

KINEMATICS OF FEEDING IN THE LIZARD *AGAMA STELLIO*

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Summary

The kinematics of prey capture, intraoral transport and swallowing in lizards of the species *Agama stellio* (Agamidae) were investigated using cineradiography (50 frames s^{-1}) and high-speed video recordings (500 frames s^{-1}). Small metal markers were inserted into different parts of the upper and lower jaw and the tongue. Video and cineradiographic images were digitized, and displacements of the body, head, upper and lower jaw and the tongue were quantified. Twenty additional variables depicting displacements and timing of events were calculated. A factor analysis performed on the kinematic data separates prey capture and swallowing cycles from intraoral transport bites. However, the intraoral transport stage cannot be separated into chewing (reduction) and transport bites. The effect of prey type and size on the feeding kinematics of intraoral transport and swallowing cycles was investigated. During the intraoral transport stage, distinct aspects (e.g. durations, maximal excursions)

of the gape and tongue cycle are modulated in response to both the size and type of the prey item. The results for *A. stellio* generally agree with a previous model, although it is the entire slow opening phase rather than solely the duration of the second part of this phase that is affected by the size of the prey. The intraoral transport cycles in *A. stellio* show the two synapomorphic characteristics of tetrapods (tongue-based terrestrial intraoral prey transport and the existence of a long preparatory period of prey compression). However, not all five characters of the feeding cycle previously proposed for amniotes are present in *A. stellio*. One major difference is that in *A. stellio* the recovery of the hyolingual apparatus does not take place during the slow opening phase but during the slow closing/powerstroke phase.

Key words: kinematics, feeding behavior, lizard, *Agama stellio*, prey-type effects.

Introduction

Following many studies on mammalian feeding mechanisms (see Weijs, 1994; De Vree and Gans, 1994, for an overview), several studies have focused on reptilian feeding mechanisms. A generalised model of the feeding cycle was proposed (Bramble and Wake, 1985) and provided a framework to which numerous results could be related. Since then, many studies have provided valuable information on reptilian feeding behavior and on the evolution of reptilian and amphibian feeding systems, but few studies describe all the successive stages (prey capture, intraoral transport and swallowing) in the feeding cycle of one animal. Such investigations provide valuable information about the relationships between different feeding stages and allow comparison between species at a broader level.

The tongue of squamates has many uses and can be highly specialised (e.g. for chemoreception in snakes and scleroglossan lizards or for prey capture in chameleons). Accordingly, tongue morphology has long been recognised to be of importance in systematics (Camp, 1923; Schwenk, 1988). In iguanian lizards, the tongue has retained many primitive characters (Gandolfi, 1908; Gnanamuthu, 1937; Smith, 1988).

One of the crucial functions of the tongue in iguanian lizards is the capturing of prey. This has been documented in several studies for chameleons (Bels and Baltus, 1987; Bell, 1990; Wainwright *et al.* 1991; Wainwright and Bennett, 1992*a,b*), agamids (Schwenk and Bell, 1988; Schwenk and Throckmorton, 1989; Kraklau, 1991; Herrel *et al.* 1995) and iguanids (Schwenk and Throckmorton, 1989; Bels, 1990; Bels and Goosse, 1990; Bels and Delheusy, 1992).

The tongue plays an important role not only during prey capture but also during the subsequent intraoral transport and during the swallowing of the prey, which has often been neglected. Intraoral transport and swallowing cycles, in general, have been studied far less than prey capture. In agamids, some data on intraoral prey transport are available only for *Agama agama* (Kraklau, 1991), *Uromastix aegyptius* (Throckmorton, 1976, 1980) and *Phrynocephalus helioscopus* (Schwenk and Throckmorton, 1989). For iguanids and chameleons, the available data are somewhat more extensive (Smith, 1984; Bels and Baltus, 1987, 1988, 1989; Schwenk and Throckmorton, 1989; Wainwright *et al.* 1991; So *et al.* 1992; Delheusy and Bels, 1992).

The ability of a predator to ingest and process a food item successfully will depend on the type and structure of that food item. However, specialisation for a specific food type might induce costs. How does a generalised lizard cope with different prey types? One option might be to develop only one specific muscle activation pattern for a certain prey type. However, this would lead to a decreased efficiency in feeding on other prey types. It might thus be advantageous to select solutions that are compatible with many prey types (De Vree and Gans, 1994). The solution expected for a generalised lizard is one of modulation, allowing plasticity in the response to the food types encountered.

The aims of the present paper are (1) to provide a quantitative kinematic analysis of the different feeding stages in *Agama stellio*, (2) to evaluate the effects of the type and size of the prey item on the kinematic properties of jaw and tongue cycles during the different feeding stages, (3) to compare tongue and jaw cycles with the model of Bramble and Wake (1985) and (4) to evaluate whether *A. stellio* shows the derived characters of the amniote feeding cycle proposed by Reilly and Lauder (1990).

Materials and methods

Specimens

Five adult specimens (body length 20 ± 3 cm; mass 42 ± 3 g; mean \pm S.D.) of the species *Agama stellio* (L.) (Agamidae) were used in the experiments. The specimens were collected in Israel and provided by Dr E. Kochva. The animals were kept in a glass vivarium on a 12 h:12 h L:D cycle and were offered water and food consisting of crickets, grasshoppers and mealworms *ad libitum*. The environmental temperature varied from 26 °C during the day to 20 °C at night; an incandescent bulb provided the animals with a basking place at a higher temperature (30 °C). An additional four animals were dissected and stained (Bock and Shear, 1972) to characterize all jaw and hyolingual muscles. Drawings were made of all stages of the dissection using a Wild M3Z dissecting microscope, provided with a *camera lucida*.

Cineradiographic and video recordings

Cineradiography was accomplished using a Siemens Tridoros-Optimatic 880 X-ray apparatus equipped with a Sirecon-2 image intensifier. Feeding bouts were recorded laterally using an Arriflex 16 mm ST camera equipped with a 70 mm lens at a film speed of 50 frames s^{-1} . Before cineradiography, small metal markers were inserted subcutaneously on the upper and lower jaws, at the base and the top of the quadratum, in the tongue, on the frontal and parietal bones and dorsally in the neck just below the skin using a hypodermic needle (Fig. 1A). During implantation of these radio-opaque markers, animals were anesthetized by an intramuscular injection of Ketalar (200 mg kg^{-1} body mass). Placement of the markers was checked using dorsoventral and lateral X-ray photographs. During the cineradiographic recordings, the prey items were injected with barium sulfate to allow visualisation of their position.

Additional recordings of the feeding process were made at higher speed (500 frames s^{-1}) to obtain more accurate data for quantification. Recordings were made using a NAC-1000 high-speed video system set at 500 frames s^{-1} . Video torches (2.4 kW; Tri-Lite, Cool Light Co. Inc., Hollywood, USA) provided the necessary illumination. In both the cineradiographic and the high-speed video recording sessions, the animals were filmed in an acrylic cage (30 cm \times 10 cm \times 10 cm) while feeding on mealworms *Tenebrio melior* (length 2.5 cm), crickets *Acheta domesticus* (2 cm) and grasshoppers *Locusta migratoria* (2–4.5 cm). The prey item was always placed less than 10 cm from the snout of the lizard.

Cineradiographic and video analysis

Only feeding sequences in which the animal remained at right angles to the axis of the camera were analyzed. Cineradiographic films were projected frame by frame onto a HIPAD-digitiser with a Vanguard projector. The position of each marker (see Fig. 1) was digitised and horizontal (x) and vertical (y) coordinates of each were recorded for each frame. High-speed video recordings were analysed by digitising seven clearly visible external markers (colored spots, see Fig. 1B) using the NAC x - y Coordinator. Horizontal (x) and vertical (y)

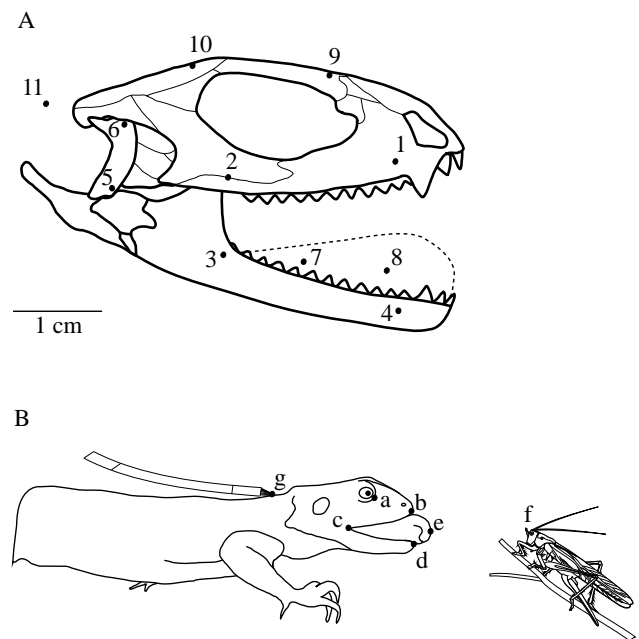


Fig. 1. (A) Positions of lead markers inserted into the skull of *Agama stellio* and used to calculate different kinematic variables. 1, anterior marker of the upper jaw; 2, posterior marker of the upper jaw; 3, posterior marker of the lower jaw; 4, anterior marker of the lower jaw; 5, lower marker of the quadratum; 6, upper marker of the quadratum; 7, posterior tongue marker; 8, anterior tongue marker; 9, marker placed on the frontal bone; 10, marker placed dorsally on the parietal bone; 11, marker placed dorsally in the neck. (B) External markers used to digitize high-speed video images. a, anterior eye margin; b, anterior margin of the upper jaw; c, anguli oris; d, anterior margin of the lower jaw; e, most anteriorly situated point of the tongue; f, point of prey contact; g, dorsal body point.

coordinates were recorded for each digitised point at intervals of two frames.

