A kinematic analysis of mesokinesis in the Nile monitor (Varanus niloticus)

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Summary. Previous investigations attempting to document cranial kinetic movements in lizards have resulted in ambiguous and contradictory results. Mesokinesis during feeding in the Nile monitor (Varanus niloticus) was investigated using a new technique. Slotted mounts were attached to the frontal and parietal segments in three adult Nile monitors (0.8-1.7 kg). Extensions which exaggerate the relative movements of the bones were attached to these mounts. All phases of feeding behavior on mice were filmed (n = 9) at 50 frames/s. Before the strike and concomitant with jaw opening the muzzle slightly dorsiflexes (2-4°). During the strike both jaws adduct simultaneously with the upper jaw ventroflexing past the rest position. During subjugation and inertial feeding the skull remains ventroflexed. Only after the prey passes into the esophagus do the cranial elements return to their rest position. The pattern of mesokinetic movements is consistent with several functional hypotheses. A mechanical analysis of the cranial skeleton predicts that mesokinetic movement of the upper jaw can be independent of lower jaw movement. Linear regression of upper jaw movement against lower jaw position and movement shows mesokinesis to be largely independent of lower jaw movement, as predicted by the model.

Key words: Cranial kinesis — Feeding — Mesokinesis — Lizards

Introduction

The skull of lizards contains several intracranial joints which divide the skull into potentially mobile bony subunits. This potential mobility is termed cranial kinesis. Versluys (1910, 1912) defines three types of cranial kinesis in lizards: metakinesis, mesokinesis and amphikinesis.

In metakinesis movement occurs between the ossified brain case and the remainder of the skull. Versluys (1912) terms the former the occipital segment and the latter the maxillary segment. In mesokinesis the maxillary segment rotates dorsoventrally about the occipital segment (brain case). In mesokinesis, the maxillary segment is hinged dorsally between the frontal and parietal bones (the mesokinetic joint) and movement occurs between portions of the maxillary segment. Amphikinetic forms combine meta- with mesokinesis. Thus cranial kinesis serves to elevate and depress all or part of the maxillary segment (and thus the upper jaw) relative to the brain case. Such movement has long been thought to function in feeding, as does cranial kinesis in other sauropsids (e.g., Gans 1961; Homberger 1980).

The functional significance of cranial kinesis in lizards is an old and persistent problem in vertebrate morphology. Functional analyses and hypotheses date to Bradley (1903) and continue to the present (Frazzetta 1986). However, the testing of functional hypotheses has been impeded by difficulty in unequivocally demonstrating that cranial movements do occur. Cinematographic analyses claiming to document cranial movements (e.g., Gerrhonotus coerules and G. multicarnatus, Frazzetta 1962, 1983; Varanus niloticus, Boltt and Ewer 1964) have been criticized on the grounds...
that elevation of the upper jaw cannot be distinguished from general head elevation about the atlanto-occipital joint (Iordansky 1966). Further, such analyses assume that skin movements accurately reflect movements of the underlying bone. Using the same technique, Iordansky (1966) failed to detect any mesokinetic movement in Agama caucasia or Lacerta agilis.

To circumvent the problems associated with cineradiographic analysis, several investigators have used cineangiography. Species investigated include Gecko gekko (De Vree and Gans 1986), Uromastix aegypti (Throckmorton 1976), Amphibolurus barbatus (Throckmorton and Clarke 1981), Varanus exanthematicus (Smith 1982) and Varanus bengalensis (Rieppel 1979). Only De Vree and Gans (1986) and Rieppel (1979) detected any cranial kinetic flexion although stereotyptic movements of the quadrate were observed in all species. Thus the results of the cineradiographic studies, like the cinematographic, are equivocal although differences among species may account for some of the variation.

While cineradiography allows direct assessment of bone movement, the technique has two limitations. First, it requires the animals to be relatively stationary. For this reason, the majority of cineradiographic studies to date have examined only the oral transport stage of feeding. Thus, if kinetics occurs during prey capture it would not be observed. Second, the technique has limited angular resolution (Throckmorton and Clarke 1981; Smith 1982; Patchell and Shine 1986) and movements below 3–4° could not be detected in published studies using the technique.

Therefore the problem in demonstrating cranial kinetics in lizards is the difficulty of detecting potentially small movements during all phases of feeding behavior. Smith and Hylander (1985) recently used strain gauges with synchronized cinemaphore to measure mesokinetic movements during feeding in Varanus exanthematicus. Extrapolating from strain levels recorded across the mesokinetic joint, they estimate that movement about the joint represents less than 0.5° of rotation. These investigaters conclude that the kinetic apparatus in lizards is not a mechanism for actual movement of the upper jaw and that re-evaluation of the function of cranial kinetics in lizards is necessary. However, as noted by these authors, it is difficult to interpret levels of strain in terms of rotational movement. Further, the surgical placement of the gauge across the joint may have impeded movement (Frazetta 1986; Smith and Hylander 1985).

Thus, all three methodologies (cinematography, cineradiography, strain gauge analysis) used to detect cranial kinetic movements in lizards have yielded ambiguous or contradictory results. This study presents a new methodology for detecting and measuring cranial kinetics in the Nile monitor (Varanus niloticus). The results are used to test, in preliminary fashion, functional hypotheses regarding cranial kinetics and also to test a mechanical model of the varanid jaw apparatus.

