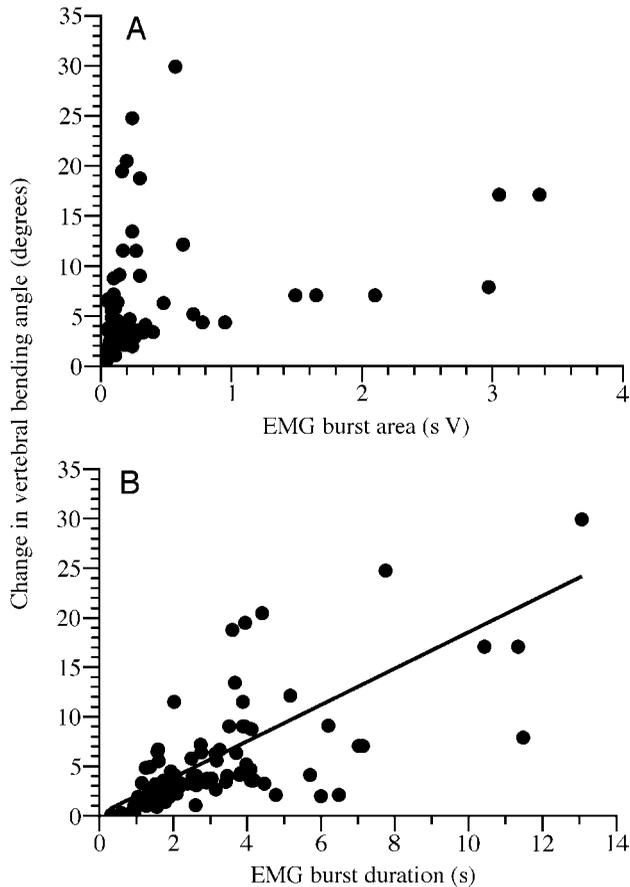


Fig. 8. The change in vertebral bending angle per joint during epaxial muscle activity *versus* electromyographic (EMG) burst area (A) and burst duration (B) in the gopher snake (*Pituophis melanoleucus*). The regression line shown in B is based on the unstandardised regression coefficients: $y = 1.85x + 0.075$, adjusted $r^2 = 0.46$, $P < 0.001$.

than 2) were removed. However, I was unable to detect a biological reason for excluding these outliers and therefore include them in the present results.

Pressure exerted on the prey

Peak pressures of 0.93–4.8 kPa (7–36 mmHg; $N = 6$) in the ingested prey corresponded to the formation and propagation of undulatory bends. These pressure peaks were most conspicuous when propagation of a bend was resumed after being temporarily stopped. However, the small sample of pressure recordings is not sufficient to support kinematic or mechanical generalisations.

Discussion

Kinematic and mechanical stages of swallowing

Snakes ingest prey using highly specialised unilateral movements of the jaws (e.g. Bolt and Ewer, 1964; Cundall, 1983; Cundall and Gans, 1979; Dullemeijer, 1956; Kardong, 1977, 1986), but the axial system then transports the prey from the throat along a substantial length of the body to the stomach.

The sequential action of the jaws and axial system during swallowing in snakes led Kardong (1986) and Janoo and Gasc (1992) to describe swallowing as a two-stage process. First, jaw and skull movements are used to ingest prey. Then, cervical and axial bending are used to transport prey to the stomach. However, a preliminary but more detailed analysis of swallowing by Kley and Brainerd (1996) indicated that swallowing in alethinophidian snakes involves four kinematic stages. The present results also indicate at least four kinematic stages with distinct mechanical functions. These stages are not always discrete; the movements of one stage may begin before the movements of the previous stage cease.