Variables calculated for both cineradiographic (X-ray) and high-speed video (HSV) recordings were (with respect to the numbered markers indicated in Fig. 1): changes in gape profile (X-ray, distance 1–4; angle subtended by the two lines 1–2 and 3–4; HSV, distance b–d; angle b–c–d), vertical displacement of the upper and the lower jaw (X-ray, changes in y-coordinates of points 1 and 4; HSV, changes in y-coordinates of points b and d), cranial elevation (X-ray, angle subtended by line 1–2 and the horizontal; HSV, angle subtended by line b–c and the horizontal) and lower jaw depression (X-ray and HSV, angle subtended by line 3–4 or c–d and the horizontal). On the cineradiographic recordings, the displacement of the tongue was also calculated from the x- and y-coordinates of both tongue markers (Fig. 1A). Prey distance (distance e–f), tongue protrusion (difference between x-coordinates of points e and d) and body position (x-coordinate of point g) were also calculated from the high-speed video recordings (Fig. 1B).

Eight cineradiographic sequences from two lizards were analysed completely and 16 other feeding bouts (in the three other lizards) were analysed partially for comparison. The eight feeding sequences were selected because they represented the whole array of bite types (from strike to swallowing) for all prey items. In four sequences, grasshoppers of average size (length 2.0 ± 0.3 cm, mean \pm s.d., $N=3$ for lizard 1 and $N=1$ for lizard 2) and in one sequence a very large grasshopper (4.5 cm, lizard 2) were presented as prey items. In two other sequences, the animals were offered crickets of average size (length 2.0 ± 0.2 cm, one each for lizards 1 and 2) and in one sequence a mealworm (2.5 cm, lizard 1) was presented to the animal as prey. The number of cycles analysed from each of these sequences is shown in Table 1. Twenty-seven bites from different stages of a feeding sequence and 21 strike sequences recorded by means of high-speed video were also analysed (Herrel *et al.* 1995).

Prey hardness was estimated as follows. The lower jaw of one of the dissection specimens was removed and partially embedded in resin, leaving the toothrows free. The hardened resin was then mounted onto a Kistler force transducer (type 9203; Kistler Inc., Switzerland) connected to a charge amplifier (model 463A-PCB, Piezotronics Inc., NY, USA) and chart recorder (Brush 481 recorder; Gould Inc., OH, USA). Prey items were crushed by pushing the jaw against the insect until failure of the chitinous exoskeleton occurred. For all prey items tested, the strength of the hardest part (usually the head and prothorax) was recorded. The relationship between the size (length and/or mass) and the hardness of the prey was investigated.

On the basis of the kinematic plots of the movements of the jaws and tongue, the following variables were determined: (1) the durations (D) of the slow opening phases (SOI and SOII), the fast opening phase (FO), the fast closing phase (FC), the slow closing/powerstroke phase (SC/PS) and the total cycle (TC); (2) the maximal values of the gape distance (GD) or angle (GA), depression of the lower jaw (MDLJ), cranial

Table 1. Number of jaw cycles used for kinematic analysis of feeding behavior of two *Agama stellio* presented with different prey items

| Food item | Feeding stage | Lizard 1 | Lizard 2 |
|---------------------------------------|---------------------|----------|----------|
| Grasshopper (2.0 cm, 0.20 g) | Strike | 21 | – |
| | Intraoral transport | 54 | 29 |
| | Swallowing | 8 | – |
| Cricket (2.0 cm, 0.23 g) | Intraoral transport | 22 | 16 |
| | Swallowing | 2 | 6 |
| Mealworm (2.5 cm, 0.13 g) | Intraoral transport | 7 | – |
| | Swallowing | 4 | – |
| Large grasshopper (4.5 cm, 1.11 g) | Intraoral transport | – | 18 |
| | Swallowing | – | 1 |

elevation (MEUJ) and horizontal (MHDTO) and vertical (MVDTO) tongue displacement; (3) the time to the maximal gape angle (TGA), the time to the most anterior (TMHDTO) and to the most dorsal (TMVDTO) tongue positions, the times to maximal depression of the lower jaw (TMDLJ) and elevation of the neurocranium (TMEUJ); and (4) the duration of horizontal and vertical tongue protraction and retraction (THTR, TVTR) (from the high-speed video images; defined as beginning when the tongue becomes visible between the half-opened jaws and ending when the tongue is no longer visible between the jaws). The different phases within a jaw cycle were determined on the basis of the changes in angular velocity of the gape cycle in conjunction with the changes in tongue movement. When sequences were partially analysed, frame 1 was arbitrarily chosen at the beginning of the slow opening of the mouth.

Several analyses were performed on the kinematic data (1) to explore the similarities between successive feeding stages (prey capture, intraoral transport, swallowing) and (2) to evaluate the effect of prey type and size on the kinematic variables. For these analyses, the SPSS-PC (Maria J. Norusis/SPSS Inc.) and the Statistica (StatSoft Inc.) statistical packages were used.

A factor analysis (Varimax rotation) containing all bite types was performed on the data set from lizard 1 feeding on grasshoppers. A one-way analysis of variance (ANOVA) was then performed on the first three factors coupled to a Duncan multiple-range significance test (at the 0.05 level) to explore the relationships between the different bite types. The original data set was then submitted to a multivariate analysis of variance (MANOVA) and subsequent univariate *F*-tests to determine which variables were significantly different between bite types. For all univariate *F*-tests performed, the significance level was corrected using a sequential Bonferroni correction (see Rice, 1989). A data set consisting of intraoral transport bites from two individuals with two prey types was constructed and submitted to a two-way MANOVA (mixed model with the individual as the random effect and prey type as the fixed effect; see Sokal and Rohlf, 1995; Zar, 1984) to investigate individual variation and the interactions between the individual

and the prey type on the kinematic characteristics of the feeding cycle. A two-way MANOVA was then performed on the intraoral transport and swallowing data set to explore possible interaction effects between bite type and prey type. A single data set per bite type was then constructed to evaluate the effect of prey type separately on the kinematic variables. On these data sets, a MANOVA was performed to evaluate the differences observed for different prey items. Finally, a MANOVA was performed on a data set containing only intraoral transport bites from one lizard for both normal (2 cm) and large (4.5 cm) grasshoppers to evaluate the effect of prey size. All analyses were performed on data sets consisting of 14 kinematic variables representing all aspects of the feeding cycle (GA, MHDT0, DSOI, DSOII, DFO, DFC, DSC/PS, DTC, THTR, TMEUJ, TMDLJ, TMHDT0, TMVDTO, TGA; for an explanation of the abbreviations used see Table 4).

Results

In the description of jaw cycles given below, we adopt the terminology of Bramble and Wake (1985). A jaw cycle is divided into five distinct phases on the basis of changes in the angular velocity of the gape angle (Fig. 2). Slow opening of the mouth (SOI and SOII) initiates a cycle and is followed by fast opening of the mouth (FO). After maximal gape has been reached, the mouth is closed rapidly (FC) until the jaws touch the prey, initiating the slow closing phase (SC) during which the closing speed decreases further. The slow closing phase may be accompanied by a prey-crushing phase (powerstroke, PS).

A feeding sequence is traditionally subdivided into a number of stages. Feeding sequences are initiated by (1) the prey capture stage, during which the food is taken between the jaws, followed by (2) the intraoral transport stage, during which the food is mechanically reduced and transported towards the back of the mouth, and ending with (3) the swallowing stage, in which the food mass is transferred from the pharynx to the esophagus (De Vree and Gans, 1989).

Subdivision of the feeding sequence

In order to investigate whether a feeding sequence could be

subdivided into different stages (i.e. different bite types) solely on the basis of kinematic variables (i.e. no *a priori* selection of cycles; all bites from the beginning to the end of a feeding sequence were used), a factor analysis was performed on a kinematic data set containing prey capture, intraoral transport and swallowing cycles for lizard 1 (prey: grasshopper, 2 cm). A plot of the factor scores of the three cycle types on the first three factors indicates that prey capture cycles are separated from intraoral transport and swallowing cycles in multivariate space (Fig. 3). However, to test the significance of this observation, a one-way ANOVA (coupled to a Duncan multiple-range test) between bite types was performed using the scores on the first ($F_{2,109}=20.92$; $F_{\text{prob}}<0.001$), second ($F_{2,109}=26.11$; $F_{\text{prob}}<0.001$) and third ($F_{2,109}=44.57$; $F_{\text{prob}}<0.001$) factors. This analysis showed that these bite types are indeed significantly different. For the first and second factors, the swallowing cycles are significantly different from prey capture and intraoral transport cycles and intraoral transport differs from prey capture. For the third factor, both swallowing and intraoral transport differ from prey capture. The first factor (51.9% variation explained; eigenvalue 7.62) is correlated strongly with the timing of maximal excursions of the jaws and tongue and the duration of the total cycle and the SO phase. The second factor (17.4% of variation explained; eigenvalue 2.43) correlates well with the maximal excursion variables and the third factor (9.1% of variation explained; eigenvalue 1.28) correlates with the durations of the FO, SC/PS and FC phases (Table 2). Differences between the three stages can thus largely be assigned to differences in timing/duration (factor 1) and maximal excursion (factor 2) variables of both the jaw and tongue cycles. A MANOVA performed on the original data set also showed that bite types were significantly different (Rao's $r=23.54$, d.f.=28, 194; $P<0.001$). The subsequent univariate F -tests (d.f.=2, 109) showed that bite types were significantly different (at the 0.01 level, after Bonferroni correction) in all variables except the duration of the SOII phase (see Table 3).