Cranial kinetics in the Nile monitor

The braincase (occipital segment) of the Nile monitor (Varanus niloticus) is fused to the parietals (Rieppel 1979) such that the skull is solely mesokinetic (mesokinetic (sensu Frazetta 1962, 1986)). That is, the skull is not amphikinetik as metakinesis is lacking. The mesokinetic skull, here and in other lizards, is composed of four bony subunits (muzzle, quadrate (paired), basal (paired) and parietal) joined together by rotational joints (mesokinetic, hypokinetic, quadrotopygoid and dorsal quadrate). The quadrate units are formed by the streptostylic quadrates which articulate dorsally with the fused pectoral unit – occipital segment. Ventrally, the quadrate articulates with the basal units at the quadrotopygoid joints and the lower jaw at the quadrate-articular (mandibular) joints. The parietal unit is formed by the paired parietals, supratemporal, squamosals and postorbitofrontals and the ossified brain case (occipital segment). Posteriorly, the parietal unit articulates with the quadrate units (dorsal quadrate joint) and anteriorly with the muzzle unit at the mesokinetic joint (frontoparietals). The basal units (paired) are each comprised by the pterygoids. The basal units articulate posteriorly with the quadrates (quadrotopygoid joints) and anteriorly with the muzzle at the hypokinetic joints (Russel 1964). The muzzle unit is comprised of the remainder of the maxillary segment (except the pterygoids): premaxillae, maxillae, nasals, septomaxillae, vomer, prefrontals, lachrymals, palatines and supraorbitalis.

The mesokinetic and hypokinetic joints are sutural articulations, the former between the frontal and parietal bones and the latter between the pterygoid of each basal unit and ectopterygoid and palatine of each side of the muzzle unit. The quadrotopygoid joints are modified sutural joints which include a stout syndesmosis. The dorsal quadrate joint is a dual joint, the quadrate forming a sutural articulation with the supratemporal (parietal unit) and a synovial joint with the intercalary of the occipital segment.

Fig. 1. A Outline of the kinematic system with the cranial, quadrotopygoid and lower jaw lines. Dots indicate points of rotation.
in *Varanus* predicts that movement of the upper jaw may be independent of lower jaw position or movement (change in gape) for both jaw opening and jaw closing.

**Varanid feeding behavior**

For purposes of description and analysis, varanid feeding behavior can be divided into three stages: ingestion, oral transport, and deglutition or swallowing (following Bramble and Wake 1985). The ingestion stage can be subdivided into strike and subjugation phases. During the strike the prey item is grasped with the jaws. Following capture, the prey is subdued (subjugation phase). While the prey may be pushed and slammed against the substrate and occasionally clawed, subjugation chiefly consists of holding the prey with the jaws until it is quiet. Depending upon the initial bite point, the jaws may be repositioned several times during subjugation. Toward the end of the subjugation phase the prey is repositioned for oral transport.

Following subjugation the prey item is transported from the jaws to the pharynx (oral transport stage). The tongue in varanids is highly specialized for sensory functions and plays no role in oral transport (Smith 1986). Instead, the prey is moved to the pharynx using a series of inertial thrusts. An inertial thrust is a highly stereotyped behavior (Gans 1969) initiated by a backward movement of the head. As head retraction accelerates, the jaws begin to open. At maximum gape the movement of the head is abruptly reversed and the inertia imparted to the prey item during retraction carries it further into the oral cavity. As the head and neck extend forward over the prey the jaws close. Thrusts are repeated until the prey has been transported to the pharynx.

Following inertial feeding, the prey is squeezed into the esophagus (deglutition phase). In varanids this is done using the hyoid apparatus (Smith 1986) as well as neck flexure.

**Functional hypotheses of cranial kinesis**

Several functions for cranial kinesis in lizards have been proposed (summarized in Table 1). Only those hypotheses dealing strictly with meso- or amphikinesis are examined. Each of these hypotheses has predictable and testable consequences in terms of the kinematics of cranial components. Bellairs (1957) suggests that cranial kinesis serves a shock absorbing function. This predicts snout dorsiflexion at the point of jaw contact with the prey during the strike. Frazzetta (1962) proposes that the kinetic skull assists in prey capture, the

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**Fig. 1.** Outline of a varanid skull with the quadric-crank mechanism superimposed (after Rieppl 1979). A Quadric-crank and lower jaw mechanisms isolated from skull and jaw outlines. Dots represent rotational joints of the mesokinetic system with the dot between Q and B also representing both the quadrateglatygoid joint and the jaw articulation. M muzzle unit; P parietal unit; Q quadrate unit; B basal unit. C Quadric-crank mechanism showing movement in dorsiflexion (d) and ventroflexion (v) from the rest position (r)
grasping of the prey by both jaws simultaneously serving to prevent deflection of the prey by the jaws. This hypothesis predicts that simultaneous adduction of both jaws should be seen during the strike. Iordansky (1966) suggests that ventroflexion of the snout past the rest position would aid in prey subjugation, the curvature of the upper jaw serving to hold the prey in a pincer-like manner with the lower jaw. This predicts ventroflexion during prey subjugation. Boltt (1974), Iordansky (1966), and Iordansky (1966) suggest that cranial kinesis functions in inertial feeding by clearing the maxillary teeth from the prey. This hypothesis predicts a pattern of snout dorsiflexion during jaw opening in inertial thrusts. Finally, Frazzetta (1962) and Auffenberg (1981) have suggested that the spreading of the pterygoids (basal units) that occurs during ventroflexion (as the basal units slide past the basiptyerygoid processes of the braincase) serves to increase the diameter of the gular passage permitting ingestion of large food items. This hypothesis predicts skull ventroflexion during oral transport.

Materials and methods

Three adult Nile monitors (Varanus niloticus) were obtained from a commercial dealer (weight: 1.7, 1.2, 0.8 kg). Nile monitors are large African carnivores which feed on a variety of vertebrate and invertebrate prey (Cisse 1972; Cowles 1930). This genus was chosen because varanids are regarded to be among the most kinetic of lizards (e.g., Frazzetta 1962; Iordansky 1966).

