

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

available at www.sciencedirect.comjournal homepage: www.intl.elsevierhealth.com/journals/arob

Jaw and hyolingual muscle activity patterns and bite forces in the herbivorous lizard *Uromastix acanthinurus*

Anthony Herrel^{a,b,*}, Frits De Vree^b

^a Département d'Ecologie et de Gestion de la Biodiversité, Muséum National d'Histoire Naturelle, 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France

^b Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerp, Belgium

ARTICLE INFO

Article history:

Accepted 4 May 2009

Keywords:

Lizard
Feeding
Electromyography
Bite force
Model
Motor control

ABSTRACT

Uromastix lizards are basal agamid lizards that are characterized by an herbivorous diet and a robust akinetic skull. Recently, lizards in general, and *Uromastix* lizards in particular, have become a model system for mechanical analyses of skull function. However, quantitative models of skull function are hampered by a lack of knowledge on the activation patterns of jaw and hyolingual muscles. Moreover, *in vivo* bite force or strain data, essential to test the validity of these modelling efforts, are lacking. Here we provide data on the muscle activation patterns and bite forces in the lizard *Uromastix acanthinurus*. Our results show that muscle recruitment patterns during intra-oral transport and swallowing, are qualitatively similar to those observed for other lizards. Whereas during the slow opening phase the hyolingual muscles show a pronounced activity, the fast opening phase is characterised by strong activity in the jaw opener and the tongue and hyoid retractors. During fast closing the jaw closers become active and at the end of this phase, the jaw closers become silent momentarily before showing a renewed and strong activity during the slow closing/power stroke phase. Measurements of bite forces indicate bite force levels similar to those of agamid lizards of similar size, and similar to those predicted based on recent modelling efforts. These data should allow further refinement and validation of recently published models of biting in lizards of the genus *Uromastix*.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Lizards are a model system to examine the evolution of cranial morphology and function as they are characterized by an enormous diversity in cranial form.^{1,2} Moreover, lizard skulls differ markedly in the degree of cranial kinesis present, ranging from completely akinetic skulls in some iguanians to skulls displaying extensive intracranial movements as observed in geckoes and cordylids.^{1–4} Recently, modelling approaches have been undertaken to assess the functional role of cranial kinesis⁵ (i.e. intracranial movements), the role

of cranial sutures in dissipating bite forces,⁶ and to infer cranial function and performance.^{7–11} Understanding the mechanical consequences of different skull designs on cranial performance is crucial to obtain insights into the selective forces that underlie the observed diversity in lizard cranial form. Theoretical models such as finite element models are especially insightful in this respect as they may provide windows onto the evolution of skull form by allowing analyses of extinct forms.^{12–14} However, the usefulness of such models may be limited if they cannot be validated first for extant organisms.^{15,16}

* Corresponding author. Tel.: +33-140798120; fax: +33-140793773.

E-mail address: anthony.herrel@mnhn.fr (A. Herrel).

0003-9969/\$ – see front matter © 2009 Elsevier Ltd. All rights reserved.

doi:10.1016/j.archoralbio.2009.05.002

Recently, lizards of the genus *Uromastix* have become a model for the analysis of cranial form and function. Although *Uromastix* is a good model system for functional analyses of lizard skulls given the availability of data on cranial structure and jaw adductor morphology,^{8,9,17} the data needed to realistically model cranial function are still lacking. One of the issues associated with the modelling of biting is how to scale muscle physiological cross sectional areas (PCSA) to obtain muscle forces. Although models with muscle forces scaled simply to PCSA can provide insights into some questions,¹⁸ it has recently been argued that scaling muscle forces relative to activation levels may be crucial in order to obtain realistic model outputs.¹⁶ However, despite some excellent earlier electromyographic work on *Uromastix aegyptius*,^{19–21} no quantitative data on jaw muscle activation patterns in *Uromastix* lizards are available in the literature. In addition to the aforementioned limitation, another potential drawback of using finite element models of cranial function in lizards is the overall lack of strain data needed to validate model output. However, the output of models mimicking biting may be validated indirectly by calculating bite forces and comparing these to bite force data recorded *in vivo*.^{10,22} Unfortunately, bite force data for *Uromastix* needed to validate such models have not been reported. As the jaw system in *Uromastix* is characterized by the presence of a unique m. pterygoideus externus published bite force estimates for closely related agamid lizards might not provide an appropriate comparison,⁸ but this needs to be tested empirically.

The goals of this study are to present a quantitative summary of the jaw and hyolingual muscle activation patterns in the herbivorous lizard *Uromastix acanthinurus*^{23,24} feeding on plant and animal prey. Additionally we present *in vivo* bite forces and compare them to bite force measurements for closely related agamid lizards of similar size, and to those obtained by recent modelling efforts.¹⁰ In addition to providing insights into the function and control of the jaw and hyolingual musculature in a highly specialised herbivorous lizard, these data can also be used to refine existing theoretical models of cranial function in lizards.

2. Materials and methods

2.1. Specimens

Four adult specimens (SVL: 162 ± 2 mm; mass 141 ± 10 g; mean \pm S.D.) of the species *U. acanthinurus* were used in the electromyographic experiments. All specimens were obtained from a commercial dealer. The animals were kept in a glass vivarium on a 12 h light/dark cycle and were offered water and food consisting of endive, salad, tomatoes, banana, and various other fruits and vegetables twice weekly. The environmental temperature varied from 35 °C during the day to 25 °C at night. An incandescent bulb provided the animals with a basking place at a higher temperature (60 °C). Two preserved specimens obtained from the Museum for Central Africa, Tervuren, Belgium, were dissected and stained²⁵ to study all jaw and hyolingual muscles.^{8,9,17} Drawings were made of all stages of the dissection using a Wild M3Z dissecting microscope with attached camera lucida.

2.2. Bite forces

Six adult *U. acanthinurus* (SVL: 159 ± 25 mm; cranial length: 31.41 ± 4.03 mm), housed at the Antwerp Zoo were used to measure bite forces. *In vivo* bite forces were measured using an isometric Kistler force transducer (type 9203, range ± 500 N; Kistler, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5995A, Kistler, Switzerland).²⁶ The place of application of bite forces was standardized for all animals by aligning the jaws with a metal stop mounted on the transducer.²⁶ Measurements were repeated five times for each animal, with an inter-trial interval of at least 30 min during which animals were placed in an incubator at 36 °C. The maximal value obtained during a recording session was considered to be the maximal bite force for that individual. For comparative purposes, data for *U. acanthinurus* were compared to a data set including 87 individuals of nine different species of agamids (*Amphibolurus muricatus*, *Chlamydosaurus kingii*, *Ctenophorus cristatus*, *Ctenophorus gibba*, *Ctenophorus nuchalis*, *Ctenophorus pictus*, *Laudakia stellerio*, *Pogona vitticeps*, *Trapelus pallida* and *Tympanocryptes lineatus*). Lizards are typically eager to bite when held and were stimulated to bite the transducer by gently tapping the sides of the jaws. This typically resulted in strong and prolonged biting.

2.3. Electromyographic recordings and analysis

The animals used in the electromyographic experiments were anaesthetized using an intramuscular injection of ketamine (125 mg/kg body mass) before electrode implantation. Bipolar electrodes (50 cm long) were prepared from Teflon-insulated 0.065 mm Ni-Cr wire. The insulation was removed at the tip, exposing 1 mm of electrode wire. The electrodes were implanted percutaneously into each muscle belly using hypodermic needles with 2 mm of the electrode bent back as it emerged from the needle barrel. During the experiments electrodes were placed in the following muscle groups: (1) jaw closers, including the musculus adductor mandibulae externus (superficial posterior, and profundus parts; MAMESP and MAMEP), and the musculus pterygoideus (medial and externus parts; MPtmed and MPttext); (2) jaw openers: the musculus depressor mandibulae (MDM); (3) hyolingual muscles including the tongue protractor (the musculus genioglossus, MGG), the hyoid protractor (the musculus mandibulohyoideus 2, MMH2), the tongue retractor (the musculus hyoglossus, MHG), and the hyoid retractors (the musculus sternohyoideus, MSH; the musculus omohyoideus, MOH). Electrode placement was confirmed on dorsoventral and lateral X-rays taken after electrode implantation.