The following description of the different feeding stages is based on feeding sequences with a 2.0 cm grasshopper unless

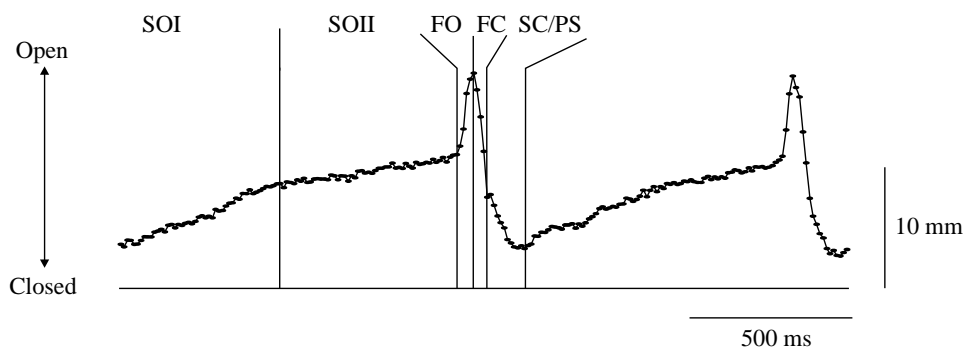


Fig. 2. Kinematic phases recognised in an intraoral bite cycle of *A. stellio* while eating a large grasshopper (terminology after Bramble and Wake, 1985). The actual data points are shown in this figure. In the other kinematic plots (Figs 4–8), only the lines connecting these points are shown; the sampling rate (high-speed video, 250 Hz; X-ray, 50 Hz) is the same for all figures. SOI, first part of the slow opening phase; SOII, second part of the slow opening phase; FO, fast opening phase; FC, fast closing phase; SC/PS, slow closing/powerstroke phase.

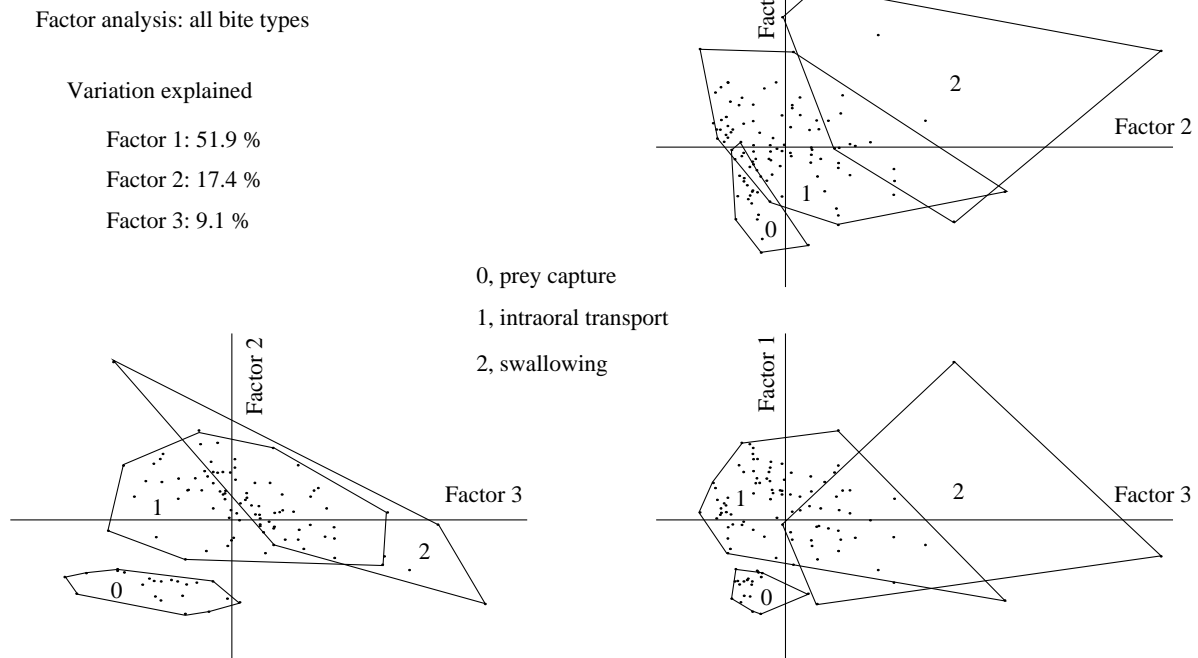


Fig. 3. Plot of the factor scores from a factor analysis of all three feeding stages (0, prey capture; 1, intraoral transport; and 2, swallowing) on the first three factors (prey: grasshopper 2.0 cm; lizard 1).

noted otherwise. All values are reported with standard deviations. Tongue movements are discussed with reference to the most posterior metal tongue marker (Fig. 1A).

Prey capture cycles will not be described here, as an extensive description of prey capture kinematics in *Agama stellio* is presented in Herrel *et al.* (1995).

Intraoral transport cycles

After a successful strike, an average of 30 ± 10 bites is needed to reduce the prey adequately and transport it to the back of the mouth. A mean bite cycle during the intraoral transport stage lasts 711 ± 235 ms (Table 4). As in prey capture cycles, the gape cycle is always initiated by a slow opening phase (SOI), during which the tongue is protracted underneath the prey and consequently the lower jaw is pushed down (Fig. 4). During tongue protraction, the posterior marker in the tongue moves a mean value of 2.4 ± 1.4 mm anteriorly and 4.4 ± 1.0 mm dorsally. The SOI phase lasts 228 ± 109 ms, which represents 32% of the total bite cycle. Once the tongue reaches the prey item, which is held between the teeth, the second part of the slow opening phase (SOII) starts. The tongue is fitted against the prey and the gape angle is kept constant at approximately 18° . The SOII phase (144 ± 141 ms) is usually not as long as the SOI phase and makes up approximately 20% of the gape cycle. The SOI and SOII phases are among the most variable phases in the jaw cycle (see Table 4).

At the end of the SOII phase, the jaws are opened rapidly (FO phase) and the tongue is retracted. The FO phase lasts 72 ± 39 ms (10% of the total cycle duration) and ends at

maximal gape ($32 \pm 7^\circ$; 8.9 ± 1.2 mm), which is achieved 443 ± 225 ms after the beginning of the cycle (Table 4).

Maximal gape distance consists of both depression of the lower jaw (6.4 ± 1.4 mm) and elevation of the neurocranium (2.4 ± 2.2 mm). The maximal elevation of the neurocranium is reached an average of 5 ± 224 ms before, and the maximal

Table 2. Results from the factor analysis

| Variable | Factor 1 | Factor 2 | Factor 3 |
|----------|----------|----------|----------|
| TMHDTO | 0.95 | 0.14 | 0.11 |
| TMDLJ | 0.94 | 0.26 | 0.18 |
| TGA | 0.94 | 0.26 | 0.19 |
| TMEUJ | 0.94 | 0.25 | 0.20 |
| DTC | 0.92 | 0.27 | 0.19 |
| DSOI | 0.84 | 0.23 | 0.11 |
| DSOII | 0.57 | -0.15 | -0.37 |
| GA | -0.17 | -0.91 | -0.01 |
| GD | -0.28 | -0.87 | -0.21 |
| THTR | 0.22 | 0.70 | 0.27 |
| DFO | 0.24 | -0.10 | 0.76 |
| DSC/PS | 0.22 | 0.41 | 0.68 |
| DFC | 0.37 | 0.21 | 0.66 |
| MHDTO | 0.33 | -0.27 | -0.62 |

For an explanation of the abbreviations used, see Table 4 (% variation explained by each factor: factor 1, 51.9%, eigenvalue 7.62; factor 2, 17.4%, eigenvalue 2.43; factor 3, 9.1%, eigenvalue 1.28).

Factor loadings are based on a data set containing all bite types for lizard 1 with 2.0 cm grasshopper prey.

Table 3. Results of the univariate analyses performed on different data sets

| Univariate analyses | GD | GA | MHDTO | DSOI | DSOII | DFO | DFC | DSC/PS | DTC | TGA | TMEUJ | TMDLJ | TMHDTO | THTR |
|--|-------|-------|---------|-------|--------|-------|-------|--------|-------|-------|-------|-------|--------|-------|
| Bite type (d.f.=2, 109) | 80.87 | 30.26 | 25.46 | 44.33 | 0.07 | 23.04 | 37.96 | 75.16 | 57.67 | 50.00 | 49.67 | 49.16 | 31.42 | 41.54 |
| Lizard 1, grasshopper | ** | ** | ** | ** | NS | ** | ** | ** | ** | ** | ** | ** | ** | ** |
| Prey size effect (d.f.=1, 43) | 1.47 | 1.50 | 0.95 | 51.40 | 37.02 | 8.61 | 7.40 | 19.48 | - | - | 68.27 | 63.67 | 23.50 | 21.29 |
| Lizard 2, intraoral transport | NS | NS | NS | ** | ** | * | * | ** | - | - | ** | ** | ** | ** |
| Prey type (d.f. = 2, 81) | 12.51 | 6.04 | 9.60 | 8.96 | 2.97 | 0.63 | 3.04 | 1.93 | 7.94 | 5.67 | 5.65 | 5.38 | 3.42 | 0.05 |
| Lizard 1, intraoral transport | ** | * | ** | ** | NS | NS | NS | NS | * | * | * | * | NS | NS |
| Individual × prey type (d.f.=1, 118) intraoral transport | 0.018 | 0.001 | 0.00002 | 0.718 | 0.0003 | 0.854 | 2.42 | 3.13 | 0.003 | 0.378 | 0.376 | 0.409 | 1.31 | 1.62 |
| Individual effect (d.f.=1, 118) intraoral transport | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| Prey type (d.f.=1, 118) intraoral transport | 0.028 | 41.26 | 2.83 | 16.81 | 9.45 | 0.424 | 0.196 | 1.73 | 17.89 | 15.29 | 14.59 | 13.92 | 11.93 | 0.016 |
| | NS | ** | NS | * | * | NS | NS | NS | ** | * | * | * | * | NS |
| Prey type (d.f.=1, 118) intraoral transport | 14.26 | 3.77 | 13.10 | 15.47 | 3.88 | 2.41 | 18.11 | 0.693 | 13.87 | 11.42 | 11.58 | 10.94 | 10.57 | 0.778 |
| | ** | NS | ** | ** | NS | NS | ** | NS | ** | ** | ** | ** | ** | NS |

Table entries are *F*-values; the first column indicates the effect investigated, the degrees of freedom, animal used, stage and prey type.
 *Significant at the 0.05 level after sequential Bonferroni correction.
 **Significant at the 0.01 level after sequential Bonferroni correction.
 NS, not significant at the 0.05 level after sequential Bonferroni correction.
 For an explanation of the abbreviations used, see Table 4.

depression of the lower jaw an average of 3 ± 230 ms after maximal gape. Tongue retraction usually begins after the tongue has reached its dorsalmost position (approximately 30 ms before maximal gape) and it takes an average of 137 ± 59 ms to reach its posteriormost position and 162 ± 57 ms to reach its ventralmost position. The posteriormost position is reached before the ventralmost position in all cycles examined.