To detect small cranial kinetic movements during all phases of feeding behavior, two mounts were attached on either side of the mesokinetic (fronto-parietal) joint. One slotted plexiglass mount was glued to the skin over the frontal just anterior to the joint. The skin over the frontal adheres to the underlying bone as evidenced by dermal pitting of the frontal bone. The skin over the parietal, however, is loose and can move independently of the underlying bone. Under anesthesia the skin over the parietal was reflected and two jeweler's screws were implanted around the screws to serve as a mold, then filled with dental acrylic. As the dental acrylic set it was slotted anteroposteriorly.

Following recovery from surgery and just prior to feeding, a protractor calibrated about the center of the mesokinetic joint was attached to the frontal mount. The parietal mount received a pointer. These extensions were kept co-planar by a transparent sleeve over the frontal extension. Total weight of the frontal apparatus was less than two grams. The extensions were rigid anteroposteriorly but flexible mediolaterally allowing bending during predatory behavior.

The use of externally visible mounts allowed mesokinetic movement throughout the entire feeding behavior to be recorded cinematographically. The length of the extension served to exaggerate rotation of the snout about the mesokinetic axis. In mesokinetic the parietal unit is fixed. Thus, during a snout dorsiflexion (elevation) the protractor rotates up and the degree marks disappear behind the parietal extension. Conversely, during snout ventroflexion (depression), the protractor rotates down exposing degree marks to view.

A total of nine feeding episodes (three per animal) were filmed. Lab mice served as food items. In one episode (±) only the strike and subjugation phases were filmed. The procedures consisted of affixing the extensions to the skull mount and introducing the lizard and a loosely tethered mouse into the feeding box. The resulting feeding behavior was filmed at approximately 50 frames/s using Kodak 4x-reversal film.

Gape (to the nearest 2.5°), mesokinetic flexion (to the nearest degree), and position of the head (X, Y coordinates of the frontal mount) were recorded for each frame using an optical digitizer. For bouts of bite point repositioning and inert feeding (behaviors involving lower jaw movement) the following variables were recorded: gape at jaw opening, change in gape during jaw opening, duration of jaw opening (ms), maximum gape, change in gape during jaw closing, duration of jaw closing (ms), degree of ventroflexion at jaw opening, degree of ventroflexion at maximum gape, amount of dorsiflexion during jaw opening, and amount of ventroflexion during jaw closing. These variables were used to test for independence of upper and lower jaw movement. Additionally, for each inert thrust, maximum velocity during head retraction (m/s), maximum velocity during head protraction (m/s) and the amount of mouse ingested (measured as a percent of total body length) was recorded.

Results

To illustrate the nature of the data, a strike sequence is shown in Fig. 2. The first frame shows the rest position of the cranial elements. Note that the parietal marker lies slightly behind the first mark posterior to the central line of the protractor.
to feeding, the mandible is held in the mesokinetic position. After an amount resembling a prey (animal #3) is weighed by a known weight of 50 g, the mandible is allowed to move. The mesokinetic and the protractor muscles then begin to be retracted by voluntary contractions, extending the mandible. The mesokinetic muscles, during the feeding period, lift the ventral part of the mandible. Contractions of the protractor muscles cause extension of the mandible.

Fig. 3. Plot of mesokinetic flexion in a monitor (animal #1) feeding on a mouse. The entire plot represents a single episode beginning at the upper left and ending at the lower right. Rest position of the upper jaw is indicated by the broken line. Vertical movement toward the top of the plot indicates muzzle dorsiflexion (df) and vertical movement towards the bottom of the plot indicates muzzle ventroflexion (vf). The vertical scale is in degrees and the horizontal axis is time. Labeled vertical bars indicate the occurrence of specific feeding behaviors: S strike, R repositioning of the bite point, L lifting of prey, T inertial thrust.

(i.e., to the right of the central line; each mark represents two degrees of rotation about the mesokinetic axis). To facilitate reading, the position of the markers is also indicated by the arrow in the insert of each frame. In frame four the strike is initiated by depression of the lower jaw. Note that the cranial markers are in their original position. In frame six further jaw opening has occurred and the upper jaw has begun to dorsiflex (elevate) about the mesokinetic joint as shown by the disappearance of the marker posterior to the central line behind the parietal extension. Frame eight shows the jaws at maximum gape as they are positioned around the prey. Note that the parietal marker now rests atop the central line indicating maximum dorsiflexion above the rest position (approximately 3°). In frame 12 both jaws have begun to adduct to grasp the prey, the upper jaw ventroflexing back to the rest position. In frame 16 jaw adduction continues and the upper jaw has ventroflexed two degrees past the rest position. By frame 20 the upper jaw has ventroflexed four degrees past the rest position as the prey is secured. Approximately 3 s later in the last frame, ventroflexion has increased to 6° past the rest position.

