

Locomotor–feeding coupling during prey capture in a lizard (*Gerrhosaurus major*): effects of prehension mode

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SUMMARY

In tetrapods, feeding behaviour in general, and prey capture in particular, involves two anatomical systems: the feeding system and the locomotor system. Although the kinematics associated with the movements of each system have been investigated in detail independently, the actual integration between the two systems has received less attention. Recently, the independence of the movements of the jaw and locomotor systems was reported during tongue-based prey capture in an iguanian lizard (*Anolis carolinensis*), suggesting a decoupling between the two systems. Jaw prehension, on the other hand, can be expected to be dependent on the movements of the locomotor system to a greater degree. To test for the presence of functional coupling and integration between the jaw and locomotor systems, we used the cordyliform lizard *Gerrhosaurus major* as a model species because it uses both tongue and jaw prehension. Based on a 3-D kinematic analysis of the movements of the jaws, the head, the neck and the forelimbs during the approach and capture of prey, we demonstrate significant correlations between the movements of the trophic and the locomotor systems. However, this integration differs between prehension modes in the degree and the nature of the coupling. In contrast to our expectations and previous data for *A. carolinensis*, our data indicate a coupling between feeding and locomotor systems during tongue prehension. We suggest that the functional integration between the two systems while using the tongue may be a consequence of the relatively slow nature of tongue prehension in this species.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/212/6/768/DC1>

Key words: capture, decoupling, tongue, jaw, lizard, feeding.

INTRODUCTION

The fitness of an individual is determined by a suite of behaviours including, for example, communication, competition, mate selection, escaping from predators, foraging and feeding, all relevant in both intra- and interspecific contexts. Feeding events can be divided into four successive stages: (i) the identification and localization of the food item using the sensory systems, (ii) the approach, largely determined by the locomotor system, (iii) the actual prey capture and processing, relying on the locomotor and feeding systems, and (iv) digestion. Clearly these stages are all crucial and rely heavily on the involvement of different functional systems. These systems, however, need to interact with each other for an individual to fully and optimally exploit potential prey resources (Higham, 2007b). For example, some long-tongued frogs rely predominantly on tongue movements when capturing small prey, but add a significant lunge component to the capture when prey are bigger, thus suggesting an intricate coupling between feeding and locomotor systems (Anderson, 1993; Valdez and Nishikawa, 1997). Yet, most functional studies of feeding consider the feeding system in isolation from other systems (e.g. Delheusy and Bels, 1992; Delheusy and Bels, 1999; Bels et al., 1994; Urbani and Bels, 1995; Herrel et al., 1995; Herrel et al., 1996; Herrel et al., 1999; Bels, 2003), and the movements involved in the approach of a potential prey and the positioning of the head prior to the strike have rarely been studied from a functional perspective (but see Kardong and Bels, 1998;

Alfaro, 2003; Higham et al., 2005; Higham, 2007a; Montuelle et al., 2008). The actual integration between feeding and locomotor systems has received even less attention to date (see Higham, 2007b).

Prey capture performance (i.e. capture success) is dependent on two elements: (i) the success of the actual capture determined by the adhesive capacity of the tongue (Bell, 1989; Delheusy et al., 1994; Herrel et al., 2000; Deban and Marks, 2002) or the ability of a predator to grasp the prey firmly and quickly between the jaws (Frazzetta, 1983), and (ii) the actual acceleration or velocity, and the precision of the predator during the approach (Webb, 1975; Webb, 1984; Webb and Skadsen, 1980; Higham et al., 2005). The use of the tongue as a prehension organ may potentially be constrained by the velocity of the predator, as tongue protrusion often requires time, and is dependent on precise sensorimotor coordination (Nishikawa et al., 1992; Deban, 1997). Indeed, most prey capture systems characterized by extreme and fast tongue elongation occur in animals using a slow approach or that remain stationary (Wainwright et al., 1991; Deban et al., 1997; Nishikawa, 1999). Moreover most animals using rapid tongue movements depend largely on feedforward modulation of the tongue and jaws (Deban, 1997; Nishikawa, 1999).

Body propulsion towards the prey, when present, is achieved by the action of the axial system, like in snakes (Kardong and Bels, 1998; Cundall and Greene, 2000), or the combined action of the axial and appendicular systems, especially in elongate tetrapods with

a parasagittal gait like lizards (Frazzetta, 1983; Kraklau, 1991; Montuelle et al., 2008). For example, the positioning of the head before capture is achieved by extension of the front limbs and bending at the cranio-cervical joint (Kraklau, 1991) but may be dependent on capture mode. Thus, the integration between feeding and locomotor systems is expected to be strong but may also be dependent on the prey capture strategy used. A recent study on feeding in lizards demonstrated that the actual feeding movements (i.e. jaw and hyolingual kinematics) were independent of the specific approach strategy used, suggesting that a direct coupling between feeding and locomotor movements may be absent in some cases (Montuelle et al., 2008).