After maximal gape, the mouth is closed rapidly (DFC: 82 ± 21 ms; 12 % of the total cycle duration) until the jaws touch the prey item. At that point, the SC/PS phase starts and the mechanical reduction of the prey takes place. This crushing phase is not always recognisable and is absent in some cycles.

The SC/PS phase lasts an average of 186 ± 67 ms (26 % of the total cycle duration).

Swallowing cycles

Once the prey has been reduced and transported to the back of the mouth, swallowing begins, resulting in the movement of the prey from the mouth to the esophagus. During the swallowing stage (Fig. 4; Table 4), a jaw cycle is mainly characterised by movements of the tongue under the prey, followed by a bulging action and subsequent retraction of the tongue. When the prey has entered the esophagus, the tongue moves anteriorly beyond the prey and then bulges. Upon

Table 4. The effect of prey size on kinematic variables during intraoral transport and swallowing

| Variable | Grasshopper (2.0 cm) | | | | Grasshopper (4.5 cm) | | | |
|----------------------|-------------------------------|-------|---------------------|-------|-------------------------------|--------|---------------------|--|
| | Intraoral transport (N=54) | | Swallowing (N=8) | | Intraoral transport (N=18) | | Swallowing (N=1) | |
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | | |
| GD (mm) | 8.9 | 1.2 | 4.7 | 2.6 | 9.5 | 1.2 | 5.9 | |
| GA (degrees) | 32.1 | 6.9 | 16.6 | 8.4 | 39.5 | 5.3 | 23.9 | |
| MEUJ (mm) | 2.4 | 2.2 | 1.2 | 1.1 | 2.8 | 1.2 | 0.5 | |
| MDLJ (mm) | 6.4 | 1.4 | 3.4 | 2.5 | 6.8 | 1.8 | 5.5 | |
| MHDTO (mm) | 2.4 | 1.4 | 4.3 | 1.4 | 3.2 | 1.5 | 4.2 | |
| MVDTO (mm) | 4.4 | 1.0 | 4.8 | 0.5 | 5.0 | 1.2 | 4.9 | |
| DSOI (ms) | 227.9 | 108.9 | 733.3 | 678.8 | 827.8 | 671.5 | 700.0 | |
| DSOII (ms) | 143.5 | 141.4 | 93.3 | 108.7 | 648.9 | 395.9 | 800.0 | |
| DSO (ms) | 371.4 | | 826.7 | | 1476.7 | | 1500.0 | |
| DFO (ms) | 72.0 | 38.6 | 195.6 | 357.9 | 84.4 | 14.2 | 80.0 | |
| DFC (ms) | 81.9 | 20.8 | 148.9 | 91.0 | 95.6 | 14.2 | 80.0 | |
| DSC/PS or DSTAT (ms) | 186.0 | 67.3 | 213.3 | 94.3 | 278.9 | 87.3 | 340.0 | |
| DTC (ms) | 710.9 | 235.4 | 1431.1 | 533.2 | 1928.9 | 969.0 | 2000.0 | |
| TGA (ms) | 443.0 | 225.2 | 1022.2 | 589.2 | 1554.4 | 979.5 | 1580.0 | |
| TMEUJ (ms) | -4.9 | 223.9 | -11.1 | 589.7 | 2.2 | 974.66 | -20.0 | |
| TMDLJ (ms) | 3.3 | 230.2 | -31.1 | 589.2 | 10.0 | 977.1 | 0.0 | |
| TMHDTO (ms) | -80.7 | 229.1 | -77.8 | 586.3 | -573.3 | 642.5 | -300 | |
| TMVDTO (ms) | -28.8 | 222.1 | -4.4 | 580.8 | -244.4 | 650.6 | -60 | |
| THTR (ms) | 136.7 | 58.6 | 215.6 | 72.9 | 194.4 | 56.1 | 720.0 | |
| TVTR (ms) | 161.9 | 56.7 | 220.0 | 69.3 | 223.3 | 35.4 | 680.0 | |
| SOI (%) | 32 | | 51 | | 43 | | 35 | |
| SOII (%) | 20 | | 7 | | 34 | | 40 | |
| SO (%) | 52 | | 58 | | 77 | | 75 | |
| FO (%) | 10 | | 14 | | 4 | | 4 | |
| FC (%) | 12 | | 10 | | 5 | | 4 | |
| SC/PS or STAT (%) | 26 | | 15 | | 14 | | 17 | |

All times are measured from the beginning of the cycle except for TMEUJ, TMDLJ, TMHDTO and TMVDTO, which are expressed in ms before (-) or after maximal gape (all values based on X-ray data, 50 frames s⁻¹).

N, number of cycles used.

During swallowing, no slow closing/powerstroke phase is present; instead a stationary phase (STAT) is recognised.

DFC, duration of the fast closing phase; DFO, duration of the fast opening phase; DSC/PS, duration of the slow closing/power stroke phase; DSOI, duration of the slow opening phase 1; DSOII, duration of the slow opening phase 2; DSTAT, duration of the stationary phase; DTC, duration of the total cycle; GA maximal gape angle; GD, maximal gape distance; MDLJ, maximal depression of the lower jaw; MEUJ, maximal elevation of the upper jaw; MHDTO, maximal horizontal displacement of the tongue; MVDTO, maximal vertical displacement of the tongue; TGA, time to maximal gape; THTR, duration of tongue retraction in the horizontal plane; TMDLJ, time to maximal depression of the lower jaw; TMEUJ, time to maximal elevation of the upper jaw; TMHDTO, time to maximal horizontal displacement of the tongue; TMVDTO, time to maximal vertical displacement of the tongue; TVTR, duration of tongue retraction in the vertical plane.

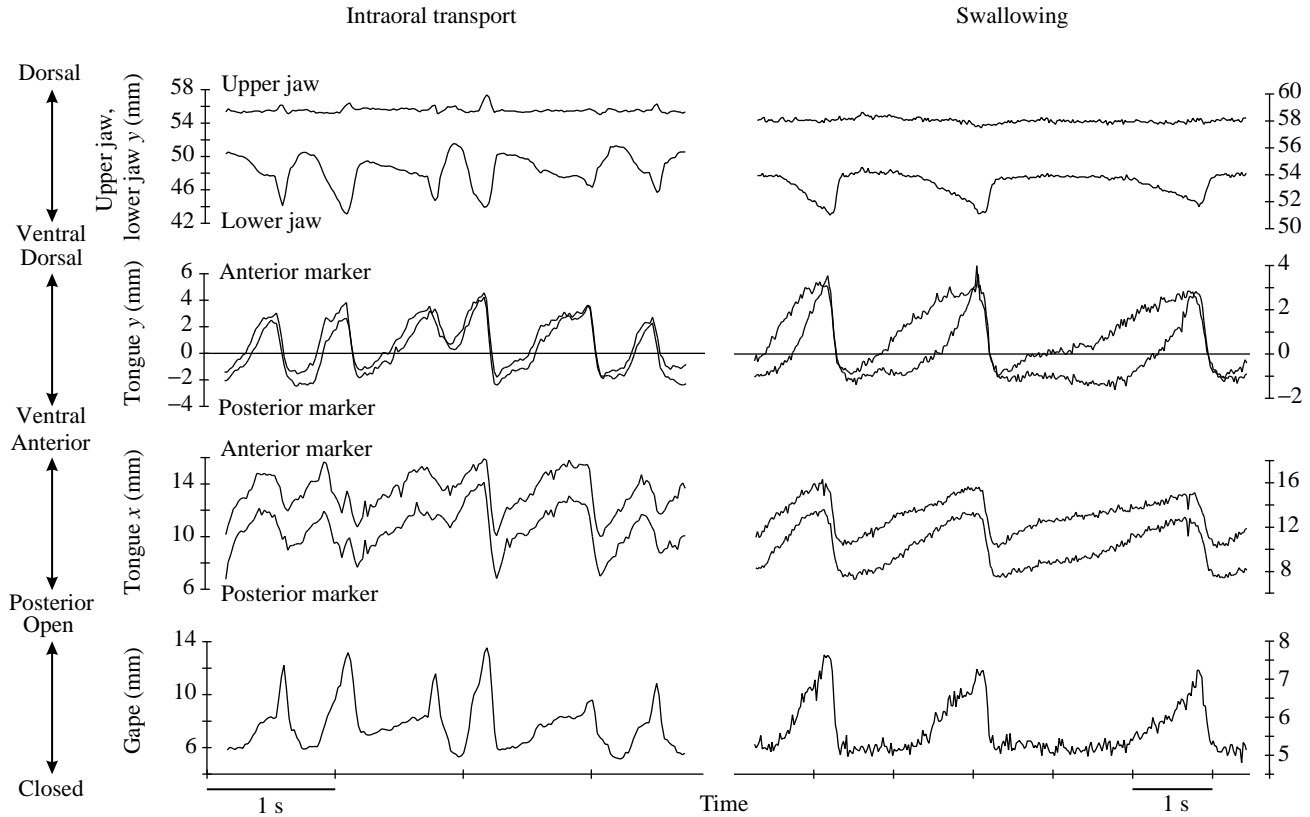


Fig. 4. Kinematic profiles (based on X-ray films, 50 frames s^{-1}) of the vertical displacements of the upper and lower jaw, the vertical displacement of the tongue, the horizontal displacement of the tongue and the gape during a number of intraoral transport and swallowing cycles in *A. stello* while eating a 2.0 cm grasshopper. Note the different scales on the y-axes for the intraoral transport and swallowing cycles.

retraction, the posterior end of the tongue pushes the prey further into the esophagus. Once inside the esophagus, constriction of the throat region pushes the prey further down. An average of 13 ± 6 bites is needed to swallow the prey.