Figure 3 shows a plot of mesokinetic flexion for an entire feeding episode (episode #2). The pattern of mesokinetic movements shown is representative of all 9 episodes in each of the three monitors. In general, dorsiflexion above the rest position is limited to the strike period. The skull remains ventroflexed throughout prey subjugation and inertial feeding. Note, however, that the

![Diagram of strike sequence](image)

Fig. 4. Plot of a strike sequence by animal #1. Shown (from top to bottom) are simultaneous readings of mesokinetic flexion (MESO), gape (GAPE), horizontal head movements (HORZ) and vertical head movements (VERT). For mesokinetics, the rest position of the skull is indicated by the broken line with movement toward the top of the plot indicating dorsiflexion (df) and movement toward the bottom of the plot indicating ventroflexion (vf). For gape, the dotted line represents the closed position (0° gape). Movement away from the line indicates lower jaw opening and movement toward the line indicates lower jaw closing. Each mark on the horizontal scales represents 20 ms.
Fig. 2. Strike sequence of a monitor (animal #1) feeding on a mouse. Background grid is 5 cm square. The frame number is shown in the lower left corner. The scale inset in the upper corner represents the frontal protractor, the longest line on the scale corresponding to the central line of the protractor. Each mark on the scale and protractor represents two degrees of rotation about the mesokinetic axis. The arrow on the scale indicates the position of the parietal marker. Movement of the arrow to the left indicates muzzle dorsiflexion and to the right muzzle ventroflexion. Frame 4 strike initiated by depression of lower jaw. Frame 6 continued lower jaw opening and beginning of muzzle dorsiflexion. Frame 8 maximum gape and maximum dorsiflexion (3°). Frame 12 simultaneous adduction of jaws to grasp prey, muzzle at rest position. Frame 16 continued lower jaw adduction and muzzle ventroflexion past the rest position (2°). Frame 20 continued ventroflexion past the rest position (4°). Last frame skull ventroflexed 6° past the rest position as prey is secured.

Table 2. Summary of episode variables:

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>Animal</td>
<td>Type of animal observed</td>
</tr>
<tr>
<td>Maximum does of gape at initiation</td>
<td>Maximum does of gape at joint of dorsiflexion</td>
</tr>
<tr>
<td>Time from jaw joint of dorsiflexion to rest position</td>
<td>Time from maximum to rest position</td>
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<tr>
<td>Time from maximum to jaw joint of dorsiflexion</td>
<td>Time from jaw joint of dorsiflexion to rest position</td>
</tr>
<tr>
<td>Time from jaw joint of dorsiflexion to maximum</td>
<td>Time from maximum to jaw joint of dorsiflexion</td>
</tr>
</tbody>
</table>

Degree of skull return:

Clearly, each strike in the tail in the series...

Strike

Due to the treatment of the head, it was observed that at least one strike is performed by each of another set of 2 showing similar movement and initiated by...

Table 3. Summary of episode variables:

<table>
<thead>
<tr>
<th>Episode</th>
<th>Animal</th>
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<td>2</td>
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<td>3</td>
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<tr>
<td>9</td>
<td>4</td>
</tr>
</tbody>
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degree of ventroflexion is not fixed and does vary. Only after inertial feeding is complete does the skull return to its rest position during deglutition.

Each stage of feeding will be examined in detail in the following paragraphs.

**Strike**

Due to the rapidity of this behavior, the strike was observed in only five of the nine sequences (at least one per animal). Jaw movements during the strike are relatively stereotyped. Figure 4 is a plot of another strike sequence (episode 4; see Table 2) showing mesokinetic flexion, gape and head movements (horizontal and vertical). The strike is initiated by opening the lower jaw. With further lower jaw abduction the upper jaw begins dorsiflexion until maximum gape is achieved. During the grasp both jaws adduct simultaneously with the upper jaw quickly ventroflexing to the rest position and then slowly ventroflexing past the rest position as the prey is secured.

Table 2 summarizes the kinematic data for the available strike sequences. Jaw opening always precedes snout dorsiflexion (40–60 ms, median 60 ms) but the amount of jaw opening at the initiation of dorsiflexion is variable (2.5–27.5°; median 17.5°). Time to maximum dorsiflexion (2–4°, median 2°) varies from 40 to 120 ms and corresponds to the amount of dorsiflexion. Time from maximum dorsiflexion to the rest position...
(0° ventroflexion) is between 20 and 40 ms but is independent of the amount of dorsiflexion. The degree of ventroflexion at point of jaw-prey contact varies from −1° (i.e. 1° of dorsiflexion) to 3° with a median of 0°. During jaw adduction, the time from maximum dorsiflexion to rest position (0°) is faster than from 0 to 2° of ventroflexion (Mann-Whitney, U = 0, P = 0.018). Time from 2 to 4° of ventroflexion was not statistically different from 0 to 2° (Mann-Whitney, U = 3.5, P > 0.35). Finally, the entire strike sequence (from the initiation of jaw opening to 4° of ventroflexion past the rest position) is very rapid with a median of 360 ms.

Subjugation

The skull remains ventroflexed (0–9°) throughout this period although the degree of ventroflexion is not fixed. Minimum, maximum and mean ventroflexion (the latter computed as the sum of ventroflexion for each frame divided by the number of frames scored) (Table 3) were not significantly different among animals (Kruskal-Wallis, P > 0.05).

Both short term and long term changes in ventroflexion during subjugation were observed. Short term changes are defined as changes associated with a specific activity. Long term changes in ventroflexion were maintained after the behavior initiating the change was over. The majority of long term changes (n = 24, 46%) were associated with lifting or lowering of the prey from the substrate. The changes were random with respect to direction (dorsiflexion, ventroflexion), the average absolute change being 1.4 ± 0.7°. However, not all lifting and lowering episodes were accompanied by a change in flexion.

Changes in ventroflexion following repositioning of the bite point accounted for 21% (n = 12) of the long term changes. Mean absolute change was 1.2 ± 0.3°. Three-quarters of these repositionings resulted in an increase in ventroflexion and one quarter in a decrease.

Increases in gape (4%, n = 2) and bouts of tether pulling (i.e., with the mouse still affixed to the substrate; 4%, n = 2) both resulted in decreases in ventroflexion. The remaining 29% of the long term changes were not accompanied by an overt change in behavior and averaged a change of 1.4 ± 0.9°. Again, the changes were largely random with respect to direction.