Electrodes were soldered into connector pins and mounted in a female amphenol 64-pin connector that could be plugged into a cable with a male connector leading to the amplifiers. Electromyographic signals were amplified 10,000 times with Tektronix 26A2 differential preamplifiers (bandwidth 100 Hz to 10 kHz) and Honeywell Accudata 117 d.c. amplifiers and recorded on a Honeywell 96 FM 14-channel tape recorder (medium bandpass) at a speed of 19.05 cm/s. The recorded EMG signals were digitized at 10 kHz using a Keithley DAS series 500 12-bit A/D converter. After digitization, the signals

were integrated following the procedure of Beach and co-workers²⁷ and the number of spikes (S) as well as the average amplitude (A) and mean number of spikes multiplied by the average amplitude ($S \times A$) were calculated. Muscles were considered active if the signal level was higher than three times the noise level determined during periods of no activity in between recording sessions.

In total, five recording sessions were performed, each consisting of several feeding sequences. The results from two of these recording sessions (from two different animals) were analyzed quantitatively. These two recording sessions were

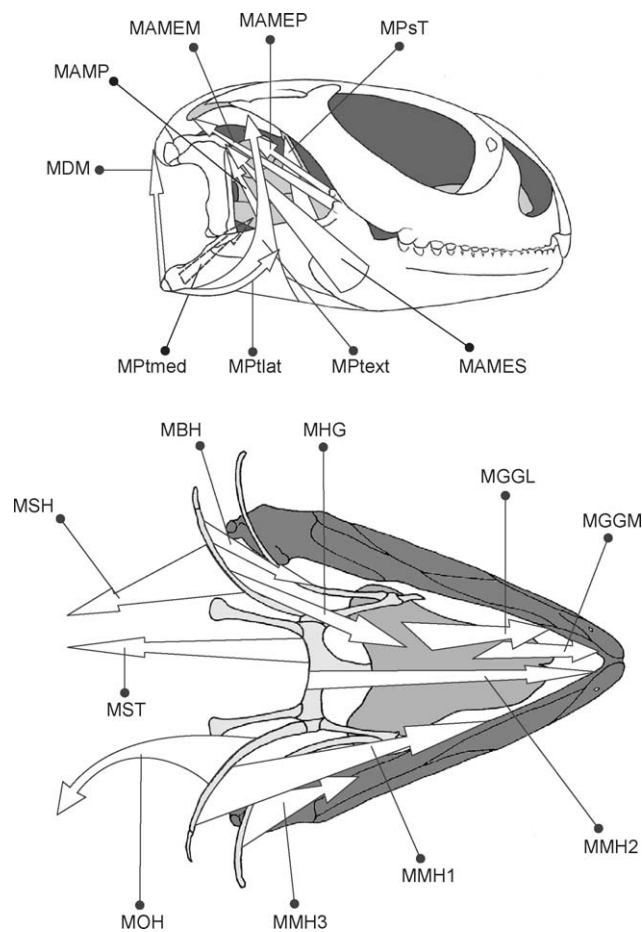


Fig. 1 – Schematic representation of jaw and hyolingual muscles of *U. acanthinurus*. (A) Lateral view of the skull; (B) ventral view of the lower jaw and the hyolingual apparatus. Arrows indicate the major jaw and hyolingual muscles and their predominant lines of action. MAMEM, m. adductor mandibulae externus medialis; MAMEP, m. adductor mandibulae externus profundus; MAMES, m. adductor mandibulae externus superficialis; MAMP, m. adductor mandibulae posterior; MBH, m. branchiohyoideus; MDM, m. depressor mandibulae; MGGL, m. genioglossus lateralis; MGGM, m. genioglossus medialis; MHG, m. hyoglossus; MMH1, MMH2, MMH3, m. mandibulohyoideus 1, 2, 3; MOH, m. omohyoideus; MPst, m. pseudotemporalis; MPtext, m. pterygoideus externus; MPtlat, m. pterygoideus lateralis; MPtmed, m. pterygoideus medialis; MSH, m. sternohyoideus; MST, m. sternothyroideus.

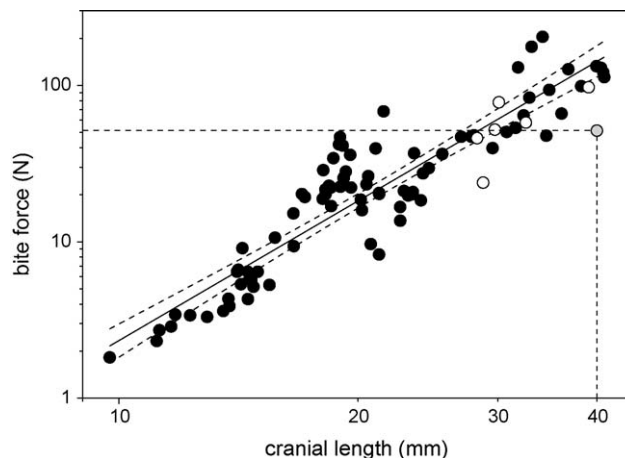


Fig. 2 – Graph illustrating the relationship of bite force to cranial length in agamid lizards. Bite forces for *Uromastix* are represented by open circles; closed circles represent a variety of agamid lizard species (see Section 2). Bite forces in *Uromastix* are similar to those of agamid lizards of similar head length. Indicated is the regression line plus the 95% confidence limits for agamid lizards. The grey symbol indicates the predicted bite force for *U. hardwickii* based on finite element models.¹⁰

chosen because they represented the maximal number of jaw and hyolingual muscles implanted. The results from the other recording sessions were used in a qualitative assessment of muscle recruitment patterns only. In the first recording session, results were obtained from several complete feeding sequences. This session included a total of four prey capture (endive), 38 intraoral transport (22 endive, 16 grasshopper) and 40 (16 endive, 24 grasshopper) swallowing cycles. Although 10 electrodes were implanted only seven of these (and the pulse from the X-ray camera) could be recorded simultaneously. Consequently, during this first recording session, activity patterns from the right MDM, the right and left MAMESP, the right and left MPtext, the right MGG, and the right MSH were recorded and quantified. The second recording session consisted of several feeding sequences during which activity patterns of the right and left MDM, the left MAMEP, the right MPtmed, the right MMH2, and the right MOH were recorded. In total 15 endive intraoral transport, and 10 endive swallowing cycles were quantified.

2.4. Quantification of recruitment patterns

After digitisation, electromyographic traces were first subdivided into separate bite cycles. Within a single cycle, however, muscle activity patterns were typically subdivided into three activity bursts on the basis of abrupt amplitude differences. For each muscle, the onset and the duration of all bursts within one cycle (and for all cycles analyzed) were recorded. Onset variables are always expressed relative to the beginning of the cycle which is defined by the onset of the first muscle to become active (typically the tongue protractor). As the number of spikes multiplied by the mean amplitude ($S \times A$) is a measure of the intensity of muscle recruitment,^{28,29}

further analyses of intensity-related variables were primarily based on this variable and mean recruitment levels were calculated for each bite. Next, the maximal recruitment values recorded for each muscle within a recording session were extracted and used to normalise muscle recruitment data.

Recruitment levels for each muscle are therefore expressed as a percentage of their maximal activity.

All experiments and procedures were approved by the institutional animal care and use committee at the University of Antwerp.