A bite cycle during the swallowing stage lasts an average of 1431 ± 533 ms. As in the intraoral transport cycles, a bite cycle is always initiated by the slow opening of the mouth (SOI phase), during which the tongue is protracted and consequently the lower jaw is pushed down. During tongue protraction, the posterior marker on the tongue moves 4.3 ± 1.4 mm anteriorly and 4.8 ± 0.5 mm dorsally. The SOI phase lasts 733 ± 679 ms (51% of the total bite cycle). Since the prey item is now positioned at the back of the mouth, the second part of the slow opening phase (SOII), which involves the fitting of the tongue against the prey, is usually absent or relatively short (93 ± 109 ms; 7% of the total cycle duration). The SOI and the SOII phases are again among the most variable phases in the jaw cycle (Table 4).

Once the tongue is positioned under or anterior to the prey, the jaws are opened (FO phase), creating a space between the tongue and the upper jaw. The tongue is then retracted and consequently the prey is transported backwards. The FO phase is difficult to recognise in certain cycles because the opening speed differs very little from that during the SOI phase. The FO phase lasts 196 ± 358 ms (14% of the total cycle duration) and

ends at maximal gape ($16.6 \pm 8.4^\circ$; 4.7 ± 2.6 mm). Maximal gape distance is achieved 1022 ± 589 ms after the beginning of the cycle. The gape distance is now mainly due to depression of the lower jaw (3.4 ± 2.5 mm), with a lesser contribution from elevation of the neurocranium (1.2 ± 1.1 mm). Maximal elevation of the neurocranium is reached an average of 11 ± 590 ms before maximal gape, whereas maximal depression of the lower jaw is reached an average of 31 ± 589 ms before maximal gape. Tongue retraction usually begins after the tongue has reached its dorsalmost position (4 ± 581 ms before maximal gape). It takes 216 ± 73 ms for the tongue to reach its posteriormost position and 220 ± 69 ms to reach its ventralmost position. The posteriormost position is usually reached before the ventralmost position.

At maximal gape, the mouth is closed rapidly (DFC, 149 ± 91 ms; 10% of the total cycle). At that point, a 'stationary phase' starts and the tongue returns to its resting position. The stationary phase lasts on average 213 ± 94 ms, which is 15% of the total cycle time.

Individual variation

To explore individual variation, a MANOVA (mixed model) was performed on a data set containing intraoral transport bites from two individuals with two different prey types (2.0 cm grasshopper and 2.0 cm cricket). In this analysis, the individual effect (random) was crossed with the effect of

prey type (fixed). The interaction effect between individual and prey type was not significant (Rao's $r=0.973$; d.f.=14, 105; $P>0.05$). Nevertheless, a significant effect of the individual was present (Rao's $r=14.83$; d.f.=14, 105; $P<0.001$). The subsequent univariate F -tests (d.f.=1, 118) (Table 3) show that these differences are significant for gape angle, the duration of the SOI and SOII phases, total cycle duration and the time to maximal gape, maximal cranial elevation, maximal lower jaw depression and maximal horizontal displacement of the tongue. However, a prey type effect is also present (Rao's $r=4.56$; d.f.=14, 105; $P<0.001$). As the univariate F -tests (d.f.=1, 118; Table 3) show, this prey type effect is significant for maximal gape distance, maximal horizontal displacement of the tongue, the duration of the SOI and the FC phases, the total cycle duration and the time to maximal gape, maximal cranial elevation, maximal lower jaw depression and maximal horizontal displacement of the tongue. Although individual lizards differ, their response to a different prey type is similar.

Effects of prey type and size

Since strike cycles were recorded only when grasshoppers were the prey item, no prey effect could be investigated in this case. However, for the intraoral transport and swallowing cycles, the effect of prey type and/or size was investigated. The effects of prey type and size on the kinematic characteristics of jaw cycles are shown in Tables 4 and 5. Gape and tongue profiles for different food types during different stages are represented in Figs 5–7. A short description of the effects of prey type and size on the major kinematic variables is given below.

Effects of prey size

To evaluate the effect of prey size, a MANOVA was performed using intraoral transport bites from one lizard with standard and very large grasshoppers as food items. Prey size had a significant (Rao's $r=19.63$; d.f.=12, 32; $P<0.001$) effect on the kinematics of a feeding cycle. Univariate F -tests (d.f.=1, 43) show that these differences are significant (Table 3) for the

Table 5. The effects of prey type on kinematic variables during intraoral transport and swallowing

| Variable | Cricket (2.0 cm) | | | | Mealworm (2.5 cm) | | | |
|----------------------|-------------------------------|-------|---------------------|-------|------------------------------|------|---------------------|-------|
| | Intraoral transport (N=16) | | Swallowing (N=6) | | Intraoral transport (N=7) | | Swallowing (N=4) | |
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| GD (mm) | 8.0 | 1.1 | 4.1 | 1.2 | 6.5 | 1.4 | 3.1 | 0.5 |
| GA (degrees) | 30.3 | 5.4 | 19.9 | 6.1 | 23.8 | 4.5 | 11.6 | 1.9 |
| MEUJ (mm) | 1.3 | 0.8 | 0.6 | 0.4 | 0.7 | 0.5 | 0.3 | 0.2 |
| MDLJ (mm) | 6.2 | 3.1 | 3.8 | 1.5 | 5.8 | 1.4 | 3.1 | 0.3 |
| MHDTO (mm) | 1.5 | 0.9 | 3.9 | 1.8 | 1.0 | 0.6 | 4.2 | 0.7 |
| MVDTO (mm) | 3.8 | 1.1 | 4.4 | 0.7 | 2.9 | 1.5 | 3.7 | 0.4 |
| DSOI (ms) | 164.7 | 95.0 | 797.5 | 515.4 | 71.4 | 23.6 | 430.0 | 234.3 |
| DSOII (ms) | 100.0 | 137.3 | 92.5 | 153.9 | 0.0 | 0 | 260.0 | 54.8 |
| DSO (ms) | 264.7 | | 890.0 | | 71.4 | | 690.0 | |
| DFO (ms) | 63.7 | 18.3 | 35.0 | 13.2 | 74.3 | 33.3 | 40.0 | 20.0 |
| DFC (ms) | 67.4 | 10.7 | 55.0 | 21.8 | 68.6 | 9.9 | 60.0 | 0.0 |
| DSC/PS or DSTAT (ms) | 180.0 | 57.3 | 380.0 | 142.5 | 151.4 | 54.4 | 280.0 | 101.0 |
| DTC (ms) | 575.8 | 215.9 | 1360.0 | 569.1 | 365.7 | 68.2 | 1070.0 | 201.2 |
| TGA (ms) | 323.2 | 198.3 | 925.0 | 533.9 | 145.7 | 43.7 | 730.0 | 264.4 |
| TMEUJ (ms) | -4.2 | 201.5 | -5.0 | 536.1 | 2.9 | 46.4 | -30.0 | 287.0 |
| TMDLJ (ms) | 3.7 | 196.5 | 2.5 | 532.6 | 2.9 | 36.8 | 0.0 | 264.4 |
| TMHDTO (ms) | -74.4 | 168.7 | -187.5 | 503.9 | -28.6 | 60.9 | -90.0 | 232.8 |
| TMVDTO (ms) | -32.1 | 192.7 | -15.0 | 530.9 | -14.3 | 47.6 | -70.0 | 312.1 |
| THTR (ms) | 144.7 | 59.2 | 255.0 | 102.8 | 145.7 | 71.5 | 220.0 | 49.0 |
| TVTR (ms) | 166.8 | 52.6 | 217.5 | 68.9 | 191.4 | 46.4 | 175.0 | 26.0 |
| SOI (%) | 29 | | 59 | | 20 | | 40 | |
| SOII (%) | 17 | | 7 | | 0 | | 24 | |
| SO (%) | 46 | | 65 | | 20 | | 64 | |
| FO (%) | 11 | | 3 | | 20 | | 4 | |
| FC (%) | 12 | | 4 | | 19 | | 6 | |
| SC/PS or STAT (%) | 31 | | 28 | | 41 | | 26 | |

All times are measured from the beginning of the cycle, except for TMEUJ, TMDLJ, TMHDTO and TMVDTO, which are expressed in ms before (-) or after maximal gape (all values based on X-ray data, 50 frames s⁻¹).

N , the number of cycles.

During swallowing, no slow closing/powerstroke phase is present; instead a stationary phase (STAT) is recognised.

For an explanation of the abbreviations used, see Table 4.

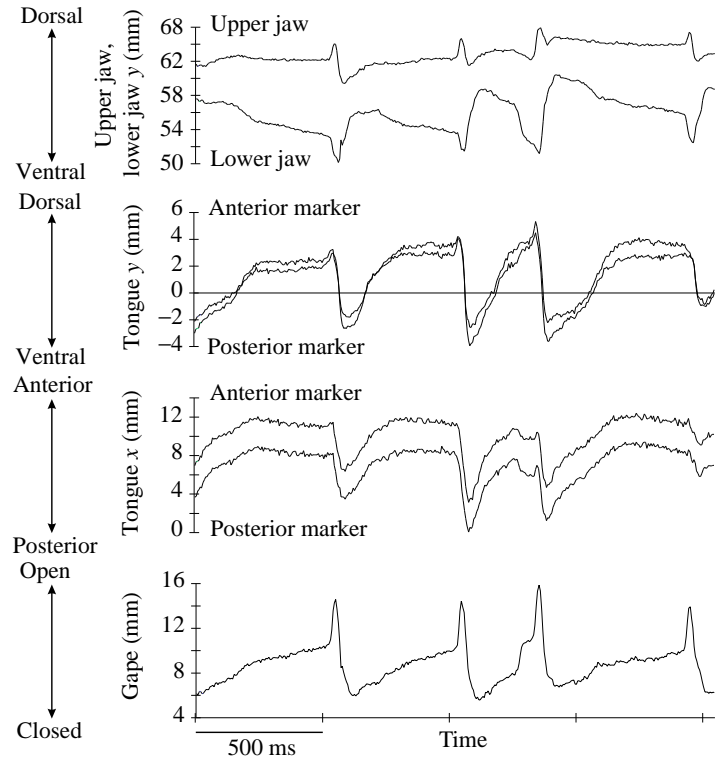


Fig. 5. Kinematic profiles (based on X-ray films, 50 frames s^{-1}) of the vertical displacements of the upper and lower jaw, the vertical displacement of the tongue, the horizontal displacement of the tongue and the gape during a number of intraoral transport cycles in *A. stellio* while eating a large (4.5 cm) grasshopper.

duration of the SOI, SOII, FO, FC and SC/PS phases as well as for the timing variables. Larger prey thus apparently results in an increase in the duration of the gape cycle, but no significant increase in the maximal excursion of the jaws and tongue.