Stage 1, snout shifting

In the first stage of swallowing, alternating unilateral movements of the jaws draw the prey into the oral cavity. Simple lateral bending of the head and anterior neck help to advance the jaws and shift the prey from the oral cavity into the oesophagus. In contrast to colubrid snakes, the basal snake *Cylindrophis ruffus* primarily uses 'snout shifting', lateral swings of head, rather than extensive pterygoid movement, to protract the upper jaws during ingestion (Cundall, 1995). Similar movements may enhance jaw protraction in macrostomatan snakes, such as pythons (Frazzetta, 1966; Kardong and Berkhoudt, 1998), colubrids (Albright and Nelson, 1959; Cundall and Gans, 1979; Kardong, 1986; Kley and Brainerd, 1996; present study) and viperids (Janoo and Gasc, 1992; Kardong, 1977). The simple lateral bending movements of the head usually decrease in amplitude as the prey moves fully into the oesophagus (Kardong, 1986).

Snakes often lift relatively small prey (less than approximately 10% of the snake's mass) off the substratum during ingestion. In these cases, the jaws and axial bends, with the help of gravity, actively pull the prey into the snake's mouth and anterior oesophagus. Lifting of the head and neck during swallowing occurs in diverse snakes, including pythons (*Python molurus*, *P. reticulatus* and *P. sebae*; Frazzetta, 1966; Kardong and Berkhoudt, 1998), colubrids (present study) and coral snakes (*Micrurus fulvius*; Greene, 1984).

Relatively large prey (in this study more than approximately 7–20% of the snake's mass) are ingested using jaw movements that pull the snake's head forward over the prey, which remains stationary relative to the substratum (Cundall, 1983; Cundall and Gans, 1979; Kardong, 1977, 1986; Kardong and Berkhoudt, 1998; Kley and Brainerd, 1996). Advance of the snake over the stationary prey, rather than pulling the prey into the snake's mouth, probably relates to mechanical effectiveness and the cost of moving the prey *versus* moving the snake's head and anterior trunk (Cundall, 1983).

Stage 2, concertina bending

In the second stage of swallowing, concertina bending of the anterior neck draws the prey further into the oesophagus in two steps. First, the bends form and draw the vertebrae and skin forwards over the prey. Then, straightening of the bends pushes

the snake's head forward relative to the prey, which thus moves farther into the oesophagus. The concertina bending pattern varies among snakes. For example, the basal snake *Cylindrophis ruffus* forms a single sharp bend per cycle (Cundall, 1995), whereas advanced snakes such as pythons, colubrids and vipers appear to form several bends per jaw cycle (Kardong, 1977, 1986; Kardong and Berkhoudt, 1998; Kardong et al., 1986; Kley and Brainerd, 1996). In *Cylindrophis ruffus*, concertina bending of the neck compresses the straight-line distance from the atlas to vertebra 13 by as much as 30% (Cundall, 1995). Concertina bending may straighten and perhaps stretch the prey and its visceral organs (Gans, 1961), so that they do not stay 'bunched up' (Kardong, 1986) in the trailing edge of the prey as it approaches the angles of the jaws. Unilateral jaw movements continue during concertina bending.

Stage 3, ventral flexion

During the transitional third stage of swallowing, the prey moves beyond the jaws, but not yet far enough for effective undulatory transport (Kley and Brainerd, 1996). Unilateral jaw movements cease, but concertina bending continues. Depression of the skull appears to aid in pushing the prey far enough into the oesophagus to allow the neck to form bends anterior to the trailing edge of the prey (Kley and Brainerd, 1996).

Stage 4, undulatory bending

The fourth and last stage of swallowing begins once the prey has moved fully into the oesophagus. Concertina bending of the anterior vertebrae shifts to undulatory bending that pushes the prey along the oesophagus to the stomach. In addition to vertebral bending, the body diameter is constricted in a peristaltic-like wave that forms anterior to the prey and aids in pushing it along the oesophagus (Cundall, 1995; Dullemeijer and Povel, 1972; Kardong, 1986). Thus, this stage of swallowing involves both unilateral bending of the vertebral column produced by the vertebral muscles and bilateral constriction of the body wall that appears to be produced by the lateral and ventral muscles of the body wall. Unlike typical locomotor undulations, swallowing undulations are often propagated intermittently.