Table 1 – Average onset and duration times and intensity-related variables of jaw and hyolingual muscle activity during endive intraoral transport.

| Muscle | Burst | Burst presence (%) | Onset (ms) | | Duration (ms) | | Average intensity (%) | | |
|-------------|-------|--------------------|------------|--------|---------------|--------|-----------------------|-------|-------|
| | | | Mean | ±S.D. | Mean | ±S.D. | Mean | ±S.D. | |
| R. MDMt | Pre | 5 | 10 | – | 20 | – | AVG S × A | 39.29 | 18.03 |
| | Main | 96 | 495.24 | 200.42 | 82.86 | 20.77 | | | |
| | Post | 82 | 701.11 | 228.70 | 73.33 | 29.90 | | | |
| L. MDM | Pre | 7 | 40 | – | 20 | – | AVG S × A | 72.76 | 20.60 |
| | Main | 100 | 716.67 | 228.93 | 69.33 | 18.70 | | | |
| | Post | 20 | 746.67 | 90.74 | 26.67 | 11.55 | | | |
| R. MAMESP | Pre | 82 | 431.11 | 232.65 | 83.33 | 64.26 | AVG S × A | 31.80 | 24.97 |
| | Main | 95 | 600 | 207.94 | 160.48 | 83.34 | | | |
| | Post | 36 | 796.25 | 300.76 | 110 | 59.04 | | | |
| L. MAMESP | Pre | 95 | 493.33 | 212.89 | 118.57 | 106.17 | AVG S × A | 52.88 | 25.87 |
| | Main | 95 | 630.48 | 195.43 | 149.52 | 62.57 | | | |
| | Post | 27 | 843.33 | 299.51 | 143.33 | 87.33 | | | |
| L. MAMEP | Pre | 80 | 287.50 | 287.84 | 93.33 | 65.13 | AVG S × A | 16.97 | 25.58 |
| | Main | 100 | 772.67 | 241.53 | 86.00 | 43.72 | | | |
| | Post | 53 | 923.75 | 282.84 | 44.00 | 24.54 | | | |
| MPtmed | Pre | 47 | 383.33 | 232.45 | 98.33 | 56.36 | AVG S × A | 50.37 | 26.03 |
| | Main | 100 | 770.07 | 222.73 | 128.00 | 62.24 | | | |
| | Post | 47 | 718.57 | 320.59 | 41.67 | 31.25 | | | |
| RMptext | Pre | 32 | 400.00 | 194.94 | 24.29 | 7.87 | AVG S × A | 36.85 | 17.83 |
| | Main | 95 | 649.52 | 231.64 | 118.57 | 61.75 | | | |
| | Post | 32 | 748.57 | 366.03 | 111.43 | 57.57 | | | |
| L. MPttext. | Pre | 13 | 366.67 | 321.92 | 23.33 | 5.77 | AVG S × A | 12.49 | 20.53 |
| | Main | 100 | 609.09 | 227.78 | 103.63 | 95.55 | | | |
| | Post | 60 | 726.92 | 271.09 | 133.85 | 55.61 | | | |
| R. MGG | Pre | 0 | – | – | – | – | AVG S × A | 43.67 | 13.05 |
| | Main | 100 | 40 | 0 | 509.55 | 101.91 | | | |
| | Post | 95 | 543.33 | 219.44 | 209.68 | 78.27 | | | |
| MHG | Pre | 20 | 123.33 | 75.72 | 126.67 | 100.17 | AVG S × A | 45.89 | 26.97 |
| | Main | 100 | 205.67 | 131.49 | 538.67 | 170.83 | | | |
| | Post | 67 | 777.00 | 240.93 | 116.00 | 36.58 | | | |
| MMH2 | Pre | 13 | 10 | 0 | 130 | 50 | AVG S × A | 56.22 | 22.39 |
| | Main | 100 | 131.11 | 118.16 | 530.67 | 164.38 | | | |
| | Post | 27 | 674.55 | 183.27 | 64.55 | 29.45 | | | |
| R. MSH | Pre | 36 | 188.75 | 103.98 | 83.75 | 45.02 | AVG S × A | 15.92 | 15.75 |
| | Main | 100 | 494.55 | 195.66 | 96.36 | 38.24 | | | |
| | Post | 82 | 677.22 | 212.21 | 77.22 | 37.86 | | | |
| L. MOH | Pre | 53 | 345.00 | 231.01 | 175.00 | 146.39 | AVG S × A | 45.71 | 19.42 |
| | Main | 100 | 707.33 | 232.67 | 136.00 | 71.39 | | | |
| | Post | 67 | 787.00 | 211.35 | 56.00 | 35.65 | | | |

Onset variables were measured from the beginning of the cycle to the onset of the muscle burst. Different bursts in the same muscle within one cycle are referred to as pre, main and post bursts. The main burst is the first activity burst in which muscles are fully active; often this burst is preceded by an activity burst of low intensity (pre) and followed by a burst of either high or low intensity (post). Burst presence indicates the number of times that burst was present in the analyzed sequences (%occurrence). The average intensity values are averaged over the total cycle and expressed relative to the maximal value recorded for each muscle in all analyzed sequences. (N = 22 for the R. MDM, R. MAMESP, L. MAMESP, L. MPttext, R. MPttext., R. MGG and R. MSH; N = 15 for the L. MDM, L. MAMEP, MPtmed, MHG, MMH2, and the MOH). MAMESP, m. adductor mandibulae externus profundus; MAMESP, m. adductor mandibulae externus superficialis posterior; MDM, m. depressor mandibulae; MGG, m. genioglossus; MHG, m. hyoglossus; MMH2, m. mandibulohyoideus 2; MOH, m. omohyoideus; MPttext, m. pterygoideus externus; MPtmed, m. pterygoideus medialis; MSH, m. sternohyoideus; S × A, number of spikes multiplied by average amplitude.

3. Results

3.1. Morphology

The cranial morphology of lizards of the genus *Uromastix* is relatively well studied. The dentition,^{30–32} cranial osteology,^{19,33–35} and the morphology of the hyoid apparatus^{36–38} have been described previously in some detail. As described by Throckmorton¹⁹ and Herrel and De Vree³⁹ the skull of *Uromastix* shows clear streptostyly (=antero-posterior rotation of the quadrate relative to the brain case), but no meso- or metakinesis (respectively, movements of the snout unit relative to the parietal, and movements of the brain case relative to the dermal cranial skeleton). The muscular system of the jaw- and hyolingual apparatus has been studied extensively^{8,7,19,40–44} and consequently only a schematic representation of these muscles is represented in Fig. 1. Characteristic for lizards of the genus *Uromastix* is the presence of a large and well developed m. pterygoideus externus which wraps around the lower jaw and attaches at the lateral aspect of the upper temporal bar (Fig. 1).

3.2. Bite force

Bite forces in *U. acanthinurus* were high (59.2 ± 25.6 N) but not significantly different from those recorded for agamids of similar head size (slopes: $F_{1,89} = 0.001$; $P = 0.98$). Bite forces predicted for *U. hardwickii* based on theoretical models fell

outside the 95% confidence limits calculated for the in vivo bite force data for agamids and *Uromastix* combined and are thus significantly different (Fig. 2).

3.3. Electromyography

Three distinct stages can be recognised during feeding in *U. acanthinurus*: food prehension, intraoral transport and swallowing.^{39,45,46} In the description of feeding cycles we use the terminology of Bramble and Wake.⁴⁷ During intraoral transport, five phases can be recognised within one cycle, based on the movements of jaws and tongue: slow opening (SO), sometimes divisible into phases I and II (SOI, SOII), fast opening (FO), fast closing (FC), and a slow close/power stroke (SC/PS) phase. During swallowing no SOI and SOII phases are discernable. Additionally, as the food item is no longer situated in between the teeth, no SC/PS phase is present. However, a stationary phase, where no jaw or tongue movements occur, is present during swallowing. As *Uromastix* is a dedicated herbivorous lizard, the description of the muscle activity patterns during the different feeding stages is based on endive feeding sequences. Below, a brief description of the muscle activation patterns during the different feeding stages is provided.