Squamate lizards may be an ideal model system to explicitly explore the coupling between locomotor and feeding movements and its dependence on prehension mode as different prey capture strategies are used by different species (Bels et al., 1994; Schwenk, 2000; Bels, 2003). For example, whereas iguanian lizards (chameleons, iguanas and agamids) rely predominantly on their tongue for prey capture, scleroglossans (all other lizards) mainly use their jaws to apprehend prey (Schwenk, 2000). The use of tongue-based prey capture may potentially allow a partial decoupling of the two systems, resulting in a lack of association between the locomotor strategy used during capture and the actual feeding movements (Montuelle et al., 2008). Indeed, in its most extreme form, as observed in chameleons for example, prey capture is completely decoupled from locomotion (Wainwright et al., 1991). The use of the jaws for prey capture, on the other hand, may imply a greater involvement of the locomotor system (i.e. limbs and vertebral axis, especially the neck) to position the head before the actual strike. Thus, comparisons between lizards that use different prey capture strategies may be especially insightful in understanding the role of prehension mode in driving the coupling between locomotor and feeding movements.

We decided to use *Gerrhosaurus major* as a model system to test for locomotor–feeding coupling. Cordyliform lizards like *Gerrhosaurus* are known to use both lingual and jaw prehension modes (Urbani and Bels, 1995; Reilly and McBrayer, 2007), allowing the role of prehension mode to be tested without potential confounding effects of phylogenetic history. Animals were offered four different prey types to elicit different prehension modes. Because the predator has to initially position and then move its jaws around the prey, jaw-based prey capture can be expected to involve the elevation of the head by extension of the forelimbs. So we predicted that during jaw prehension, coupling and integration of the feeding and locomotor systems will be strong. During tongue prehension, however, the tongue is the organ contacting and transporting the prey and may potentially eliminate the need for extensive forelimb and body involvement during capture. Thus, the integration between the locomotor and feeding systems may be reduced in the case of tongue prehension as previously observed for *A. carolinensis* (Montuelle et al., 2008).

MATERIALS AND METHODS

Animals and husbandry

Five adult male individuals of the species *Gerrhosaurus major* Duméril 1851 of similar size (snout–vent length 208.6±8.0 mm, cranial length 39.0±1.2 mm, mass 235.6±22.3 g), housed at the University of Antwerp, Belgium, were transported to the Muséum National d'Histoire Naturelle in Paris, France, for the feeding trials. Animals were allowed to rest for 24 h before the start of the feeding trials. While at the Muséum, animals were housed together in a large wooden terrarium (1 m×1 m×40 cm) with

multiple hiding places consisting of PVC pipes. Water was always available to the animals.

Experimental protocol

We offered four different food items that reflect the natural diet of *Gerrhosaurus major* (Spawls et al., 2002): a piece of fruit (banana, length 10.5±2.8 mm), mealworms (*Tenebrio molitor*, length 36.8±7.5 mm), grasshoppers (*Locusta migratoria*, length 45.0±1.3 mm) and newborn mice (*Mus musculus*, length 29.8±3.6 mm). These prey types were selected to provide the animal with prey of different size, shape and mobility, and are known to elicit different prehension modes. The experimental set-up consisted of a 2 m long, 30 cm wide wooden trackway covered with a non-slip green plastic carpet. Before the experiments, animals were free to roam across the track to induce naturalistic foraging behaviour. On one side of the track, three synchronized high-speed cameras (AVT Pike F-032B, Allied Vision Technologies, Stadroda, Germany) were set up and used to film the capture of prey at 200 frames s⁻¹. One camera was set in frontal view, a second one in lateral view and the third one tilted down in an oblique dorsal view. During filming, all five animals (marked individually by paint codes on their backs) were positioned at one side of the track. Food items were offered at the opposite side of the track and we waited for lizards to detect the prey and spontaneously initiate an approach and capture sequence.

Three-dimensional reconstruction

A custom-written Matlab routine (Loco 2.8) was used to digitize the landmarks (markers painted on the body and head using non-toxic white paint) on multiple synchronized views. This allowed us to calculate the screen coordinates of the following landmarks (Fig. 1): the upper jaw, the lower jaw, the corner of the mouth, the anterior corner of the eye, the mid-sagittal point between the eyes, the back of the parietal bones, the pectoral girdle, the neck mid-way between the back of the parietal bones and the pectoral girdle, the pelvic girdle, two markers mid-way between the neck marker and the parietal bones and pectoral girdle markers, respectively, the left shoulder, the left elbow, the left wrist, and finally one landmark on the prey. The digitization provided us with three sets of 2-D coordinates (one set per camera) which were used to calculate the 3-D coordinates using a DLT-routine (Hartley and Sturm, 1995). A checkerboard composed of nine by nine squares of 1 cm×1 cm was used to calibrate the cameras and scale the images.

Kinematic analysis

Based on the 3-D coordinates of the landmarks we calculated five kinematic profiles from which we extracted 23 spatiotemporal kinematic variables describing the actions of the cranial system (jaws and head positioning; seven variables; Table 1), the movements of the post-cranial system (forelimb and vertebral axis; 11 variables; Table 1) and the strike features (five variables; Table 1). For all profiles, time 0 was set to coincide with prey contact, such that events occurring before predator–prey contact have negative time values, whereas those occurring after are represented by positive time values.