These four stages of swallowing represent functionally distinct stages of prey transport in snakes. As swallowing progresses, the elements involved in prey transport shift from the jaws to concertina bends of the anterior vertebrae, then to undulations of the vertebral column from the skull to the stomach. In particular, the transition from concertina to undulatory bending (stages 3–4) reflects a shift from pulling small prey into the mouth and throat (or advancing the snake's head over large prey) to pushing the prey along the rest of the oesophagus towards the stomach. The kinematic patterns and mechanical roles of the vertebral column and body wall clearly indicate that vertebral bending is critical to prey transport in snakes. Therefore, future studies of snake feeding mechanics should be careful to describe the relationship between

movements of the jaws and skull and those of vertebral column.

Pressure exerted on prey during swallowing

Swallowing undulations produce pressure in the body cavity of the ingested prey. These pressure pulses are most conspicuous whenever the swallowing movements resume after briefly stopping. These results indicate that vertebral bending transmits force from the epaxial muscles to the body wall and then to the internal prey. During continuous swallowing, pressure in the prey generally remains low and relatively steady; pressure pulses, if present, are small and probably reflect distortions of the soft prey as it moves along the oesophagus.

Muscular control of swallowing

Concertina bending

Concertina bending during the early stages of swallowing is similar to concertina locomotion and may involve similar muscular activity patterns. However, the present trunk muscle recordings cannot be used to test this hypothesis because concertina bending appears to involve only the anterior neck muscles. Recordings from anterior cervical muscles would be valuable for studying concertina bending and cervical function in general. In addition, recordings from the anterior muscles would be valuable for comparing cranial and cervical movements during feeding in snakes and other reptiles (see *Evolutionary patterns*).

Lateral bending

The anteriormost epaxial muscles that insert on the skull and the first few cervical vertebrae (Pregill, 1977; Ruben, 1977b) are probably the flexors of the head and neck during left–right and concertina bending. In addition, lateral bending of the anterior neck during ingestion, prior to concertina bending, can involve the epaxial muscles as far posterior as vertebra 25. These muscles insert *via* long tendons on the first few cervical vertebrae but are not modified for insertion on the skull (Fig. 1). The roles of these muscles in flexing the anterior *versus* posterior vertebrae of insertion remain unclear.

In swallowing undulations, the muscles become active slightly before the point of maximal stretching and cease activity when maximally shortened or when being stretched again. Vertebral bending, produced by the epaxial muscles, causes the body wall to push the prey along the oesophagus (Fig. 6B). Longer EMG bursts were significantly correlated with sharper vertebral bending (Fig. 8B). EMG burst area shows a tendency to be related to vertebral bending angle, but the trend is not significant even when outliers are excluded (Fig. 8A).

Lifting

Lifting of the head and anterior neck during swallowing was often associated with bilateral activity of the epaxial muscles, although the correlation was not significant in the small sample tested. During lifting, usually only one muscle (the SSP) was

active bilaterally and two muscles (the LD and IL) were active unilaterally in producing bending (Fig. 7). Therefore, the SSP can act independently of the other epaxial muscles and is an important dorsiflexor when active bilaterally. The SSP is also active bilaterally during lifting in other movements, such as sidewinding locomotion (Jayne, 1988b).

Cranial lifting during swallowing in gopher snakes is similar to the lifting used during foraging by whipsnakes (*Masticophis flagellum*; Ruben, 1977b). This postural similarity suggests that differences in cervical myology do not mechanically constrain gopher snakes from lifting the head and neck to steep angles, as suggested by Ruben (1977b).