3.4. Food prehension

The first muscles to become active during food prehension (i.e. food 'capture') are the hyoid protractor (MMH2), the tongue

Table 2 – Average onset and duration times and intensity-related variables of jaw and hyolingual muscle activity during grasshopper intraoral transport.

| Muscle | Burst | Burst presence (%) | Onset (ms) | | Duration (ms) | | Average intensity (%) | | |
|-----------|-------|--------------------|------------|---------|---------------|--------|-----------------------|-------|-------|
| | | | Mean | ±S.D. | Mean | ±S.D. | Mean | ±S.D. | |
| R. MDM | Pre | | 167.5 | 182.64 | 30 | 18.27 | AVG S × A | 26.21 | 16.91 |
| | Main | | 522.5 | 308.15 | 62.63 | 28.74 | | | |
| | Post | | 733.33 | 346.70 | 58.00 | 47.69 | | | |
| R. MAMESP | Pre | 88 | 498.57 | 312.36 | 30.71 | 26.15 | AVG S × A | 50.00 | 25.24 |
| | Main | 100 | 591.25 | 316.48 | 67.50 | 43.59 | | | |
| | Post | 94 | 659.33 | 347.76 | 129.33 | 63.52 | | | |
| R. MPtext | Pre | 13 | 830 | – | 15.00 | 7.07 | AVG S × A | 44.88 | 29.53 |
| | Main | 100 | 618.13 | 323.51 | 81.25 | 67.22 | | | |
| | Post | 75 | 719.17 | 368.99 | 169.17 | 181.48 | | | |
| L. MPtext | Pre | 38 | 168.00 | 286.304 | 36.67 | 26.58 | AVG S × A | 9.14 | 6.55 |
| | Main | 100 | 595.63 | 323.60 | 93.13 | 74.45 | | | |
| | Post | 75 | 775.00 | 307.73 | 173.33 | 180.52 | | | |
| R. MGG | Pre | 6 | 50 | – | 140 | – | AVG S × A | 45.76 | 26.89 |
| | Main | 100 | 88.75 | 102.32 | 508.13 | 300.47 | | | |
| | Post | 38 | 600 | 378.42 | 83.33 | 33.86 | | | |
| RMSH | Pre | 13 | 40 | – | 25 | 7.07 | AVG S × A | 26.88 | 27.37 |
| | Main | 100 | 525.63 | 311.40 | 93.75 | 28.49 | | | |
| | Post | 100 | 668.75 | 332.44 | 109.38 | 79.79 | | | |

Onset variables were measured from the beginning of the cycle to the onset of the muscle burst. Different bursts in the same muscle within one cycle are referred to as pre, main and post bursts. The main burst is the first activity burst in which muscles are fully active; often this burst is preceded by an activity burst of low intensity (pre) and followed by a burst of either high or low intensity (post). Burst presence indicates the number of times that burst was present in the analyzed sequences (%occurrence). The average intensity values are averaged over the total cycle and expressed relative to the maximal value recorded for each muscle in all analyzed sequences. ($N = 16$ for all muscles). $S \times A$, number of spikes multiplied by average amplitude. See Table 1 for definitions of muscle abbreviations.

protractor (MGG) and somewhat later the tongue retractor (MHG). The activity of these muscles gradually increases during the SOI (MMH2) and SOII (MGG, MHG) phases. About halfway through the SO phase, at the transition from SOI to SOII, some jaw closers such as the medial pterygoid (MPtmed) may show a short activity burst, and the activity in the MMH2 decreases. During the SOII phase, the tongue is protruded beyond the anterior jaw margin as observed in other agamid lizards.⁴⁸⁻⁵¹ At the end of the SOII phase, the MGG and MHG

become silent, and shortly after the jaw opener (MDM) shows a distinct activity burst initiating the FO phase. Simultaneous with this burst in the MDM, a renewed pronounced activity in the MHG and an activity burst in the hyoid retractors (the MSH and MOH) cause tongue retraction. Remarkably, the activity of one of the jaw closers (the MAMESP) consistently starts about halfway through the FO phase. The other jaw closers (MAMEP, MPttext, MPtmed) become active at the end of the FO phase and show a single, long activity burst, thus closing the jaws.

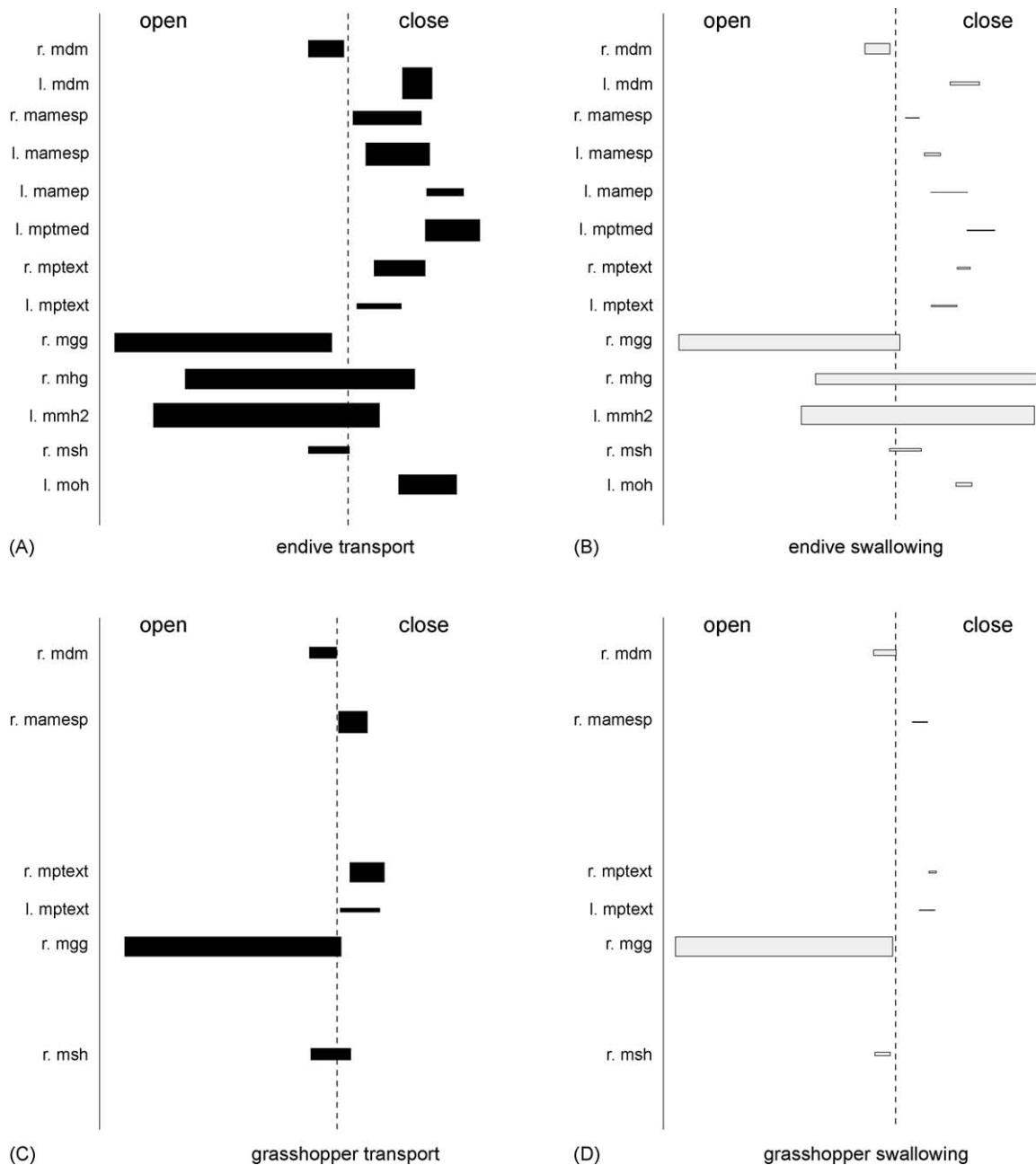


Fig. 3 – Summary of muscle activity patterns during intra-oral transport (A and C) and swallowing (B and D) in *U. acanthinurus* while eating endive (A and B) and grasshoppers (C and D). Only the onset and duration of the main activity burst in each muscle are represented for reasons of clarity. The vertical dashed line represents maximal gape. Note how the activation levels of the muscles decrease considerably during swallowing resulting in lower magnitude and duration of the recruitment. Unexpectedly, activation patterns are very similar for endive and grasshoppers suggesting only limited modulation of jaw muscle activity relative to food type in *U. acanthinurus*. The height of the bars is proportional to the recruitment level of the muscle.