Kinematic variables describing the movements of the cranial system were based on two profiles. First, the gape angle was defined as the angle subtended by the line interconnecting the tip of the upper jaw and the corner of the mouth, and the line interconnecting the tip of the lower jaw and the corner of the mouth (Fig. 1B). From the gape profile we extracted the maximal gape angle, the time to the onset of opening and the time to maximal gape. Second, the

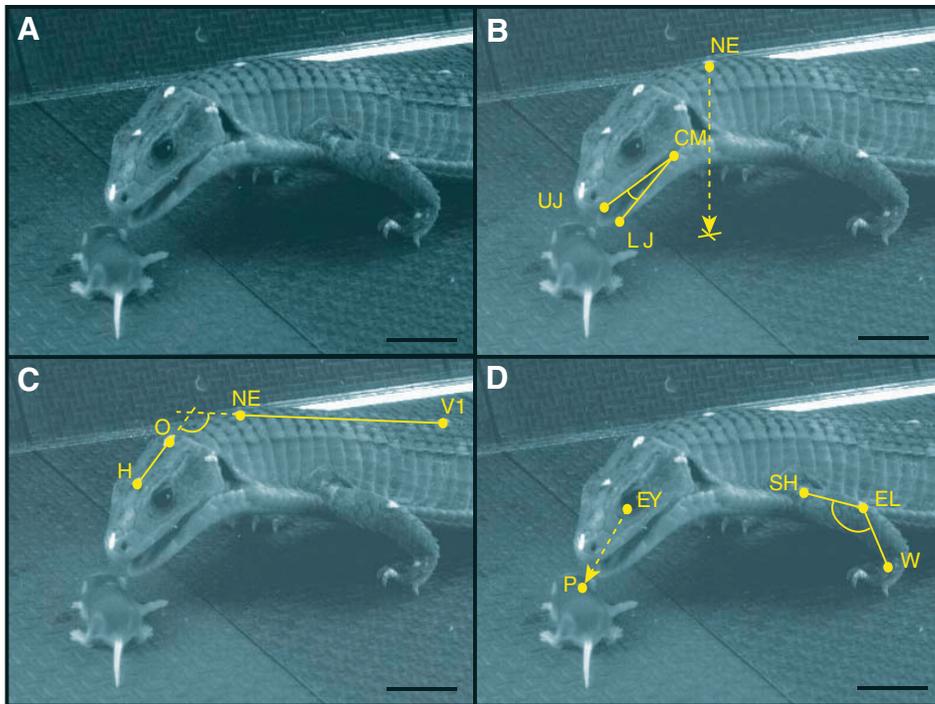


Fig. 1. Illustration of the kinematic variables quantified in this study. (A) Typical frame extracted from one of the three synchronized high-speed cameras (camera tilted down in oblique dorsal view). (B) Illustration of the gape angle and the elevation of the neck (3-D Z-coordinate of the point NE). (C) Illustration of the head angle. (D) Illustration of the predator-prey distance and the angle of the elbow. UJ, upper jaw; LJ, lower jaw; CM, corner of the mouth; NE, neck, mid-way between the back of the parietal and the pectoral girdle; H, mid-sagittal point between the eyes; O, back of the parietal bones; V1 and V2, two markers, mid-way between the neck marker and the parietal bones and pectoral girdle markers, respectively; EY, anterior corner of the eye; SH, left shoulder; EL, left elbow; W, left wrist (W); P, prey. Scale bar 2 cm.

head angle was calculated as the angle between the long axis of the head (line O–H, Fig. 1C) and the long axis of the neck (line V1–NE; Fig. 1C). From the changes in head angle over time, the angle at the onset of mouth opening, the head angle at prey contact, the

Table 1. Summary of the kinematics of movements associated with the cranial and post-cranial systems as well as those specifically related to the strike during jaw and tongue prehension events in *Gerrhosaurus major*

	Jaw prehension	Tongue prehension
Cranial kinematics		
Time to mouth opening (ms)	-171±28	-111±15
Maximal gape (deg.)	27.9±1.3	21.6±1.4
Time to maximal gape (ms)	3±8	85±8
Head angle at mouth opening (deg.)	126.1±3.3	131.4±3.1
Head angle at prey contact (deg.)	131.2±3.7	132.0±3.5
Minimal head angle (deg.)	118.9±4.6	124.0±3.0
Time to minimal head angle (deg.)	-91.0±40.5	56.7±36.0
Post-cranial kinematics		
Elevation of the neck at mouth opening (mm)	16.8±2.1	12.4±1.3
Elevation of the neck at prey contact (mm)	12.9±1.9	12.9±1.1
Maximal elevation of the neck (mm)	20.4±2.3	14.8±1.1
Time to maximal elevation of the neck (ms)	-90±48	116±32
Elbow angle at mouth opening (deg.)	78.9±7.0	76.4±4.4
Elbow angle at prey contact (deg.)	89.4±6.5	81.6±4.6
Maximal elbow angle (deg.)	103.8±6.8	94.4±5.3
Time to maximal elbow angle (ms)	3±44	135±32
Minimal elbow angle (deg.)	66.2±5.2	69.0±3.8
Time to minimal elbow angle (ms)	-139±63	-222±43
Total variation of elbow angle (deg.)	37.7±5.5	25.3±3.2
Strike kinematics		
Strike distance (mm)	45.4±4.5	31.6±1.4
Prey distance at mouth opening (mm)	37.1±2.7	29.8±1.4
Distance run at mouth opening (%)	15.0±3.4	5.7±1.0
Speed of strike (cm s ⁻¹)	9.18±2.59	2.10±0.20
Time to maximal speed of strike (ms)	-10±4	-0±6

Table entries are means ± s.e.m. See Materials and methods for details.

minimal head angle (describing the most flexed position of the head) and the time to the minimal head angle were extracted.