Kinematics and muscular control of locomotion and feeding

Different environments and behaviours impose distinct mechanical demands on organisms and can dramatically alter musculoskeletal function (Biewener and Gillis, 1999). Comparisons of diverse behaviours can, therefore, illustrate how muscle recruitment varies in response to the different mechanical demands of each behaviour.

Swallowing is a kind of inside-out locomotion. During terrestrial lateral undulation, forces are exerted unilaterally against rigid external points of resistance. In contrast, swallowing forces must be exerted bilaterally inward against the soft internal prey (Fig. 6). When swallowing large prey, the snake often advances (literally crawls) forward over the prey, resulting in the swallowing bend and prey being propagated along the snake body but remaining stationary relative to the substratum (Cundall, 1983; Cundall and Gans, 1979; Kardong, 1977, 1986; Kley and Brainerd, 1996).

Swallowing undulations are kinematically similar to those of lateral undulatory locomotion (Janoo and Gasc, 1992; Kardong, 1977; Moon and Gans, 1998). In gopher snakes, swallowing bends involve 7–19 vertebrae per half-wavelength and are propagated at frequencies of 0.04–0.63 Hz, and locomotor undulations involve 22–59 vertebrae and cycling frequencies of 0.24–1.32 Hz (Moon and Gans, 1998). The mean bending angle of 7.1° per joint during swallowing is consistent with the 3–8° per vertebral joint in lateral undulatory locomotion (determined from the axial curvatures recorded by Moon and Gans, 1998). These results indicate that the vertebral bending angles and undulation frequencies are qualitatively similar in these two behaviours but tend to be quantitatively different. The qualitative similarities between swallowing and locomotor undulations show that the two kinds of bending involve similar patterns (timing) of muscle recruitment. However, the quantitative differences in the bending angles and frequencies show that the muscle activation patterns differ quantitatively in the two behaviours.

During lateral undulatory locomotion in colubrid snakes, the epaxial muscles are active on the convex sides of lateral bends between the region of maximal convexity and the straight (Moon and Gans, 1998) or concave (Jayne, 1988a) region. This activation pattern causes the body to push against and deform around points of force exertion (Moon and Gans, 1998).

During swallowing, the muscles are often activated substantially before reaching the point of maximal convexity, while still over the internal prey, and are usually deactivated well after maximal concavity (Table 3). Thus, the epaxial muscles are activated at similar phases of the bending cycle in locomotion and swallowing, but are deactivated later in the swallowing cycle. The EMG duty factor during undulatory swallowing is significantly longer than that during lateral undulation (mean 0.60 versus 0.34, unpaired $t_{131} = -5.07$, $P < 0.01$); this was the case even when the few long EMG bursts (duty factor > 1) that occurred during swallowing were excluded from the analysis.

The large EMG duty factors of swallowing suggest that swallowing forces must overcome relatively large drag on prey as it is pushed along the narrow, muscular oesophagus. Furthermore, the larger duty factor in swallowing undulations suggests that the force required for swallowing is larger than that required for unrestrained lateral undulation. During lateral undulation, gopher snakes increase the epaxial muscle duty factors when drag is increased (Moon and Gans, 1998), as do other animals such as eels moving on land compared with swimming in water (Gillis, 2000). Swallowing forces may be enhanced by activation of the epaxial muscles before the point of maximal bending convexity, while they are still being stretched (Table 3). In particular, the LD is actively stretched prior to and during activation by the SSP and IL segments connected to it anteriorly (see Fig. 1; Moon and Gans, 1998). This pattern of activation during lengthening should enhance muscular force production (Cavagna and Citterio, 1974; Cavagna et al., 1968, 1975; Gordon et al., 1966; Katz, 1939).

In contrast to the undulatory bending of locomotion and swallowing, constriction of prey involves the rapid formation of sharp bends, which are then held relatively static for long periods. The epaxial muscles are active during the formation of small-radius bends in a constriction coil, but other muscles must then be recruited as the sharp bends squeeze the prey (Moon, 2000).