Although no distinct SC/PS phase is observed during prehension cycles, the MAMEP tends to become active somewhat later than the other jaw closers. During the FC phase the MDM and the MGG usually show an activity of low intensity lasting for the entire duration of this phase.

3.5. Intra-oral transport (Figs. 3 and 4; Tables 1 and 2)

Intra-oral transport cycles are somewhat similar to capture cycles, but are characterized by the presence of a clear SC/PS phase. As during capture, the first muscles to become active are the hyoid protractor, the tongue protractor, and the tongue retractor (Tables 1 and 2). Again, these muscles show a gradual increase of activity causing simultaneous hyoid protraction, tongue protraction and tongue bulging. Activity in the MMH2 generally stops about halfway through the SO phase. Generally the activity in the jaw closers is of very low to low intensity during the SO phase. The transition from the SO to the FO phase is characterised by the absence of activity in both the MGG and the MHG, and the onset of activity in the MDM, and the hyoid retractors (MSH, MOH). After a short pause of about 30 ms (see Tables 1 and 2), the MHG shows a new, short but strong activity burst causing tongue retraction. At maximal gape most jaw closers (MAMESP, MPtext) become active simultaneously, and show a distinct activity burst during the FC phase. Both the MAMEP and the MPtmed become active somewhat later, coinciding with the onset of the SC/PS phase. At that moment, the other jaw closers become active again after a short pause (in between 20 and 60 ms) and show prolonged and strong activity throughout the SC/PS phase.

3.6. Swallowing (Figs. 3 and 5; Tables 3 and 4)

Swallowing cycles are distinct in comparison to both intraoral transport and capture cycles, and are characterised by the absence of a SC/PS phase, and a short FO phase. Muscle activity patterns are dominated by hyolingual muscles, and during late swallowing both the jaw opener and the jaw closers no longer show any activity (see Tables 3 and 4; burst presence). Additionally, the SO phase cannot be subdivided into separate SOI and SOII phases,³⁹ which is also reflected in the activity patterns of the jaw and hyolingual muscles. Again, activity in the MGG and the MMH2 initiates a cycle with the MHG becoming active somewhat later. Hyoid and tongue protractors show a gradually increasing activity level during the SO phase. During the first couple of swallowing cycles, the MDM still shows a short activity burst at the end of the SO phase. Similarly the jaw closers also show short activity bursts of low intensity (less than 5%) during the first couple of swallowing cycles. Later during the swallowing stage no jaw opener or closer activity is observed in the muscles sampled here. Similarly, the activity in the hyoid retractors decreases (see Tables 3 and 4; burst presence and average intensity), and may be absent during late swallowing (Figs. 3 and 5).

A comparison of the activation patterns illustrated in Fig. 3 suggests only marginal effects of food type on the jaw and hyolingual activity patterns during intraoral transport (see also Tables 1–4). Principal differences are situated in the onset of the hyoid retractor relative to maximal gape, being slightly later during grasshopper transport. During swallowing,

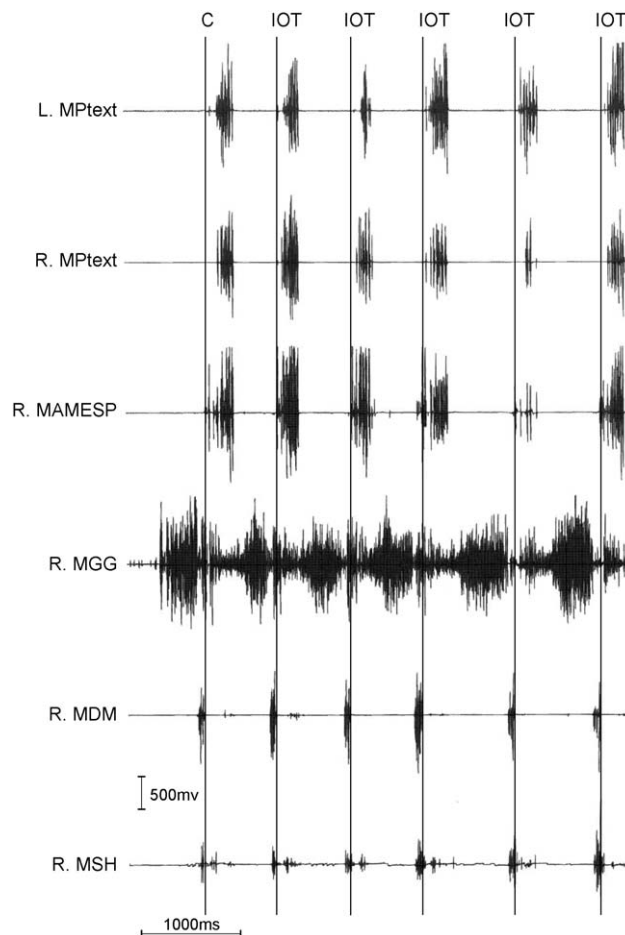


Fig. 4 – Representative electromyograms during intra-oral transport from the first recording session from an individual *U. acanthinurus* feeding on endive. Vertical lines indicate time of maximal gape. Note the near-simultaneous activation of left and right side MPtext and the double burst pattern in the hyolingual muscles. C, capture; IOT, intraoral transport; L, left; MAMESP, m. adductor mandibulae externus superficialis posterior; MDM, m. depressor mandibulae; MGG, m. genioglossus; MPtext, m. pterygoideus externus; MSH, m. sternohyoideus; R, right.

differences in activation patterns of the muscles are also small, but here the activity of the hyoid retractor during the swallowing of grasshoppers has shifted to an earlier onset.

4. Discussion

The overall muscle activity patterns in *U. acanthinurus* are qualitatively similar to those observed for other lizards. As in the closely related agamid *P. stellio*^{51,52} and the scincids *T. rugosa* and *C. zebra*^{53,54} jaw closers are generally activated bilaterally simultaneously and approximately during the same kinematic phases (FC and SC/PS phases). Thus, our results for this species generally support conclusions from previous studies,^{52,53} together suggesting a fairly simple motor pattern (but see^{55,56}). The results on the activation patterns of the

Table 3 – Average onset and duration times and intensity-related variables of jaw and hyolingual muscle activity during endive swallowing.