To describe the movements of the post-cranial system we quantified two profiles. First, the elevation of the neck was calculated as the difference between the Z-coordinate of the neck point with the Z-coordinate of the neck at rest position (Fig. 1B). Based on the change in this variable over time we calculated neck elevation at the onset of mouth opening and at prey contact, the maximal elevation of the neck and the time to the maximal elevation of the neck. Second, the elbow angle was defined as the angle subtended by the shoulder, the elbow and the wrist markers (Fig. 1D). From this profile we quantified the elbow angle at the onset of mouth opening, the elbow angle at prey contact, the minimal and maximal elbow angle, and the time to the minimal and the maximal angle. Additionally, we calculated the absolute magnitude of the variation in elbow angle as the difference between the maximal and minimal angles.

The strike features are based on the predator-prey distance profile over time. The predator-prey distance was defined as the distance between the anterior corner of the eye and the anterior point of the prey (Fig. 1D). In this matrix, we include the strike distance, the predator-prey distance at the onset of mouth opening, and the distance run by the lizard between the start of the strike and the onset of mouth opening (% of the total strike distance). Finally, we calculated peak strike velocity and the time to the peak strike velocity.

Data set

Consequently, our data set is divided into three matrices, each of them representing a different component of prey capture in *Gerrhosaurus major* (Table 1). The cranial matrix is composed of seven variables (three for jaw system and four for head positioning): time to mouth opening, maximal gape angle and time to maximal gape; head angle at the onset of mouth opening, head angle at prey contact, minimal head angle and time to minimal head angle. Next, the post-cranial matrix is composed of 11 variables (four for neck

movements and seven for elbow angle): neck elevation at the onset of mouth opening, neck elevation at prey contact, maximal neck elevation and time to maximal neck elevation; elbow angle at the onset of mouth opening, elbow angle at prey contact, maximal elbow angle, time to maximal elbow angle, minimal elbow angle, time to minimal elbow angle and absolute magnitude of elbow angle variation. Finally the strike matrix comprises five strike variables: strike distance, predator–prey distance at the onset of mouth opening, distance run by the lizard at mouth opening, peak strike velocity and time to peak strike velocity.

For a total of 37 capture sequences, the three synchronized views were digitized and 3-D reconstructions were performed. Overall, the data set is composed of 16 sequences describing the kinematics of jaw prehension and 21 sequences describing tongue prehension. In both prehension modes, all five individuals are represented, and for each prey type the data set includes at least four of the five individuals.

Statistical analysis

All statistical analyses were performed using SPSS 15.0 for Windows (SPSS, Chicago, IL, USA). All kinematic data were \log_{10} transformed to fulfil assumptions of normality and homoscedasticity. Prior to analysis, we performed a MANCOVA on the complete data set (cranial, post-cranial and strike variables) to test for an effect of individual size. Size was not significant and thus will no longer be considered in our analysis.

First, we performed a factor analysis with varimax rotation on a composite matrix combining both the cranial and post-cranial matrix to reduce the dimensionality of the data. Factors with eigenvalues greater than 1 were extracted and factor scores were saved. Individuals were entered as random factor, and prehension mode was entered as a fixed factor in a full factorial two-way MANOVA coupled to univariate F -tests. Non-significant interaction terms were removed from the final model. Next, we ran a discriminant function analysis (DFA) on the factor scores to determine which kinematic variables discriminated best between prehension modes (Quinn and Keough, 2002).

The strike variables were analysed through two consecutive statistical procedures. First, we tested for a prehension mode effect by performing an ANOVA coupled to univariate F -tests. In this analysis, individuals were set as random factor and prehension modes as fixed factor, and non-significant interaction terms were removed from the final model. Then, we used a correlation matrix to test for associations between the strike variables and the factor scores obtained previously that summarize the kinematics of the cranial and post-cranial movements.

To test for associations and the integration between the cranial and post-cranial systems during prey capture, the data set was split into two data sets, one representing the kinematics for jaw prehension and one representing tongue prehension. For both data sets, the cranial and post-cranial matrix were separately subjected to a factor with varimax rotation, and factors with eigenvalues greater than 1 were extracted. These factors were then introduced into a correlation matrix to test for associations between the kinematics of the cranial and post-cranial systems, and to compare jaw and tongue prehension modes.