The kinematic variables of intraoral transport cycles of *Agama stellio* while eating a very large grasshopper (4.5 cm, which is more than twice the size of those usually eaten) thus differ significantly from those for smaller prey in several ways (Fig. 5; Table 4). The cycles are more than twice as long (1929 ± 969 ms) and all the different kinematic phases last longer. The most striking difference is for the SO phase; the duration of both SOI and SOII is more than three times (SOI, 828 ± 672 ms, SOII, 649 ± 396 ms) that of intraoral transport cycles while eating standard prey items. Both the SOI and SOII phases increase in importance (percentage of total cycle) (SOI, 43%; SOII, 34%) whereas the FO (4%), the FC (5%) and the SC/PS (14%) phases decrease in relative importance.

Tongue displacements are also affected by the size of the prey. Both the duration of tongue protraction (TMHDTO, TMVDTO) and the duration of tongue retraction (THTR, TVTR) are significantly larger than those with standard prey items. It is interesting that the maximal anterior and dorsal positions of the tongue are reached more than 200 ms before maximal gape. This indicates that the SOII phase becomes of greater importance when large prey items are processed. When the tongue is completely protracted, more time is presumably needed to ensure close contact between the tongue and prey to prevent loss of the prey upon retraction of the tongue.

Unfortunately, only one swallowing cycle was recorded with

the large grasshopper prey and thus the following description can only be considered as preliminary (Table 4). During the swallowing stage, the cycle duration is similar to that of intraoral transport. The relative importance of the different phases during a swallowing cycle resembles that of the intraoral transport cycle for the same prey (Table 4) in which the SO phase constitutes 75% of the total cycle and the FO and FC phases each constitute less than 5%.

Effects of prey type

The effect of prey type (2.0 cm grasshopper, 2.0 cm cricket, 2.5 cm mealworm) on the kinematic variables was also investigated. In order to explore the possible interaction between prey type and bite type, a MANOVA was performed using both intraoral transport and swallowing data. This analysis shows a significant (Rao's $r=2.137$; d.f.=28, 160; $P=0.002$) interaction effect between prey type and bite type; different prey types have different effects on intraoral transport and swallowing cycles. The effect of prey type was then investigated for a single bite type. Unfortunately, the data set for swallowing bites (for different prey types) was too limited to perform a statistical analysis. However, for the intraoral transport bites, a significant difference between prey types was found (Rao's $r=2.87$; d.f.=28, 138; $P<0.001$). The univariate F -tests (d.f.=2, 81) show that differences are significant (at the 0.05 level after sequential Bonferroni correction; see Rice, 1989) for the maximal gape, the maximal horizontal displacement of the tongue, the duration of the SOI phase, the total cycle duration and the time to maximal gape, cranial elevation and lower jaw depression (Table 3). The type of prey

thus results in modulation of both maximal excursions, the time to maximal jaw displacements and the duration of the SOI phase (and thus also the TC).

These prey type effects could be due to the prey structure and/or form. Different prey differ in length, width, mass and hardness. For one prey type, the length, mass and hardness will covary. However, a 2.5 cm mealworm has a completely different body form (with an elongated cylindrical body) and is much lighter (0.13 g) than a 2.0 cm cricket (0.23 g) or a 2.0 cm grasshopper (0.20 g). The cricket has a harder exoskeleton than that of the grasshopper (2 N *versus* 1.5 N). These differences will affect the kinematic characteristics of intraoral transport and swallowing cycles (Figs 6, 7; Table 5).

Intraoral transport cycles for mealworm prey have shorter total cycle duration and smaller maximal gape (GD=6.5±1.4 mm; GA=23.8±4.5°; MEUJ=0.7±0.5 mm; MDLJ=5.8±1.4 mm) and tongue-related values (MHDTO=1.0±0.6 mm; MVDTO=2.9±1.5 mm) than for grasshopper prey (compare Tables 4 and 5). The SOI phase lasts for only 71±24 ms (20% of the total cycle). Remarkably, no SOII phase could be recognised with mealworm prey (Fig. 7). The FO phase lasts 74±33 ms, which is not significantly different from that for other prey types. However, the relative duration of this phase is double (20% of total cycle duration) that of grasshopper intraoral transport cycles (Table 4). The FC phase lasts only 69±10 ms (19% of total

cycle duration). Remarkably the SC/PS phase lasts 151±54 ms (41% of total cycle duration). Although relative durations are rather different, absolute phase durations are not significantly different in comparison with other prey.

A second type of prey item given to the lizards was crickets (Fig. 7; Table 5). Comparing cricket intraoral transport cycles with those of standard grasshoppers, maximal gape values are rather similar (see Tables 4, 5). The absolute durations of the total cycle are significantly different, whereas the durations of the different kinematic phases do not differ significantly between prey types. The relative durations, especially those of FO and FC phases, are similar for both crickets and grasshoppers.

As no statistical analysis could be performed on the swallowing cycles, only a short qualitative description of the effects of prey type can be given. Mealworm swallowing cycles generally show smaller absolute values for gape and tongue variables (Fig. 6; Table 5) when compared with those for grasshoppers (Table 4), while the total cycle length is similar. However, FO (40±20 ms) and FC (60 ms) are shorter for mealworm swallowing cycles, whereas the stationary phase lasts longer (280 ms). The relative durations of the SO phase (64%) are similar for both prey but that of FO (4%) and FC (6%) decrease. The stationary phase (26%), in contrast, increases in relative duration when swallowing mealworms.

Cricket swallowing cycles are similar to standard prey

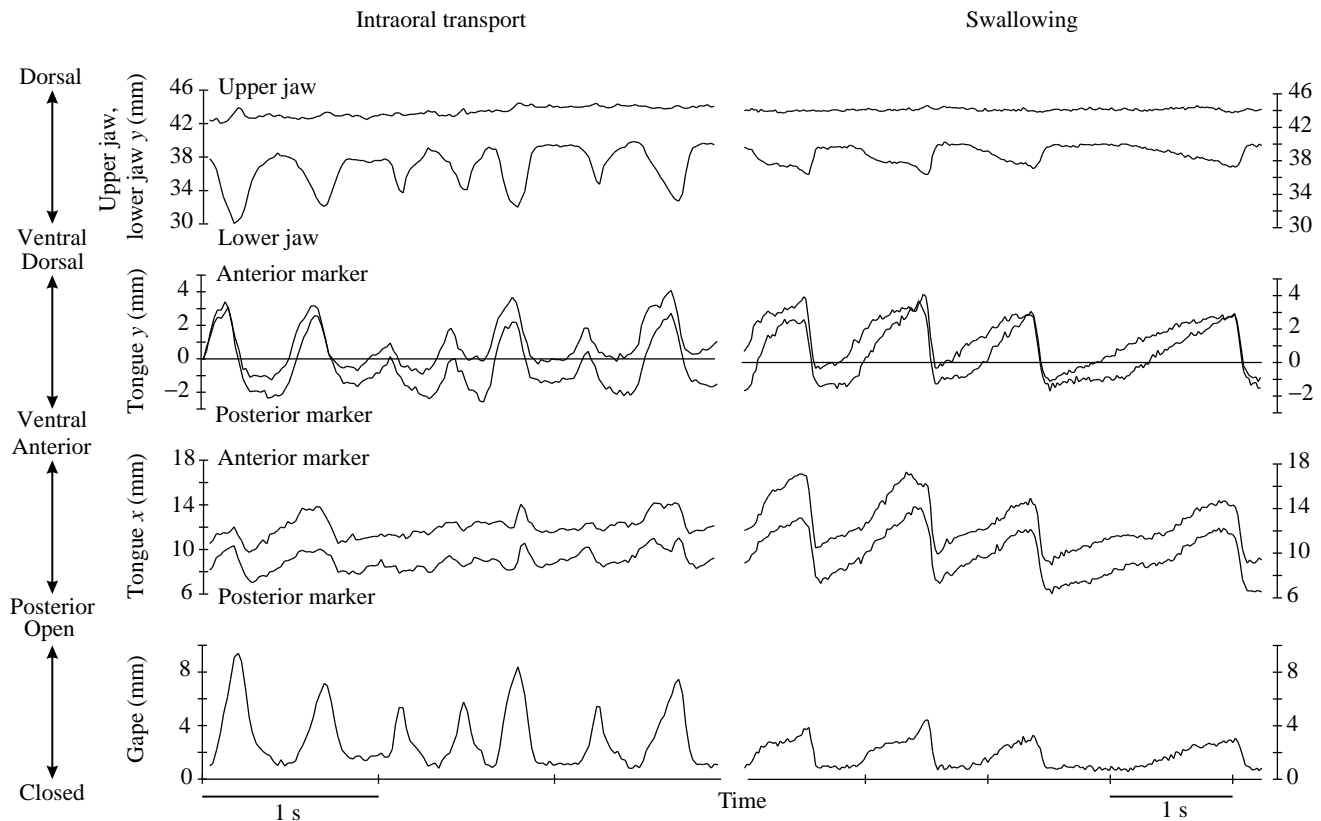


Fig. 6. Kinematic profiles (based on X-ray films, 50 frames s^{-1}) of the vertical displacements of the upper and lower jaw, the vertical displacement of the tongue, the horizontal displacement of the tongue and the gape during a number of intraoral transport and swallowing cycles in *A. stellio* while eating a 2.5 cm mealworm. Note the different scale on the y-axes for the intraoral transport and swallowing cycles.

swallowing cycles regarding gape values and tongue displacements (Fig. 7; Table 5). The duration of a swallowing cycle and the duration of tongue retraction during swallowing are also similar for both prey. The most notable difference during swallowing lies in the duration of the FO, FC and stationary phases. Whereas the FO and FC phases tend to be much shorter, the stationary phase lasts much longer when swallowing a cricket.