| Muscle | Burst | Burst presence (%) | Onset (ms) | | Duration (ms) | | Average intensity (%) | | |
|------------|-------|--------------------|------------|--------|---------------|--------|-----------------------|-------|-------|
| | | | Mean | ±S.D. | Mean | ±S.D. | Mean | ±S.D. | |
| R. MDM | Pre | 13 | 190 | 259.81 | 30 | 17.32 | AVG S × A | 25.06 | 29.83 |
| | Main | 54 | 518.46 | 136.37 | 58.46 | 29.96 | | | |
| | Post | 21 | 768.00 | 238.58 | 32.00 | 17.89 | | | |
| L. MDM | Pre | 10 | 840 | – | 20 | – | AVG S × A | 6.53 | 4.79 |
| | Main | 60 | 716.67 | 228.93 | 69.33 | 18.70 | | | |
| | Post | 0 | – | – | – | – | | | |
| R. MAMESP | Pre | 38 | 445.57 | 216.17 | 38.89 | 19.65 | AVG S × A | 1.23 | 1.57 |
| | Main | 50 | 611.67 | 162.08 | 32.50 | 27.01 | | | |
| | Post | 13 | 876.67 | 80.83 | 46.67 | 5.77 | | | |
| L. MAMESP | Pre | 25 | 571.67 | 94.96 | 61.67 | 18.35 | AVG S × A | 6.03 | 4.42 |
| | Main | 33 | 656.67 | 92.33 | 36.67 | 24.49 | | | |
| | Post | 17 | 795.00 | 133.04 | 82.50 | 74.11 | | | |
| L. MAMEP | Pre | 20 | 115.00 | 35.36 | 35.00 | 7.07 | AVG S × A | 0.52 | 0.35 |
| | Main | 30 | 690.00 | 170.88 | 50.00 | 34.64 | | | |
| | Post | 20 | 680.00 | 42.43 | 45.00 | 49.50 | | | |
| MPtmed | Pre | 40 | 640.00 | 280.83 | 17.50 | 9.57 | AVG S × A | 1.94 | 3.50 |
| | Main | 60 | 753.33 | 224.74 | 65.00 | 18.71 | | | |
| | Post | 20 | 875.00 | 219.20 | 35.00 | 7.07 | | | |
| RMptext | Pre | 0 | – | – | – | – | AVG S × A | 4.29 | 3.25 |
| | Main | 33 | 731.25 | 121.94 | 30.00 | 20.70 | | | |
| | Post | 8 | 800.00 | 212.13 | 25.00 | 7.07 | | | |
| L. MPtext. | Pre | 4 | 140.00 | – | 30.00 | – | AVG S × A | 3.27 | 3.69 |
| | Main | 29 | 674.29 | 109.07 | 60.00 | 66.08 | | | |
| | Post | 17 | 750.00 | 113.43 | 75.00 | 71.41 | | | |
| R. MGG | Pre | 8 | 40 | – | 140.00 | 28.28 | AVG S × A | 36.91 | 14.56 |
| | Main | 100 | 81.05 | 75.20 | 519.17 | 132.37 | | | |
| | Post | 42 | 550 | 159.30 | 64.00 | 49.95 | | | |
| MHG | Pre | 30 | 285.00 | 77.78 | 230.00 | 113.14 | AVG S × A | 24.99 | 18.25 |
| | Main | 100 | 403.00 | 309.52 | 516.00 | 380.42 | | | |
| | Post | 70 | 760.00 | 225.02 | 148.57 | 70.58 | | | |
| MMH2 | Pre | 30 | 110.00 | 81.85 | 36.67 | 15.28 | AVG S × A | 42.74 | 31.31 |
| | Main | 100 | 367.78 | 263.14 | 548.00 | 329.23 | | | |
| | Post | 40 | 992.50 | 240.47 | 50.00 | 28.28 | | | |
| R. MSH | Pre | 17 | 157.50 | 168.20 | 32.50 | 25.00 | AVG S × A | 5.35 | 8.39 |
| | Main | 88 | 574.76 | 153.87 | 74.76 | 41.79 | | | |
| | Post | 25 | 666.67 | 169.90 | 55.00 | 31.46 | | | |
| L. MOH | Pre | 20 | 640.00 | – | 25 | 21.21 | AVG S × A | 7.44 | 2.72 |
| | Main | 30 | 733.33 | 215.95 | 36.67 | 46.19 | | | |
| | Post | 10 | 1040.00 | – | 10 | – | | | |

Onset variables were measured from the beginning of the cycle to the onset of the muscle burst. Different bursts in the same muscle within one cycle are referred to as pre, main and post bursts. The main burst is the first activity burst in which muscles are fully active; often this burst is preceded by an activity burst of low intensity (pre) and followed by a burst of either high or low intensity (post). Burst presence indicates the number of times that burst was present in the analyzed sequences (%occurrence). The average intensity values are averaged over the total cycle and expressed relative to the maximal value recorded for each muscle in all analyzed sequences. (N = 24 for the R. MDM, R. MAMESP, L. MAMESP, L. MPtext, R. MPtext., R. MGG and R. MSH; N = 10 for the L. MDM, L. MAMEP, MPtmed, MHG, MMH2, and the MOH). S × A: number of spikes multiplied by average amplitude. See Table 3 for definitions of muscle abbreviations.

MPtmed are, however, not in accordance to previously published data obtained for the closely related species *Uromastix aegyptius*.²⁰ In the latter species the deep part of the pterygoid muscle (=MPtmed in this study) is only active during jaw opening when eating dog food, and during both opening and closing when feeding on slices of sweet potato tuber.²⁰ Together with the data reported here, this suggests

that the Mptmed is active during closing only when consuming tough food items such as sweet potato, endive, or grasshoppers. Based on our data, we suggest that this muscle typically functions as a true jaw closer and presumably also as quadrature stabiliser.²⁰ An additional role as protractor of the lower jaw²⁰ is not supported by our data and needs to be investigated further.

Table 4 – Average onset and duration times and intensity-related variables of jaw and hyolingual muscle activity during grasshopper swallowing.

| Muscle | Burst | Burst presence (%) | Onset (ms) | | Duration (ms) | | Average intensity (%) | | |
|-----------|-------|--------------------|------------|---------|---------------|--------|-----------------------|-------|-------|
| | | | Mean | ±S.D. | Mean | ±S.D. | Mean | ±S.D. | |
| R. MDM | Pre | 6 | 180 | – | 10 | – | AVG S × A | 13.28 | 4.71 |
| | Main | 19 | 503.33 | 180.37 | 53.33 | 5.77 | | | |
| | Post | 13 | 620 | 226.27 | 15 | 7.07 | | | |
| R. MAMESP | Pre | 31 | 502 | 180.19 | 18 | 13.04 | AVG S × A | 1.85 | 2.81 |
| | Main | 31 | 594 | 200.57 | 36 | 24.08 | | | |
| | Post | 6 | – | – | – | – | | | |
| R. MPtext | Pre | 6 | 530 | – | 10 | – | AVG S × A | 4.34 | 2.53 |
| | Main | 19 | 633.33 | 192.18 | 16.67 | 11.55 | | | |
| | Post | 6 | 910 | – | 20 | – | | | |
| L. MPtext | Pre | 19 | 120 | 156.205 | 26.27 | 15.28 | AVG S × A | 0.72 | 0.61 |
| | Main | 19 | 610 | 190.79 | 36.67 | 11.54 | | | |
| | Post | 6 | 910 | – | 60 | – | | | |
| R. MGG | Pre | 0 | – | – | – | – | AVG S × A | 45.26 | 11.61 |
| | Main | 100 | 36.67 | 13.71 | 511.25 | 131.65 | | | |
| | Post | 6 | 700 | – | 50 | – | | | |
| RMSH | Pre | 0 | – | – | – | – | AVG S × A | 7.66 | 14.04 |
| | Main | 69 | 506.36 | 100.82 | 35.45 | 33.57 | | | |
| | Post | 13 | 625 | 304.06 | 45 | 7.07 | | | |

Onset variables were measured from the beginning of the cycle to the onset of the muscle burst. Different bursts in the same muscle within one cycle are referred to as pre, main and post bursts. The main burst is the first activity burst in which muscles are fully active; often this burst is preceded by an activity burst of low intensity (pre) and followed by a burst of either high or low intensity (post). Burst presence indicates the number of times that burst was present in the analyzed sequences (%occurrence). The average intensity values are averaged over the total cycle and expressed relative to the maximal value recorded for each muscle in all analyzed sequences. ($N = 16$ for all muscles). $S \times A$: number of spikes multiplied by average amplitude. See Table 1 for definitions of muscle abbreviations.