RESULTS

Prey prehension modes

In accordance with previous studies on cordyliform lizards (Urbani and Bels, 1995), *Gerrhosaurus major* used two prehension modes to capture prey: jaw and tongue prehension. The selection of

prehension mode was strongly influenced by the type of food captured; jaw prehension was typically used for newborn mice (78.6%) and grasshoppers (91.3%), whereas tongue prehension was used for banana (92.9%) and mealworms (100%). In both prey prehension modes, attacks were highly successful in all individuals, the predator rarely, if ever, missing the target.

After detecting the prey, individuals oriented and moved towards the prey, tongue flicking occasionally. In prey capture sequences involving the use of the tongue, the lizard stopped closer to the prey compared with those involving the jaws. During the preparatory phase, a distinctive body configuration was associated with each prehension mode suggesting that the selection of prehension modes is completed prior to the strike and is based on sensory stimuli gathered during the approach. During tongue prehension sequences, the body remained close to the substratum with the vertebral column in an extended horizontal position; in contrast, during jaw prehension the forelimbs were extended, thus elevating the head and neck (see supplementary material Movies 1 and 2, respectively). After the extension of the forelimbs the head was flexed ventrally and positioned above the prey. Next the mouth was opened and gape increased rapidly; the speed of mouth opening being distinctly greater during jaw prehension than during tongue prehension. The strike itself was also more rapid during jaw prehension and the forward velocity of the predator was largely determined by the extension and subsequent flexion of the forelimbs. Occasionally, the vertebral axis was also curved in an S-shape during the preparatory phase of jaw prehension, and extended rapidly during the strike, thus providing an additional acceleration component, similar to that observed previously in snakes (Kardong and Bels, 1998). During both jaw and tongue prehension, the head of the predator was typically oriented perpendicular to the long axis of the prey. Tongue protrusion in *G. major* appears to be qualitatively similar to that described for iguanians and scincids using this capture mode (Schwenk and Throckmorton, 1989; Kraklau, 1991; Herrel et al., 1995; Smith et al., 1999). The tongue is protracted outside the mouth, curls ventrally and bulges, thus exposing the dorsal surface anteriorly towards the prey. Next, the tongue contacts the prey and retracts, bringing the prey inside the mouth. During jaw prehension, however, the tongue is retracted backwards at the onset of jaw opening. Once the prey has passed the jaw margins, the mouth closes rapidly, and a power stroke occurs upon prey contact. Given the more extended initial position of the head and body during tongue prehension events, the power stroke is performed with the head positioned horizontally, in contrast to jaw prehension events where the power stroke occurs while the head is bent ventrally (Table 1).

Variables in the strike matrix were strongly modulated according to prehension mode. Indeed, the prehension mode had a significant effect on the strike distance ($F_{1,31}=11.259$; $P<0.01$), indicating jaw prehension is induced further from the prey. The distance of mouth opening ($F_{1,31}=5.248$; $P=0.03$) was also affected by prehension mode suggesting the mouth opens further from the prey in jaw prehension than in tongue prehension. Moreover, the prehension mode had a significant effect on the distance run by the lizard between the start of the strike and mouth opening ($F_{1,31}=6.098$; $P=0.02$), providing evidence that a predator using jaw prehension has covered a greater portion of the total strike distance when the mouth opens. Finally, the peak strike velocity was greater during jaw prehension than during tongue prehension ($F_{1,31}=58.503$; $P<0.01$). No individual effect was detected for any variables. Interaction term was only significant for the time to peak strike velocity, so we treated each

Table 2. Results of a factor analysis performed on the kinematics of cranial and post-cranial movements during jaw and tongue prehension in *Gerrhosaurus major*

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Eigenvalues	5.77	2.90	1.97	1.76	1.58	1.43
% of variance explained (cumulative %)	20.55	15.21 (35.76)	14.27 (50.03)	13.63 (63.65)	11.80 (75.45)	10.12 (85.57)
Cranial kinematics						
Time to mouth opening	0.07	-0.07	-0.07	0.88	0.23	0.05
Maximal gape	-0.01	-0.08	0.24	0.77	-0.11	0.28
Time to maximal gape	0.06	-0.14	0.02	0.57	0.71	-0.15
Head angle at mouth opening	-0.15	-0.33	0.83	0.14	0.13	-0.07
Head angle at prey contact	-0.23	-0.25	0.85	0.30	-0.03	-0.10
Minimal head angle	-0.10	0.01	0.90	-0.14	0.02	-0.02
Time to minimal head angle	0.25	-0.11	-0.10	-0.29	0.75	0.23
Post-cranial kinematics						
Elevation of the neck at mouth opening	0.37	0.76	-0.13	-0.02	-0.25	-0.13
Elevation of the neck at prey contact	0.35	0.81	-0.18	-0.31	0.17	-0.07
Maximal elevation of the neck	0.09	0.91	-0.20	0.06	-0.06	0.13
Time to maximal elevation of the neck	-0.13	-0.44	0.23	0.07	0.60	-0.33
Angle of elbow at mouth opening	0.93	0.18	-0.24	-0.01	-0.05	0.06
Angle of elbow at prey contact	0.84	0.23	-0.16	0.08	-0.01	0.36
Maximal elbow angle	0.83	0.13	-0.09	0.15	-0.01	0.48
Time to maximal elbow angle	-0.36	0.35	0.14	0.20	0.68	0.19
Minimal elbow angle	0.90	0.18	-0.06	-0.06	0.05	0.17
Time to minimal elbow angle	0.02	0.09	0.07	0.56	-0.19	-0.57
Total variation of elbow angle	0.25	0.03	-0.08	0.24	0.01	0.87

Values in bold represent loadings greater than 0.70.

of the five individuals separately. The effect of prehension mode was only significant for one individual ($F_{1,3}=12.550$; $P=0.04$), not for the others.