Short term changes in ventroflexion lasted less than 200 ms and were associated with repositionings of the bite point, crushing bites and jaw stubbing. In jaw stubbing (n = 1) the lower jaw was pushed against the substrate and ventroflexion increased 1°. The increase lasted as long as the mandible was in contact with the substrate. In three instances the animals could be seen to be biting or crushing the prey as evidenced by momentary decreases in gape. These behaviors were accompanied by small increases in ventroflexion (1–2°). The greatest amount of ventroflexion observed (9°) was associated with a hard bite.

The most frequent short term changes in ventroflexion were associated with repositionings of the bite point. A total of 53 repositionings were observed in the nine feeding sequences. Figure 5A shows a repositioning with the mouse against the ground and Fig. 5B a repositioning with the mouse held aloft. Note that in both repositionings the skull is in a ventroflexed position. Dorsiflexion is associated with jaw opening in both cases but does not pass the rest position in either. Similarly, ventroflexion is associated with jaw closing.

Dorsiflexion during jaw opening occurred in 62% of the repositionings and ranged from 1 to 3° with a mean of 1.6°. Dorsiflexion during jaw opening never passed the rest position of the skull, i.e., the muzzle remained in a ventroflexed position at all times during subjugation. Regression of the amount of dorsiflexion during jaw opening showed no significant correlation with the degree of gape at jaw opening or change in gape during jaw opening (Table 4). Multiple re-
regression of these lower jaw variables did not produce a statistically significant fit.

Ventroflexion during jaw closing ranged from -1 to 4° and occurred in 82% of the cases with a mean of 1.6°. The amount of ventroflexion during jaw closing was not significantly correlated with maximum gape or change in gape during jaw closing (Table 4). Multiple regression of these lower jaw variables produced a linear combination which explained approximately 40% of the variation in ventroflexion.

Kinematically, repositionings could be classified into five types based upon upper jaw movement during lower jaw opening and closing. Type 1 shows no upper jaw movement with either lower jaw opening or lower jaw closing. Type 2 shows dorsiflexion of the muzzle accompanying jaw opening but no ventroflexion with jaw closing. Dorsiflexion with jaw opening and ventroflexion with jaw closing defines type 3. No dorsiflexion during jaw opening but ventroflexion with jaw closing defines type 4. Type 5 shows no upper jaw movement during jaw opening but dorsiflexion with lower jaw closing.

Type 3 was the most frequent repositioning type (65%) followed by equal frequencies of type 1 and type 4 (14% each). Types two and five each account for less than 5% of the remaining episodes. There was no statistical difference in the proportion of types between animals ($X^2 = 7.5, df = 8, P > 0.3$). A two-way analysis of variance (ANOVA) by repositioning type (types 2 and 5 deleted due to small sample size) and animal showed no significant differences ($P > 0.05$) among the types for lower jaw variables or upper jaw position. However, the degree of ventroflexion before repositioning, the change in gape during jaw opening and duration of jaw opening did differ significantly among animals.

**Inertial feeding**

Ventroflexion is maintained throughout this stage ranging from 0 to 8° with means ranging from 2.2 to 6.2° per episode (Table 5). In seven of the eight episodes mean ventroflexion during inertial feeding was less than or equal to mean ventroflexion during subjugation. There were no significant differences among animals in maximum, minimum or mean ventroflexion (Kruskal Wallis, $P > 0.05$).

Short term changes in mesokinetic flexion were associated with two behaviors, inertial thrusts ($n=156$) and tooth clearings ($n=3$; see below). The latter occurred in only on episode.

Figure 6A shows a series of three inertial thrusts by animal #4. Note that head retraction is

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**Table 4. Linear regression of dorsiflexion and ventroflexion during prey repositioning**

<table>
<thead>
<tr>
<th>Variable</th>
<th>$n$</th>
<th>$r$</th>
<th>$r^2$</th>
<th>$P$</th>
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<td>29</td>
<td>0.162</td>
<td>0.026</td>
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<tr>
<td>DGAPJO</td>
<td>27</td>
<td>0.130</td>
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<tr>
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<tr>
<td>(2) DGAPIC</td>
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<tr>
<td>(1) + (2)</td>
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</table>

**DF dorsiflexion; GAPJO gape at jaw opening; DGAPJO change in gape during jaw opening; MAXGAP maximum gape; DGAPIC change in gape during jaw closing; VF ventroflexion; n sample size, r correlation coefficient; r² proportion of explained variance; P probability**

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**Table 5. Summary data for inertial feeding stage**

<table>
<thead>
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<th>Episode</th>
<th>Animal</th>
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<th>Duration of inertial feeding stage (%)</th>
<th>Maximum ventroflexion (degrees)</th>
<th>Minimum ventroflexion (degrees)</th>
<th>Mean ventroflexion (degrees)</th>
<th>Standard deviation (degrees)</th>
<th>Number of inertial thrusts</th>
<th>Class 1 inertial thrusts (%)</th>
<th>Class 2 inertial thrusts (%)</th>
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<td>-</td>
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<td>5</td>
<td>-</td>
<td>60</td>
<td>27</td>
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correlations were weak (Table 6). Multiple regression of the two variables increased the explained variance to 9%.

Ventroflexion of the upper jaw during jaw closing was associated with 59% of the inertial thrusts with the amount ranging from 1 to 4° with a mean of 1.6°. The amount of ventroflexion was significantly correlated with both maximum gape and change in gape during jaw closing (Table 6). Stepwise regression of the lower jaw variables showed that maximum gape alone to be the best predictor of the amount of ventroflexion, explaining 13% of the total variance.