Interestingly, only minor differences in muscle activation patterns were observed for feeding cycles associated with different prey types (Fig. 3). Such small changes in activation patterns are rather unexpected, as changes in food type in other lizards readily result in large changes in a number of timing and intensity related variables^{52–54}. Even in comparison to another herbivorous lizard (*C. Zeburata*⁵⁴), *Uromastix* shows a marked decrease in the variability of the motor pattern. Considering the large difference in mechanical properties such as size, mass and toughness (endive being much tougher than grasshoppers) and behavioural characteristics (i.e. the mobility) of the food items used here (endive vs. grasshopper) this suggest a rather stereotyped activation pattern that may be related to its dietary specialization. This observation is supported by an analysis of the kinematics of jaws and tongue in the same species.³⁹

Although the activity of only a limited amount of hyolingual muscles was sampled here, the overall pattern is similar to the results published for other lizard species.^{51,52,57} Kinematic patterns of prey prehension in *Uromastix* are highly similar to those observed for agamid lizards (A.H. pers. obs.) and suggests that the m. verticalis in *Uromastix*^{44,58} causes sliding of the tongue on the entoglossal process, similar to the function of the ring muscle in agamids. Tongue movements mediated by the activity of the MGG and the MHG (mainly intraoral tongue protraction, and tongue bulging during transport and swallowing) are similar to those observed in the agamid lizard *P. stellio*, suggesting strong similarities in overall motor control.

Our bite force data for *U. acanthinurus* were not different from data gathered for agamid lizards suggesting that the m.

pterygoideus externus may not provide a performance advantage as has been suggested previously.⁸ Interestingly, our *in vivo* data for *Uromastix* are slightly higher than the predicted data based on the MDA model developed by Moazen et al.¹⁰ However, the predictions based on the Moazen model¹⁰ are strikingly close to *in vivo* data gathered here suggesting that the model provides an accurate prediction of biting in this species. However, given that muscle forces in the model were simply scaled proportional to muscle cross-sectional area, a more realistic model using muscle forces scaled to actual recruitment data will likely result in even lower bite force estimates. Although it is hard to determine why the model underestimates bite forces at this point, we suggest that either the cranial system in *U. hardwickii* is slightly different from that in *U. acanthinurus* or alternatively that the scaling of PCSA to force may be underestimated. However, given that the 30 N/cm² used by Moazen et al.¹⁰ is on the high end for specific tension values in vertebrates, we suggest that there may be significant differences in cranial design between the two species. However, this needs to be investigated further by measuring *in vivo* bite forces for *U. hardwickii* or alternatively by modelling the jaw system in *U. acanthinurus*.

The data provided here in combination with previously published data on muscles masses, cross-sectional areas and data on excitation–contraction coupling (i.e. time to peak force generation¹⁷) should allow future workers to generate more realistic models for *U. acanthinurus* that can be tested using bite force data provided here. Future strain-gauge based analyses of strain patterns in this species are needed to provide additional validation of theoretical models.

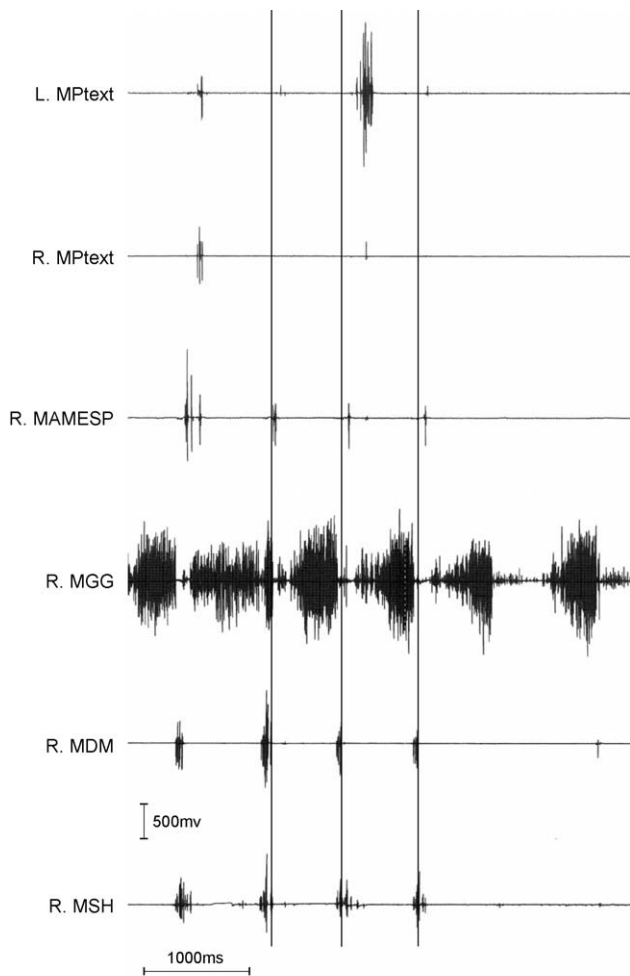


Fig. 5 – Representative electromyograms during swallowing from the first recording session from an individual *U. acanthinurus* feeding on endive. Vertical lines indicate time of maximal gape. Note how the jaw closers and openers are active to a much smaller degree compared to intraoral transport cycles and even become silent at the end of the swallowing stage. L, left; MAMESP, m. adductor mandibulae externus superficialis posterior; MDM, m. depressor mandibulae; MGG, m. genioglossus; MPtext, m. pterygoideus externus; MSH, m. sternohyoideus; R, right.

Acknowledgements

We thank Dr. D. Meirte (Museum for Central Africa, Tervuren) for providing us with the preserved *U. acanthinurus* specimens used for dissection; P. Jouk for allowing us to measure bite forces in the lizards housed at the Antwerp Zoo and Mrs J. Fret and J. Cleuren for help with the electromyographic experiments.

Funding: FWO-Vlaanderen.

Competing interests: None declared.

Ethical approval: Ethical approval was provided by the University of Antwerp Institutional Animal Care and Use Committee.

REFERENCES

- Evans SE. At the feet of the dinosaurs: the early history and radiation of lizards. *Biol Rev* 2003;**78**:513–51.
- Herrel A, Schaerlaeken V, Meyers JJ, Metzger KA, Ross CF. The evolution of cranial design and performance in squamates: consequences of skull-bone reduction on feeding behavior. *Integr Comp Biol* 2007;**47**:107–17.
- Herrel A, De Vree F, Delheusy V, Gans C. Cranial kinesis in gekkonid lizards. *J Exp Biol* 1999;**202**:3687–98.
- Herrel A, Aerts P, De Vree F. Cranial kinesis in geckoes: functional implications. *J Exp Biol* 2000;**203**:1415–23.
- Moazen M, Curtis N, Evans SE, O'Higgins P, Fagan MJ. Combined finite element and multibody dynamics analysis of biting in a *Uromastix hardwickii* lizard skull. *J Anat* 2008;**213**:499–508.
- Moazen M, Curtis N, O'Higgins P, Jones MEH, Evans SE, Fagan MJ. Assessment of the role of sutures in a lizard skull: a computer modelling study. *Proc R Soc Lond B* 2009;**276**:39–46.
- Sinclair AG, Alexander RMCN. Estimates of forces exerted by the jaw muscles of some reptiles. *J Zool Lond* 1987;**213**:107–15.
- Herrel A, Aerts P, De Vree F. Ecomorphology of the lizard feeding apparatus: a modelling approach. *Neth J Zool* 1998;**48**:1–25.
- Herrel A, Aerts P, De Vree F. Static biting in lizards with a primitive skull: functional morphology of the temporal ligaments. *J Zool Lond* 1998;**244**:135–43.
- Moazen M, Curtis N, Evans SE, O'Higgins P, Fagan MJ. Rigid body analysis of a lizard skull: modelling the skull of *Uromastix hardwickii*. *J Biomech* 2008;**41**:1274–80.
- Moreno K, Wroe S, Clausen P, McHenry C, D'Amore DC, Rayfield EJ, Cunningham E. Cranial performance in the komodo dragon (*Varanus komodoensis*) as revealed by high-resolution 3-D finite element analysis. *J Anat* 2008;**212**:736–46.
- Fastnacht M, Hess N, Frey E, Weiser HP. Finite element analysis in vertebrate paleontology. *Senckenbergiana Lethaea* 2002;**82**:195–206.
- Wroe S, McHenry CR, Thomason JJ. Bite club: comparative bite force in big biting mammals and the prediction of predatory behavior in fossil taxa. *Proc R Soc Lond B* 2005;**272**:619–25.
- Rayfield EJ. Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. *Annu Rev Earth Planet Sci* 2007;**35**:541–76.
- Dumont ER, Piccirillo J, Grosse IR. Finite-element analysis of biting behavior and bone stress in the facial skeletons of bats. *Anat Rec A* 2005;**283**:319–30.
- Ross CF, Patel BA, Slice DE, Strait DS, Dechow PC, Richmond BG, Spencer MA. Modeling masticatory muscle force in finite element analysis: sensitivity analysis using principal coordinate analysis. *Anat Rec A* 2005;**283**:288–99.
- Herrel A, Cleuren P, Fret J, De Vree F. Morphology of the feeding system in agamid lizards; ecological correlates. *Anat Rec* 1999;**254**:496–507.
- Cleuren J, Aerts P, De Vree F. Bite and joint force analysis of *Caiman crocodilus*. *Belg J Zool* 1995;**125**:79–94.
- Throckmorton GS. Oral food processing in two herbivorous lizards *Iguana iguana* (Iguanidae) and *Uromastix aegyptius* (Agamidae). *J Morphol* 1976;**148**:363–90.
- Throckmorton GS. Action of the pterygoideus muscle during feeding in the lizard *Uromastix aegyptius* (Agamidae). *Anat Rec* 1978;**190**:217–22.
- Throckmorton GS. The chewing cycle in the herbivorous lizard *Uromastix aegyptius* (Agamidae). *Arch Oral Biol* 1980;**25**:225–33.