Modulation of capture kinematics according to prehension mode

To test for differences in the kinematics of the feeding and locomotor systems associated with different prehension modes we performed a factor analysis with varimax rotation on the full kinematic data matrix. Six factors with eigenvalues greater than 1 were extracted (Table 2), the first two factors jointly explaining 35.76% of the total variance. The MANOVA performed on the factor scores detected significant prehension mode (Wilk's $\lambda=0.357$; $F_{6,26}=7.789$; $P<0.01$) and individual effects (Wilk's $\lambda=0.095$; $F_{24,91.913}=3.693$; $P<0.01$). Interaction effects were non-significant, suggesting that all individuals change their kinematics in a similar fashion when switching from jaw to tongue prehension.

The first factor was positively correlated with variables describing the movement of the elbow: the elbow angle at mouth opening, the maximal flexion of the elbow (minimal angle), the elbow angle at prey contact, and the maximal extension of the elbow (maximal angle; Table 2). However, neither prehension mode nor individual effects were significant. The maximal elevation of the neck, and the elevation of the neck at prey contact and mouth opening loaded positively on the second factor (Table 2). Only individual effect ($F_{4,31}=4.255$; $P<0.01$) was significant on the second factor.

The third factor was associated with head positioning kinematics: minimal head angle (the most flexed position of the head), the head angle at prey contact and the head angle at the onset of mouth opening all loaded positively (Table 2). As for the second factor, individual effect was significant on the third factor ($F_{4,31}=6.148$; $P<0.01$). The fourth factor was positively correlated with jaw movements and especially the time to mouth opening and the maximal gape angle (Table 2). Prehension mode effect was strong on the fourth factor ($F_{1,31}=12.905$; $P<0.01$; Fig. 2), and so was

individual effect ($F_{4,31}=3.844$; $P=0.01$). This suggests that jaws open later and wider in jaw prehension events than in tongue prehension events. The timing of cranial system movements (time to minimal head angle and time to maximal gape angle) loaded positively on the fifth factor (Table 2). This factor was strongly affected by prehension mode ($F_{1,31}=11.808$; $P<0.01$; Fig. 2), indicating that head flexion is more rapid and maximal gape occurs sooner in jaw

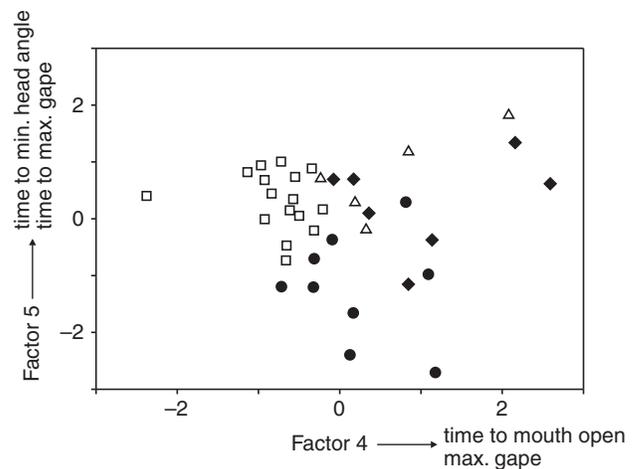


Fig. 2. Scatter plot illustrating the results of a factor analysis performed on the full data set including the kinematic variables of cranial and post-cranial systems associated with prey capture in *Gerrhosaurus major*. The proportion of the total variance explained by each factor is indicated. Factors 4 and 5 significantly discriminated between capture modes. Open symbols represent tongue prehension events; filled symbols represent jaw prehension events. Squares represent capture events on mealworms, triangles represent the capture of banana, circles represent the capture of grasshoppers and diamonds represent the capture of newborn mice. Variables with loading greater than 0.70 are indicated on the factor axes.

prehension. The sixth factor (correlated with the total extension of the elbow) did not discriminate between either individuals or prehension modes.

A DFA performed on the six factor scores extracted a single discriminant function defined by factors 4 and 5. Consequently, jaw prehension differs from tongue prehension by a more rapid positioning of the head, a retarded opening of the mouth, and a wider maximal gape that occurs earlier. Interestingly, most variables that discriminated between prehension modes were timing-related variables of the cranial system, suggesting that the speed and timing

of jaw movements are the dominant features characterizing each prehension mode.