Five classes of inertial thrusts were defined on the basis of upper jaw movement. Class 1 shows no movement with either jaw opening or jaw closing. Class 2 shows dorsiflexion with jaw opening but no ventroflexion with jaw closing. Dorsiflexion with jaw opening and ventroflexion with jaw closing defines class 3. No dorsiflexion during lower jaw opening but ventroflexion during jaw closing defines class 4. Class 5 is defined on the basis of a complex movement of the upper jaw during lower jaw closing, exhibiting a pattern of first ventroflexion then dorsiflexion followed again by ventroflexion.

Lizards #2 and #4 displayed all five classes (Table 5) while #1 showed only classes 1 and 2. The proportion of classes differed significantly among animals (X² = 91.5, 28 df, P < 0.001). The modal frequency for animal #2 was class 1. Animals #2 and #4 both showed a modal frequency of class 3 but differed in their second most frequent class (type 4 and 1, respectively).

A two-way ANOVA by inertial thrust class (classes 1, 3, and 4 only) and individual (Table 7) showed gape at jaw opening, change in gape during jaw opening, maximum gape, degree of ventroflexion before jaw opening, and degree of ventroflexion at maximum gape to differ significantly between the types. All variables but change in gape during jaw closing, maximum velocity during head protraction were statistically different among individuals.
Table 7. Mean values for the five classes of inertial thrusts

<table>
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<tr>
<th>Type</th>
<th>Variable</th>
<th>1</th>
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<th>4</th>
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<td>VFMAXGAP</td>
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Probabilities of F-ratios for two-way ANOVA, P₁ between classes; P₂ between individuals. NS not significant; VFB degree of ventroflexion prior to inertial thrust; VFMAXGAP degree of ventroflexion at maximum gape; DURJO duration of jaw closing; DURJC duration of jaw closing; VELHR maximum velocity during head retraction; VELHP maximum velocity during head protrusion; ADVPER percent of mouse ingested per thrust. Other abbreviations as in Table 4.

The remaining short term changes in ventroflexion (n = 3) during the inertial feeding stage were associated with a behavior termed tooth-clearing. Tooth-clearing occurred during one episode when the legs of a mouse hooked around the corner of the lizard’s mouth during inertial feeding. Inertial feeding was halted and three tooth-clearings were observed. During tooth clearing the head was moved posteriorly and raised. Snout dorsiflexion preceded jaw abduction (Fig. 6B) and carried past the rest position. Snout ventroflexion accompanied jaw adduction. Following this behavior inertial feeding was resumed and the mouse passed into the pharynx.

Deglutition

Jaw movements are minimal during this stage and the skull returns to its rest position. This occurs between 1 and 40 s after the last inertial thrust.

Discussion

First, consideration must be given to potential sources of error in the technique used here. It has been suggested that inertia may serve as a possible source of error, the frontal extension flexing during the rapid head movement of the strike and thus producing exaggerated readings on the goniometer. Examination of the strike sequence (Fig. 4) shows that the degree of ventroflexion achieved during such movements is maintained after both vertical and horizontal head movements have stopped. Thus, there is no evidence of a whip-lash effect which would require that the indicator show some dorsiflexion following the ending of the head movements. Further, if inertia was a problem, it would be most evident during inertial feeding when maximum head velocities occur. In these cases, inertia would produce a significant correlation between maximum head velocity and the amount of dorsiflexion during head retraction. Similarly, a correlation would exist between maximum head velocity and the amount of ventroflexion during head protrusion in inertial thrusts. Linear regression for dorsi and ventroflexion produces a non-significant correlation of 0.110 (P < 0.178). For ventroflexion, the correlation is statistically significant (r = 0.209, P < 0.014) but explains only 4% of the variation in the amount of ventroflexion. These relationships are demonstrated empirically in Fig. 6A which shows three inertial thrusts with approximately equal velocities during head retraction and head protration, yet the amount of dorsiflexion and ventroflexion registered is different for all three with absolutely no movement of the goniometer for the second thrust. Thus, inertia appears to have no quantitative effect on the goniometer.

In the Nile monitor both mesokinetic dorsiflexion and ventroflexion occur during feeding. Dorsiflexion above the rest position is usually limited to the strike although it can occur during the inertial feeding stage in tooth-clearing behavior. The skull remains ventroflexed past the rest position throughout subjugation and inertial feeding but the degree of ventroflexion is not fixed. Maximum dorsiflexion (4°) occurred during the strike. The greatest degree of ventroflexion past
the rest position (9°) occurred during subjugation. Total range of movement (maximum dorsiflexion above the rest position to maximum ventroflexion past the rest position) varied among animals from 7 to 11° with maximum ventroflexion always being greater than maximum dorsiflexion. Total range did not seem to vary with size as the largest animal had a range of 10° and the smallest 11°.

Aside from the strike, where mesokinetic movement ranged between 6 and 8°, changes in mesokinetic flexion during other behaviors rarely exceeded 3°. For both inertial thrusts and repositionings of the bite point, dorsiflexion and ventroflexion averaged less than 2°. The small amplitude of the movement during these behaviors may explain why mesokinetic movements were not observed in the cineradiographic studies of oral transport in other lizards as this degree of movement is below the level of resolution of this technique.

During the strike, ventroflexion of the upper jaw from maximum dorsiflexion to rest position was significantly faster than ventroflexion past the rest position. This difference may be the result of resistance to ventroflexion caused by the basipterygoid processes (of the chondrocranium) which slide along and separate the basal units in ventroflexion past the rest position. Alternatively or additionally, the longer time may be due to resistance from the prey item.