Discussion

Prey capture, intraoral transport and swallowing all play important roles in the feeding process. The generalised feeding cycle in the Bramble and Wake (1985) model was based on intraoral transport cycles from a number of species, and they suggested that the intraoral transport cycle is the basis of all other feeding cycles (i.e. prey capture, swallowing, drinking, tongue flicking, etc.). Most authors recognise this, but still divide the feeding process into subsequent stages; generally, these are prey capture, reduction (chewing), transport and swallowing (pharyngeal packing).

Several authors have used multivariate statistics on kinematic data in order to demonstrate the presence of such subdivisions. For *Agama agama* (Kraklau, 1991), no difference was found between strike cycles and 'chewing' using a principal component analysis. Similarly, for *Oplurus cuvieri*

(Delheusy and Bels, 1992), strikes and reduction bites or transport and transport bites were not clearly separated in multivariate space. Only the 'cleaning' cycles represent a significantly different bite type in *O. cuvieri*. In *Zonosaurus laticaudatus* (Urbani and Bels, 1995), only the deglutition (swallowing) cycles are separated in multivariate space. However, the different cycle types were not significantly different. In the two species (*Phrynocephalus helioscopus*, Agamidae; *Dipsosaurus dorsalis*, Iguanidae) for which quantitative data on intraoral transport and prey capture are presented in Schwenk and Throckmorton (1989), little difference was found in gape angle and cycle duration when comparing prey capture with transport cycles. The principal difference noted by these authors between bite types is the proportion of maximal gape achieved during the SO phase.

In *A. stellio*, both capture and swallowing cycles are separated from intraoral transport bites in multivariate space (Fig. 3). Additionally, bite types are significantly different in almost every aspect of the jaw and tongue cycles (with the exception of the duration of the SOII phase; Table 3). Although the absolute durations of the different kinematic phases differ, the relative durations of the different kinematic phases do not differ greatly between capture, intraoral transport and swallowing (Fig. 8). Aspects of duration and maximal excursion are thus modulated in relation to the specific demands of each food processing stage. In the plot of the factor

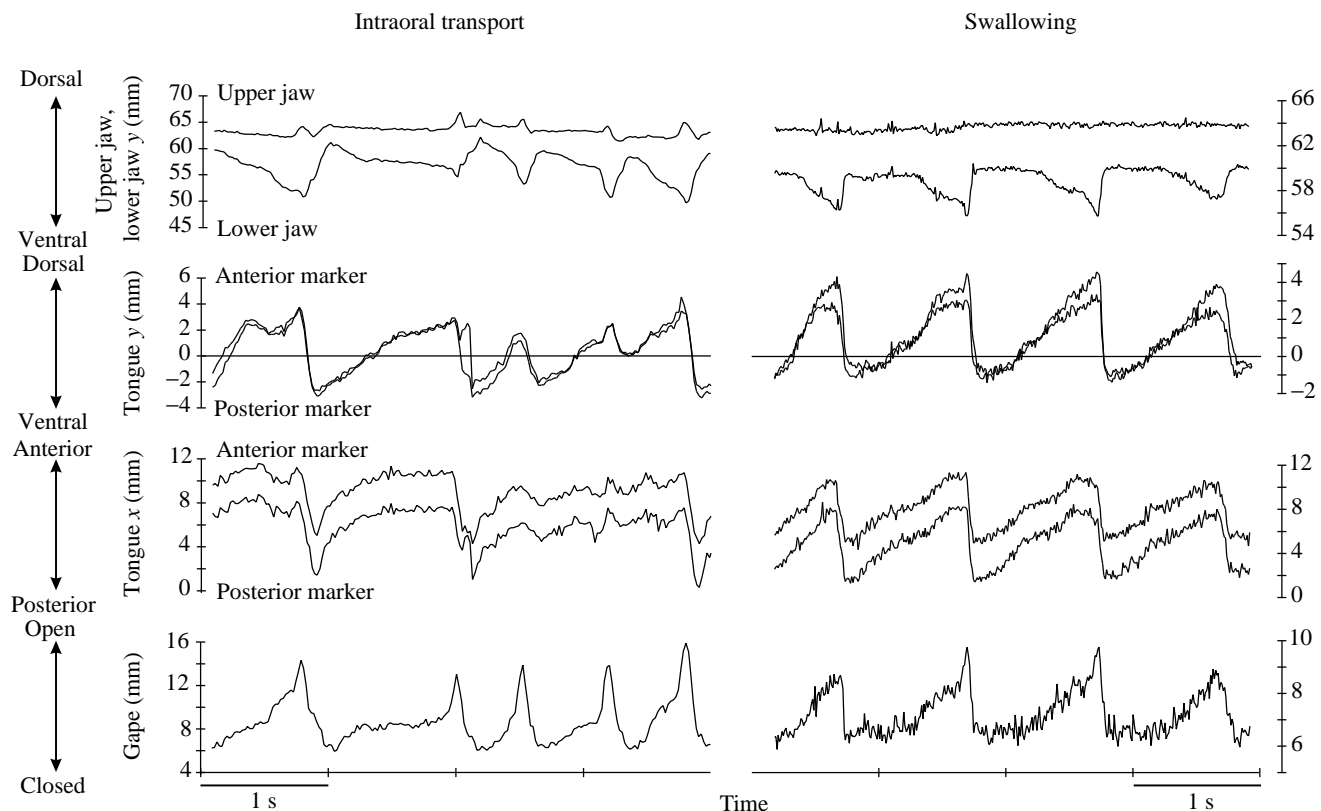


Fig. 7. Kinematic profiles (based on X-ray films, 50 frames s^{-1}) of the vertical displacements of the upper and lower jaw, the vertical displacement of the tongue, the horizontal displacement of the tongue and the gape during a number of intraoral transport and swallowing cycles in *A. stellio* while eating a 2.0 cm cricket. Note the different scale on the y-axes for the intraoral transport and swallowing cycles.

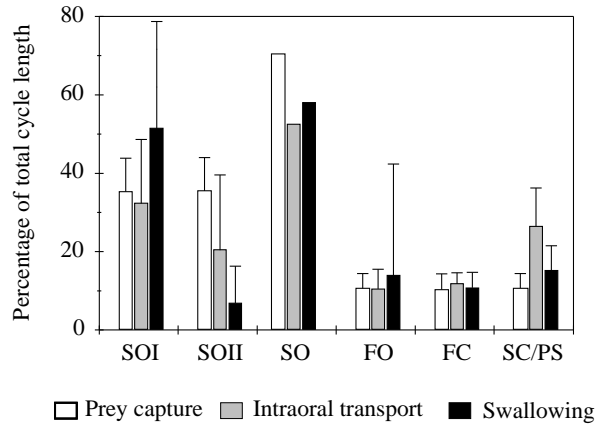


Fig. 8. Histogram representing the relative phase durations (percentage of total cycle duration) of prey capture (open columns), intraoral transport (stippled columns) and swallowing (filled columns) bites in *A. stellio* while eating a 2.0 cm grasshopper. During swallowing, no SC/PS phase is present; instead, the bar represents the stationary phase. Error bars indicate standard deviations; values of N are given in Table 4. SOI, slow opening I; SOII, slow opening II; SO, slow opening (SOI+SOII); FO, fast opening; FC, fast closing; SC/PS, slow closing/powerstroke.

scores (Fig. 3) for the different bite types, most overlap is present between the intraoral transport bites and the two other bite types. This observation supports the hypothesis of Bramble and Wake (1985) regarding the ancestral status of intraoral transport bites.

The only lizard for which a difference was found previously within the intraoral transport stage (between 'chewing' and transport) is *Chameleo jacksonii* (So *et al.* 1992). However, in *A. stellio*, no subdivision of the intraoral transport stage into separate chewing (reduction) and transport bites can be made from our kinematic data. It is likely that quantitative electromyographical data from the jaw closer muscles during the SC/PS phase are the only way in which reduction can be differentiated from the other intraoral transport bites.

Comparative kinematics

Intraoral transport cycles

The only agamids for which intraoral transport cycles have been analysed are *Uromastix aegyptius* (Throckmorton, 1976), *Phrynocephalus helioscopus* (Schwenk and Throckmorton, 1989) and *Agama agama* (Kraklau, 1991). Somewhat more extensive data exist on the kinematics of intraoral transport cycles in iguanids: an arboreal (*Anolis equestris*; Bels and Baltus, 1989) and several ground-dwelling species (*Ctenosaura similis*, Smith, 1984; *Dipsosaurus dorsalis*, Schwenk and Throckmorton, 1989; *Oplurus cuvieri*, Delheusy and Bels, 1992). Although the absolute excursions of the jaws and tongue may vary between species, great similarities in the kinematics of the intraoral transport cycles are present. The only iguanian lizard that differs greatly from the others (mainly in increased aspects of cycle duration) is *Chameleo jacksonii* (So *et al.* 1992). It is likely that the extreme specialisation of the tongue in relation to the ballistic

prey capture mechanism in this species has led to a decreased efficiency during the intraoral transport stage.

The similarity between results for *A. stellio* and the other agamid (Throckmorton, 1976; Schwenk and Throckmorton, 1989; Kraklau, 1991) and iguanid species (Smith, 1984; Schwenk and Throckmorton, 1989; Bels and Baltus, 1989) suggests a basic motor pattern for moving the jaw and hyolingual apparatus during the intraoral transport cycles. This could be confirmed using electromyographical recordings.