22. Herrel A, De Smet A, Aguirre LF, Aerts P. Morphological and mechanical determinants of bite force in bats: do muscles matter? *J Exp Biol* 2008;**211**:86–91.
23. Dubuis A, Faurel L, Grenot C, Vernet R. Sur le régime alimentaire du lézard saharien *Uromastix acanthinurus* Bell. *C R Acad Sci Ser D Sci Naturelles* 1971;**273**:500–3.
24. Grenot C. Ecophysiologie du lézard saharien *Uromastix acanthinurus* Bell, 1825 (Agamidae herbivore). *Ecole Norm Supér Publ Lab Zool* 1976;**7**:1–323.
25. Bock WJ, Shear CR. A staining method for gross dissection. *Anat Anz* 1972;**130**:222–7.
26. Herrel A, Spithoven L, Van Damme R, De Vree F. Sexual dimorphism of head size in *Gallotia galloti*; testing the niche divergence hypothesis by functional analyses. *Funct Ecol* 1999;**13**:289–97.
27. Beach J, Gorniak GC, Gans C. A method for quantifying electromyograms. *J Biomech* 1982;**15**:611–7.
28. Basmajian JV, De Luca CJ. *Muscles alive: their functions revealed by electromyography*. Baltimore: Williams and Wilkins; 1985.
29. Loeb GE, Gans C. *Electromyography for experimentalists*. Chicago: The University of Chicago Press; 1986.
30. Cooper JS, Poole DFG. The dentition and dental tissues of the agamid lizard, *Uromastix*. *J Zool Lond* 1973;**169**:85–100.
31. Robinson PL, How Sphenodon and *Uromastix* grow their teeth and use them. Bellairs ADR, Cox CB, editors. *Morphology and biology of reptiles Linnean society symposium series*, vol. 3. 1976:p. 43–6.
32. Throckmorton GS. The effect of wear on the cheek teeth and associated dental tissues of the lizard *Uromastix aegyptius* (Agamidae). *J Morphol* 1979;**160**:195–208.
33. Beddard FE. Some notes on the cranial osteology of the Mastigure lizard *Uromastix*. *Proc Zool Soc Lond* 1905;**119**:887–904.
34. El Toubi MR. Notes on the cranial osteology of *Uromastix aegyptia* (Forsk.) *Bull Fac Sci Cairo Fouad I Univ* 1945;**25**:1–10.
35. Jollie MT. The head skeleton of the lizard. *Acta Zool* 1960;**41**:1–64.
36. Fürbringer M. Das Zungenbein der Wirbeltiere Insbesondere der Reptilien und Vögel. *Abhandlungen der Heidelberger Akademie der Wissenschaften, II Abhandlung*; 1922.
37. Gnanamuthu CP. Comparative study of the hyoid and tongue of some typical genera of reptiles. *Proc Zool Soc Lond B* 1937;**107**:1–63.
38. Tilak R. The hyoid apparatus of *Uromastix hardwickii* Gray. *Sci Cult* 1964;**30**:244–6.
39. Herrel A, De Vree F. Kinematics of intraoral transport and swallowing in the herbivorous lizard *Uromastix acanthinurus*. *J Exp Biol* 1999;**202**:1127–37.
40. Lakjer T. *Studien über die Trigemini-versorgte Kaumuskulatur der Sauropsiden*. Kopenhagen: C.A. Reitzel; 1926.
41. George JC. The muscular system of *Uromastix hardwickii* (Gray). *J Univ Bombay* 1948;**17**:1–17.
42. Haas G. Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. Gans C, Parsons T, editors. *Biology of the Reptilia* vol 4, London: Academic Press; 1973. p. 285–490.
43. Gomes NMB. Anatomie comparée de la musculature trigéminal des lacertiliens. *Mem Mus Natl Hist Nat Ser A (Zool)* 1974;**90**:1–107.
44. Smith KK. Form and function of the tongue in agamid lizards with comments on its phylogenetic significance. *J Morphol* 1988;**196**:157–71.
45. De Vree F, Gans C. Functional morphology of the feeding mechanisms in lower tetrapods. Splechtma H, Hilgers H, editors. *Fortschritte der Zoologie* vol 35, New York: Gustav Fischer Verlag; 1989. p. 115–27.
46. Herrel A, Cleuren J, De Vree F. Kinematics of feeding in the lizard *Agama stellio*. *J Exp Biol* 1996;**199**:1727–42.
47. Bramble D, Wake DB. Feeding mechanisms of lower tetrapods. In: Hildebrand M, Bramble D, Liem K, Wake D, editors. *Functional vertebrate morphology*. Cambridge, MA: Harvard University Press; 1985. p. 230–61.
48. Schwenk K, Throckmorton GS. Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics. *J Zool Lond* 1989;**219**:153–75.
49. Kraklau DM. Kinematics of prey capture and chewing in the lizard *Agama agama*. *J Morphol* 1991;**210**:195–212.
50. Delheusy V, Bels VL. Kinematics of feeding behaviour in *Oplurus cuvieri* (Reptilia: Iguanidae). *J Exp Biol* 1992;**170**:155–86.
51. Herrel A, Cleuren J, De Vree F. Prey capture in the lizard *Agama stellio*. *J Morphol* 1995;**224**:313–29.
52. Herrel A, Cleuren J, De Vree F. Quantitative analysis of jaw and hyolingual muscle activity during feeding in the lizard *Agama stellio*. *J Exp Biol* 1997;**200**:101–15.
53. Gans C, De Vree F, Carrier D. Usage pattern of the complex masticatory muscles in the shingleback lizard *Trachydosaurus rugosus*: a model for muscle placement. *Am J Anat* 1985;**173**:219–40.
54. Herrel A, Verstappen M, De Vree F. Modulatory complexity of the feeding repertoire in scincid lizards. *J Comp Physiol A* 1999;**184**:501–18.
55. Smith KK. An electromyographic study of the function of the jaw adducting muscles in *Varanus exanthematicus*. *J Morphol* 1982;**173**:137–58.
56. Herrel A, Schaerlaeken V, Ross CF, Meyers JJ, Nishikawa KC, Abdala V, Manzano A, Aerts P. Electromyography and the evolution of motor control: limitations and insights. *Integr Comp Biol* 2008;**48**:261–71.
57. Smith KK. The use of the tongue and hyoid apparatus during feeding in lizards (*Ctenosaura similis* and *Tupinambis nigropunctatus*). *J Morphol* 1984;**202**:115–43.
58. Herrel A, Timmermans J-P, De Vree F. Tongue flicking in agamid lizards: morphology, kinematics and muscle activity patterns. *Anat Rec* 1998;**252**:102–16.