Five types of repositioning were defined on the basis of upper jaw movement. However, these types did not differ with respect to measures of upper or lower jaw position or of lower jaw movement. The lack of correlation may be due to the highly variable nature of the repositionings (all variables had high coefficients of variation) or insufficient sample size for some of the types. In contrast, three variables showed significant differences among individuals. Two of these variables dealt with the duration of jaw opening and jaw closing. The data show that the two animals with shorter duration times more frequently repositioned the prey while holding it aloft, presumably necessitating quick movements to avoid dropping the prey. With respect to the third variable, two of the animals began repositionings at slightly lower degrees of ventroflexion.

Similarly, five classes of inertial thrusts could be defined on the basis of upper jaw movement. An ANOVA showed that only the variables associated with the jaw opening phase of inertial thrusts differed significantly among types whereas those associated with jaw closing were statistically indistinguishable. These results suggest that behavior during the jaw opening phase (including movement of the upper jaw) is being adjusted to individual conditions whereas behavior during jaw closing phase is more stereotyped. With respect to variation among individuals, eight of ten variables were significantly different. Again, the two variables which were not different measured aspects of the jaw closing phase, supporting the notion that the jaw closing phase of inertial thrusts is more stereotyped. The levels of individual variation seen in inertial thrusting are consistent with those reported by Shaffer and Lauder (1985) in another relatively stereotyped behavior, prey capture in the salamander Ambystoma.

Maintenance of ventroflexion throughout inertial feeding suggests that ventroflexion of the skull is the preferred position for this behavior. This is supported by two episodes in which inertial feeding was halted and behavior characteristic of deglutition began, followed by the return of the cranial elements to their rest position. After several seconds, inertial feeding was resumed (presumably due to difficulty in passing the prey into the esophagus). In both cases the skull was re-ventroflexed prior to initiating the second series of inertial thrusts. While it can be argued that ventroflexion during inertial feeding is a by-product of jaw adductor activity, this fails to explain the re-establishment of ventroflexion prior to the first thrust of the second series.

Comparison with other studies

Mesokinetic movements during the strike phase in the Nile monitor are essentially identical to those reported by Frazzetta (1983) for Gerrhonotus multicarnatus feeding on mealworms and crickets and by De Vree and Gans (1986) for Gecko gecko. Both studies report a pattern of dorsiflexion with jaw opening and ventroflexion past the rest position with jaw closing. Comparable ranges of movement are illustrated by Frazzetta (1983; taken from Figs. 10 to 13) with a maximum dorsiflexion of 5° above the rest position and ventroflexion of 8° past the rest position. Whether or not ventroflexion was maintained after the strike is unknown as both studies examined only the strike phase.

A pattern of dorsiflexion with jaw opening and ventroflexion with jaw closing during inertial thrusts has been reported by Bolt and Ewer (1964) and Rieppel (1979) in two species of varanids. However, in both studies the reported range of movement is greater than observed here. Bolt and Ewer (1964; Fig. 12) show a maximum
of 15° of dorsiflexion and 15° of ventroflexion in a plot of two inertial thrusts in a juvenile Nile monitor. Rieppel (1979) reports dorsiflexion of 9° with jaw opening and 15° of ventroflexion with jaw closing in a Bengal monitor (Varanus bengalensis).

In this study, inertial thrusts were always initiated with the skull in a ventroflexed position. This is also true of Varanus bengalensis (Rieppel 1979; see Fig. 5) and is suggested by Boltt and Ewer's study of Varanus niloticus (1964; see Fig. 12). Not all thrusts utilized mesokinesis, but where they did mesokinesis could occur either with lower jaw opening or lower jaw closing or both. This variability was not reported by Rieppel (1979) or Boltt and Ewer (1964), but is consistent with variability in quadrate movement during inertial feeding in Varanus exanthematicus as reported by Smith (1982) since quadrate movement and mesokinesis are linked.

Although Smith and Hylander (185) report no mesokinetic movement in their study of savannah monitor feeding, the pattern of strain across the mesokinetic joint is essentially identical to the plot of mesokinetic flexion seen in Fig. 3 (compare with Fig. 4 in Smith and Hylander 1985). Specifically, compression (dorsiflexion) was recorded just prior to the strike and tension (ventroflexion) was recorded throughout subjugation and inertial feeding with a return to rest position during glottion. However, Smith and Hylander (1985) report increases in tension (ventroflexion) associated with jaw opening in inertial thrusts and decreases in tension (dorsiflexion) during jaw closing until resistance. This is opposite to the pattern reported here and by Boltt and Ewer (1964) and Rieppel (1979).

Functional hypotheses

The simultaneous adduction of the jaws seen in the strike is consistent with Frazzetta's (1962) hypothesis that kinesis serves to allow both jaws to simultaneously grasp the prey, thus reducing the risk of deflecting the prey away from the mouth if only one jaw was moving. A corollary of Frazzetta's hypothesis is that simultaneous adduction of the upper and lower jaws also decreases the duration of the strike (from maximum gape until the jaws contact the prey), relative to the akinetic condition of only the lower jaw moving Bock (1964). Calculations from the four successful strikes observed here (episodes 1, 2, 3 and 8), show that the simultaneous adduction of both jaws reduces the time relative to an akinetic strike by 12-18%. However, in absolute terms this represents a decrease of only 3-6 ms. The calculations assume that the arc of the strike traversed by the upper jaw in the kinetic system would be traversed by the lower jaw moving at its maximum velocity in an akinetic system. Thus the figures are conservative. These calculations suggest that this function is of minimal importance in grasping mice but may be of increased importance in predation upon smaller, lighter and faster prey, such as insects.