For non-iguanid lizards, a description of intraoral transport cycles is available only for *Tupinambis nigropunctatus* (Smith, 1984), *Lacerta viridis* (Goosse and Bels, 1992) and *Zonosaurus laticaudatus* (Urbani and Bels, 1995). Despite specialisation of the tongue for chemoreception, these cycles in scleroglossans show similar kinematic profiles to those of *A. stellio*. Again, this suggests a basic ancestral pattern for all lizards that has been at least partially retained in highly derived species such as lacertid lizards.

Not all lower tetrapods use lingual intraoral transport. In *Varanus* sp. (Smith, 1982, 1986), intraoral transport cycles are composed of an inertial thrust of the craniocervical complex accompanied by fast opening of the mouth, followed by fast closing. Both the FO (40 ms) and FC (60 ms) phases are shorter than in *A. stellio* (FO, 70 ms; FC, 80 ms). A similar situation is present in *Caiman crocodilus* (Cleuren and De Vree, 1992). The short duration of both the FO and FC phases in these two species appears to be an adaptation to inertial feeding.

Data from the rhynchocephalian *Sphenodon punctatus* are useful for comparisons among lepidosaurians. The intraoral transport stage is composed of specific reducing and repositioning movements (Gorniak *et al.* 1982). Both reducing and repositioning movements consist of SO, FO, FC and SC phases. The SC phase in *Sphenodon punctatus* consists of a dorsal and propalinal shift of the lower jaw producing a unique shearing bite. No quantitative data concerning durations or maximal values of these phases are given by the authors. However, their general description of the cycles indicates similarities with those of *A. stellio*. If the intraoral transport cycle of *Sphenodon punctatus* is considered to be plesiomorphic with respect to that of *A. stellio*, the intraoral transport cycles in *A. stellio* can be considered to be the result of retention of a primitive set of characters. However, to test this hypothesis, electromyographical data from the jaw and hyolingual muscles during the intraoral transport stage in *A. stellio* should be compared with data already obtained for *Sphenodon punctatus* (Gorniak *et al.* 1982).

Swallowing cycles

Quantitative data for swallowing cycles are scarce. The only agamid for which data exist is *Uromastix aegyptius* (Throckmorton, 1980). Differences between the swallowing cycles of *U. aegyptius* and *A. stellio* are mainly in the duration of the SO and the stationary phases. The stationary phase is of greater importance in *U. aegyptius* than in *A. stellio*. These differences might be related to the different types of food eaten by the herbivorous *U. aegyptius*. Tongue protraction (which

corresponds to the SO phase) is apparently not as extensive in *U. aegyptius* as in *A. stellio*. Pieces of vegetable matter are probably easier to swallow (presumably due to their 'one bite' size).

For iguanids, quantitative data exist only for *Oplurus cuvieri* (Delheusy and Bels, 1992). Comparison of swallowing cycles between *A. stellio* and *O. cuvieri* indicates that, although the absolute timing of events is rather different, both animals apparently use a similar strategy to swallow their prey.

In scleroglossan lizards, swallowing of prey is performed by combined movements of the jaws and hyolingual apparatus (Smith, 1984, 1986; Goosse and Bels, 1992; Urbani and Bels, 1995). Although differences in tongue structure between scleroglossans (slender, elongated tongues) and iguanian lizards such as *A. stellio* (thick, fleshy tongue) result in differences in maximal gape values, the gape profile of the swallowing cycles is similar in both groups (compare Fig. 4, this study, with Fig. 8 in Urbani and Bels, 1995).

In *Varanus* sp. (Smith, 1986), swallowing or hyobranchial packing occurs during small inertial thrusts and during lip-licking cycles that follow ingestion of the prey. Because of the highly specialised tongue structure in this species, the role of the tongue during swallowing in *A. stellio* is performed by the hyobranchial apparatus in *Varanus* sp. However, the hyobranchial packing operates in an analogous way to the tongue cycles in *A. stellio*. In *Caiman crocodilus* (Cleuren and De Vree, 1992) a similar situation occurs. Apparently, the development of inertial feeding has increased the importance of the hyoid apparatus during swallowing. However, the primitive antero-posterior movement of the hyolingual apparatus has been retained in these species.

In *Sphenodon punctatus*, swallowing or terminal movements are composed of clear SO, FO, FC and SC/PS phases. Furthermore, terminal movements are characterised by a wider opening of the mouth and for a longer interval (Gorniak *et al.* 1982). This differs from the swallowing cycles in *A. stellio*, which are characterised by a smaller gape and the absence of a SC/PS phase. However, similarities do occur regarding tongue movements. The tongue movements during swallowing in *A. stellio* might thus be considered to be the retention of a primitive set of characters.

Swallowing in *A. stellio* and lizards in general appears to be mainly determined by tongue movements. These tongue movements have probably been retained from an ancestral feeding cycle. The jaw movements in *A. stellio* during swallowing appear to be determined by tongue movements rather than by an active component of the swallowing cycle. Electromyographical analysis of both jaw and tongue muscles during swallowing cycles could confirm this proposal.

Effects of prey type and size

The effects of different food items on the feeding cycle in *Anolis equestris* were examined by Bels and Baltus (1989). In this study, the effects of the size and mass of the food items on the number of cyclic movements were examined. The number of transport cycles was correlated with the size of the

prey, but the number of reduction cycles showed no relationship to the size or mass of the food item. During feeding, the mechanical resistance of food items apparently affects the number of cyclic movements. Surprisingly, Urbani and Bels (1995) did not find any significant effect of prey type on the kinematic variables (except for the time to maximal gape) in *Zonosaurus laticaudatus*.

In *A. stellio*, not only the size but also the structure, mass and form of the prey play an important role in the modulation of the intraoral transport cycles. The effect of a larger prey (compare standard with large grasshoppers; Table 4) is translated into an increase in the duration of the gape cycle, without a significant increase in maximal excursion of the jaws and tongue. Although the type of prey is the same, they differ in length, mass and hardness. The effect of a different prey type (grasshopper, mealworm or cricket), however, is a modulation of both maximal excursions, the time to maximal jaw displacements and the duration of the SOI phase. Here, the prey differ in mass, hardness and form. The duration of the total cycle and of the different phases (size effect) as well as the absolute excursions of jaws and tongue (prey type effect) are modulated.

Urbani and Bels (1995) found no effect of prey type on the swallowing cycles of *Zonosaurus laticaudatus*. In *A. stellio*, prey type and size do affect the kinematic variables during swallowing, but to a lesser extent than during intraoral transport. This might be because mechanical reduction of the prey has occurred during the previous intraoral transport stage. However, a thorough investigation of the effects of prey size and type during swallowing is needed and these conclusions can only be considered as preliminary.

On the basis of our results, we suggest that a single central pattern generator could be responsible for both intraoral transport and swallowing cycles, at least as far as tongue movements are concerned. However, modulation of this pattern can involve different aspects of the gape and tongue cycle and active feedback from the jaw and hyolingual apparatus is therefore likely to occur. An observation supporting this proposal is that while different individuals differ in their kinematics, their responses to specific prey types are similar. The effects of modulation can be seen most clearly in the SO phase of the cycle (the most variable phase of a cycle). Information regarding the prey item (structure, mass, state of reduction of the prey) is probably collected during the SC/PS phase (or stationary phase for swallowing cycles) of the previous cycle and the SO phase of the cycle in progress (see Bramble and Wake, 1985). How such information regarding the prey is gathered and the sensory receptors that are used remain to be studied.

Evolutionary implications

As discussed above, the kinematics of the intraoral transport cycles of lizards share many similarities and have a number of features in common with the Bramble and Wake (1985) model. Swallowing cycles seem to be more varied but share several characteristics with intraoral transport cycles, especially with

respect to tongue movements. Thus, most results justify the Bramble and Wake (1985) model of a generalised feeding cycle.

In general, our results also support the Bramble and Wake (1985) model. However, one major difference lies in the duration of the SOII phase. Whereas the model proposes a longer duration of the SOII phase than the SOI phase, our results indicate that the reverse situation applies. However, note that subdivision of the SO phase into SOI and SOII phases is not always straightforward. For all food types examined, the SOI phase was invariably longer than the SOII phase during intraoral transport. Only for prey capture cycles did the SOII phase last longer than the SOI phase. However, the Bramble and Wake model predicts that the duration of the SOII phase will increase for heavy prey items, and this is supported by our results. The relative duration of the SOII phase for standard food items was about 20% of the total cycle duration (SOI 32%), whereas for large grasshoppers the relative duration of the SOII phase increases to 34% of the total cycle (SOI 43%). In addition, for relatively light prey items, the SOII phase decreases in importance and is absent during mealworm intraoral transport cycles. The relative duration of the SOI phase is also increased when eating large prey items and thus the whole of the SO phase is affected by the size and mass of the food. This might be explained by an increase in the frictional forces between the tongue and the prey during the SOI phase (related to the forward movement of the hyolingual complex under the food, see Delheusy and Bels, 1992). In *U. aegyptius* (Throckmorton, 1976), the SO phase has less importance, possibly related to the much lighter (and thus easier to transport) vegetable diet. A link between the duration of the SO phase and modulation of the feeding cycle is thus clearly present.

Reilly and Lauder (1990) proposed five derived characters of the prey transport cycle for all amniotes and two synapomorphic characters for all tetrapods. Our results show that *A. stellio* possesses the two synapomorphic characters of tetrapods, but does not show all five derived characters proposed for amniotes. In *A. stellio*, inertial feeding does not play a significant role in the intraoral transport of the prey. More importantly, the recovery phase of the hyolingual apparatus does not take place during the SO phase. Recovery, if any, takes place during the SC/PS phase in *A. stellio*. The SO phase consists of an active protraction of the tongue under the prey. As far as the extensive food processing is concerned, our results agree with those of Reilly and Lauder (1990). Intraoral transport is composed of a number of cycles, all relating to the reduction, repositioning or transport of the prey to the back of the oral cavity.

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