Additionally we compared the six factor scores with the strike variables using bivariate correlations, in order to investigate how the combined actions of the cranial and post-cranial kinematics result in the strike efficiency. The strike distance was correlated with factor 5 ($R=-0.45$, $P<0.01$), suggesting cranial movements are quicker when the prey is closer to the predator (Fig. 3A). Peak strike velocity was correlated with factor 5 ($R=-0.40$, $P=0.01$) and factor 6 ($R=0.40$, $P=0.02$; Fig. 3B,C). This indicates fast strikes are supported

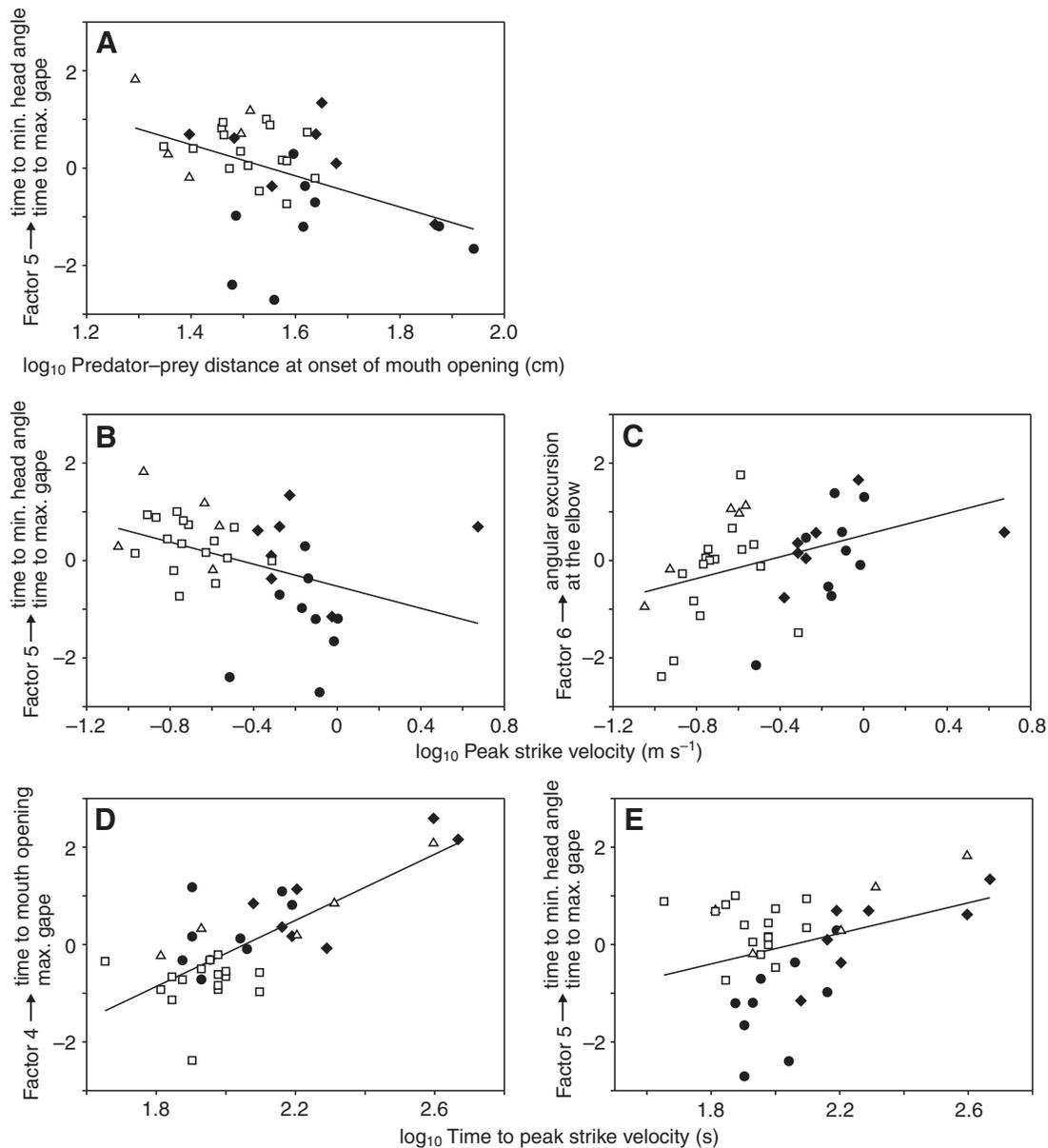


Fig. 3. Correlations between strike variables and the multivariate indicators of the kinematics of cranial and post-cranial systems associated with prey capture in *Gerrhosaurus major*. (A) Predator–prey distance at mouth opening is negatively correlated with factor 5 ($P<0.01$), indicating the head flexion and the maximal gape are quicker when the prey is closer. (B,C) Peak strike velocity is negatively correlated with both factor 5 (negatively; $P=0.01$; B) and factor 6 (positively; $P=0.02$; C), indicating quick cranial movements and wide extension of the elbow are major components of strike velocity. (D,E) Time to peak strike velocity is positively correlated with both factor 4 ($P<0.01$; D) and factor 5 ($P=0.03$; E), indicating late peak strike velocities are associated with slow cranial movements. Open symbols represent tongue prehension events; filled symbols represent jaw prehension events. Squares represent capture events on mealworms, triangles represent the capture of banana, circles represent the capture of grasshoppers and diamonds represent the capture of newborn mice. Variables with loading greater than 0.70 are indicated on the factor axes.

by quick cranial movements and wide extension of the elbow. The time to peak strike velocity was correlated with factor 4 ($R=0.76$, $P<0.01$; Fig. 3D) and factor 5 ($R=0.35$, $P=0.03$; Fig. 3E), suggesting that when peak strike velocity occurs later the cranial movements are slower than when the peak strike velocity is achieved earlier in the capture events. No correlations were found between the distance at the onset of mouth opening or the distance run by the lizard between the start of the strike and mouth opening, with any of the six factors. Thus, most of the strike variables were associated with cranial movements, but note elbow extension is one major component for strike velocity.