The absence of dorsiflexion at the moment of prey contact in the strike negates the shock absorbing hypothesis (Bellairs 1957), at least for grasping behavior. The maintenance of ventroflexion throughout subjugation is consistent with Jordansky's (1966) hypothesis that ventroflexion serves to hold the prey in a pincer-like manner. Patchell and Shine (1986) note that this positions also maximizes the number of teeth in contact with the prey, further enhancing the grip on the prey.

The maintenance of ventroflexion during inertial feeding is consistent with the hypothesis that ventroflexion serves to increase the gular passage diameter (Frazzetta 1962; Auffenberg 1981). Measurements from a ligament preparation of a Nile monitor show that the inner quadrato (which determines the horizontal gular passage diameter) increases 10% at 4° of ventroflexion. However increases beyond that produced by ventroflexion of the mesokinetic apparatus may be possible due to the considerable abdication of the quadrato allowed by the dorsal quadrato joint. Thus the prey item may passively serve to increase gular passage diameter by adducting the quadrates.

Dorsiflexion during the jaw opening stage occurred in 48% of the inertial thrusts and is consistent with the hypothesis of Boltt and Ewer (1964), MacLean (1974) and Rieppel (1979) that this movement serves to clear the maxillary teeth from the prey and thus facilitate inertial feeding. However, an ANOVA between kinematic classes shows that no more of the prey is ingested per thrust for those thrusts involving dorsiflexion than those without (Table 9). This analysis does not really test the hypothesis, however, as it can be argued that dorsiflexion was not required on those thrusts in which it did not occur. Ventroflexion during jaw closing occurred in 39% of the thrusts. Rieppel (1979) suggests that this movement serves to push the prey further into the oral cavity. However, an ANOVA between kinematic classes suggests that this function may be negligible as no more of the prey is ingested per thrust.
for those thrusts involving ventroflexion than those without (Table 9).

Tooth-clearing behavior, although not predicted a priori is consistent with the hypothesis that dorsiflexion serves to clear the maxillary teeth from the prey item.

**Mechanical hypotheses**

The amount of dorsiflexion accompanying repositioning of the bite point was not significantly correlated with lower jaw position (gape) or movement. A maximum of 9% of the total variance in dorsiflexion during jaw opening was explained by lower jaw position and movement during inertial feeding. These results demonstrate that upper and lower jaw abduction are essentially independent and support the mechanical model of the varanid cranial skeleton as a jaw apparatus with two degrees of freedom. Dorsiflexion of the skull past the rest position independent of jaw adduction can be accomplished by the protractor pterygoideus muscle. This muscle arises from the chondrocranium and inserts to the basal unit (Haas 1973). Its contraction does not affect the lower jaw. Dorsiflexion of the skull from a ventroflexed position can result from either of two forces, 1) muscular contaction of protractor pterygoideus and 2) elastic recoil of the skull. The dorsiflexion seen in repositioning and in inertial feeding could be the result of either force as dorsiflexion associated with both behaviors never carries above the rest position. However, if dorsiflexion during the above activities were strictly a function of elastic recoil, one would predict a strong positive correlation between degree of ventroflexion prior to jaw opening and the amount of dorsiflexion. This correlation was non-significant in repositioning and accounted for only 7% of the total variance in the amount of dorsiflexion in inertial feeding. Further tests of these hypotheses will require electromyography.

Ventriculation during jaw closing was significantly correlated with lower jaw position and movement in both repositioning and inertial feeding. However, a linear combination of these two variables explained only 40% and 14%, respectively, of the total variation in the amount of ventroflexion. Like dorsiflexion, ventroflexion of the upper jaw appears to be largely independent of the lower jaw. The greater correlation between upper and lower jaw movement for adduction is not surprising given that the jaw adductors are responsible for both actions. However, the fact that 60–86% of upper jaw adduction cannot be explained by lower jaw adduction suggests that motor control of the two jaws can be operated somewhat independently.

**Conclusions**

Mesokinetic movements during all stages of feeding behavior occur. The total range of movement among individuals was 7–11° representing 5–9° of ventroflexion past the rest position and 2–4° of dorsiflexion above the rest position. Except for the strike, the mean change in skull flexion (less than 2°) during feeding behaviors is below the resolution of the cineradiographic technique. Thus the absence of mesokinesis cannot be determined by cineradiography.

The pattern of mesokinetic movements during feeding is consistent with several functional hypotheses. The simultaneous adduction of both jaws during the strike is consistent with Frazetta’s (1962) hypotheses that mesokinesis aids in grasping the prey. The maintenance of ventroflexion during subjugation is consistent with Iordansky’s (1966) hypothesis that ventroflexion past the rest position serves to hold the prey in a pincer-like manner. Similarly, maintenance of ventroflexion during inertial feeding is consistent with the hypothesis that this position increases the width of the gular passage as proposed by Frazetta (1962) and Auffenberg (1981). Finally, the dorsiflexion that accompanies jaw opening in some inertial thrusts is consistent with the hypothesis that this action aids in clearing the maxillary teeth from the prey (Bolt and Ewer, 1964; MacLean, 1974; Rieppel 1979). Bellair’s (1957) shock absorbing hypothesis is not supported.

Linear regression of upper jaw movement shows both dorsiflexion and ventroflexion to be largely independent of lower jaw movement. Lower jaw movement explains a greater proportion of variance for ventroflexion than for dorsiflexion but never more than 40%. These findings support the modeling of the varanid cranial skeleton as a jaw apparatus with two degrees of freedom, i.e., independent movement of the upper and lower jaw.

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