The kinematic and EMG results support the hypothesis that the epaxial muscles are important lateral flexors in diverse behaviours that involve large-radius bending. These results also support the hypothesis that locomotion and swallowing involve similar undulatory bending and muscular control patterns. However, the EMG duty factors of the epaxial muscles differ quantitatively between locomotor and swallowing undulations in response to the distinct mechanical demands of each behaviour.

Evolutionary patterns

Although snakes have highly derived skulls and feeding systems, some of their swallowing movements are similar to, and apparently derived from, those of lizards. The unusual feeding mechanism of scolecophidian (blind) snakes (Kley and Brainerd, 1999) appears to be unique and not representative of the ancestral feeding system of snakes. Therefore, basal alethinophidian snakes may better reflect the ancestral features of the snake feeding system. Here, I use data from diverse

lizards and snakes to hypothesise broad evolutionary patterns in snake feeding behaviours.

At least three swallowing movements are shared by lizards and snakes, and thus may be ancestral features in snakes. Lateral bending of the head and neck, including concertina bending, occurs during swallowing in some lizards (e.g. some anguids and varanids; B. R. Moon, personal observations) and snakes (e.g. Cundall, 1995; Greene, 1984; Kardong, 1977, 1986; Kardong and Berkhoudt, 1998; Kardong et al., 1986; present study). Similarly, the head and neck are lifted during swallowing, after inertial ingestion, when present, in diverse lizards (e.g. Bels and Delheusy, 1992; Gans et al., 1985; Herrel et al., 1995; Smith, 1982; Urbani and Bels, 1995) and snakes (e.g. Greene, 1984; present study; Janoo and Gasc, 1992). In the late stages of swallowing, depression of the snout occurs in varanid and other lizards (e.g. Condon, 1987; Elias et al., 2000; Gans et al., 1978; Smith, 1982, 1986) as well as in diverse snakes (Cundall, 1995; Frazzetta, 1966; Janoo and Gasc, 1992; Kardong and Berkhoudt, 1998; present study). The phylogenetic distributions of lateral bending, craniocervical lifting and snout depression suggest that snakes inherited these swallowing movements from lizards. Furthermore, lifting of the head and neck during swallowing occurs in the tuatara *Sphenodon punctatus* (Gorniak et al., 1982) and in crocodylians (Cleuren, 1996) and may be an ancestral feature of all squamates.

In alethinophidian snakes, cervical and axial undulation during swallowing appear to be derived movement patterns relative to swallowing in scolecophidian snakes and lizards, in which axial undulation has not been reported. In the present study, the qualitative similarities in kinematic and motor patterns between the gopher snakes and the single king snake suggest that both species have similar bending mechanics and motor control when swallowing similar prey. However, further generalisations about interspecific differences among colubrid snakes must remain tentative until more specimens, species and prey types can be tested.

In colubroid snakes, a trade-off between locomotor and feeding (constriction) movements (Ruben, 1977a) is hypothesised to have limited the capacity for locomotor, and hence evolutionary, diversification (Savitzky, 1980; Smith, 1993). Savitzky (1980) further argued that the evolution of venom uncoupled feeding and locomotor movements, and thus allowed further evolutionary diversification of colubroid snakes. However, the hypothesised trade-off between constriction and locomotor capacity is refuted by three lines of evidence: the lack of correlation between epaxial muscle and tendon elongation and constriction behaviour (Jayne, 1982), the use of constriction by many fast snakes (including some venomous snakes; Shine and Schwaner, 1985), and the activity of epaxial muscles during constriction coil formation (Moon, 2000). Furthermore, swallowing and locomotor movements are still integrated by the use of the epaxial muscles in both behaviours. The evolution of venom was probably a key innovation in the evolution of advanced snakes, but not because it uncoupled the feeding and locomotor systems.

Locomotor and feeding movements remain highly integrated in most living snakes.

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