Functional integration of cranial and post-cranial systems

Given that jaw and tongue prehension are characterized by different kinematic variables, we split our initial data set into two matrices: one for the kinematics of jaw prehension, and one for tongue prehension. For each data set we performed a factor analysis for kinematic features associated with the cranial and post-cranial systems separately. Factors with eigenvalues greater than 1 were retained and bi-variate correlations were performed to test for a functional integration (i.e. co-variation in kinematics) between cranial and post-cranial systems during jaw and tongue prehension events, respectively.

For jaw prehension, three factors were extracted for the cranial system (explaining 83.3% of the total variance), and four factors for the post-cranial system (explaining 89.3% of the total variance; Table 3). Loadings of the variables on the factors were similar to those on the factors retained in the factor analysis performed previously (see Tables 2 and 3). Bi-variate correlations between the seven factors indicated one significant and negative correlation: between cranial factor 3 and post-cranial factor 4 ($R=-0.49$, $P=0.05$; Fig. 4A). This correlation describes a functional link between the

time of the maximal flexion of the head and the elbow. Interestingly, this association is independent of prey type and thus appears to describe the functional coupling between the two systems (Fig. 4A). However, note the correlated factors are the ones that explained the least of the variance (17.1% and 11.15%, respectively) and, consequently, most cranial (e.g. head positioning, jaw movements) and post-cranial movements (e.g. neck elevation) remain independent.

For tongue prehension, the multivariate analysis performed on the kinematics associated with the cranial system is summarized by two factors (explaining 78.1% of the total variance), whereas the post-cranial kinematics can be summarized by three factors (explaining 80.7% of the total variance; Table 4). Bi-variate correlations of the five factors indicated only one significant correlation: between cranial factor 2 and post-cranial factor 2 ($R=-0.56$, $P<0.01$; Fig. 4B). Consequently, tongue prehension events involving a greater elevation of the neck during the preparatory phase are associated with faster jaw movements (both time of mouth opening and maximal gape). Maximal gape also loaded positively on the second cranial factor indicating that tongue prehension events involving a greater lifting of the neck are associated with lower maximal gape angles. Interestingly, tongue prehension cycles involving higher neck elevation, faster strikes and lower gape angles were mostly associated with the capture of mealworms (Fig. 34). Moreover, as for jaw prehension, the correlated factors only represent 35.5% and 28.76% of their respective total variance (Table 4). Indeed, the factors that explain most of the variance were surprisingly not correlated, indicating head positioning and neck elevation are independent.

DISCUSSION

Once within strike distance, *Gerrhosaurus major* selects a distinct prey capture mode: jaw prehension for small mice and grasshoppers,

Table 3. Results of a factor analysis performed on the kinematics of cranial and post-cranial movements during jaw prehension in *Gerrhosaurus major*

	Factor 1	Factor 2	Factor 3	Factor 4
Cranial kinematics				
Eigenvalues	2.62	2.21	1.00	
% of variance explained (cumulative %)	34.75	31.43 (66.18)	17.09 (83.26)	
Time to mouth opening	0.14	0.97	0.12	
Maximal gape	0.58	0.43	-0.21	
Time to maximal gape	-0.10	0.95	0.08	
Head angle at mouth opening	0.82	0.05	-0.15	
Head angle at prey contact	0.89	0.07	-0.38	
Minimal head angle	0.76	-0.36	0.34	
Time to minimal head angle	-0.21	0.16	0.92	
Post-cranial kinematics				
Eigenvalues	5.29	2.28	1.23	1.03
% of variance explained (cumulative %)	43.63	19.28 (62.91)	15.20 (78.11)	11.15 (89.25)
Elevation of the neck at mouth opening	0.82	0.36	0.29	0.23
Elevation of the neck at prey contact	0.72	0.24	0.53	-0.09
Maximal elevation of the neck	0.43	0.57	0.64	0.22
Time to maximal elevation of the neck	0.09	-0.73	-0.30	-0.33
Angle of elbow at mouth opening	0.97	-0.03	-0.14	0.03
Angle of elbow at prey contact	0.89	0.23	-0.08	-0.20
Maximal elbow angle	0.88	0.40	-0.14	-0.15
Time to maximal elbow angle	-0.21	0.06	0.86	-0.17
Minimal elbow angle	0.90	-0.33	0.02	0.11
Time to minimal elbow angle	-0.01	-0.00	-0.12	0.90
Total variation of elbow angle	0.25	0.87	0.00	-0.31

Values in bold represent loadings greater than 0.70.

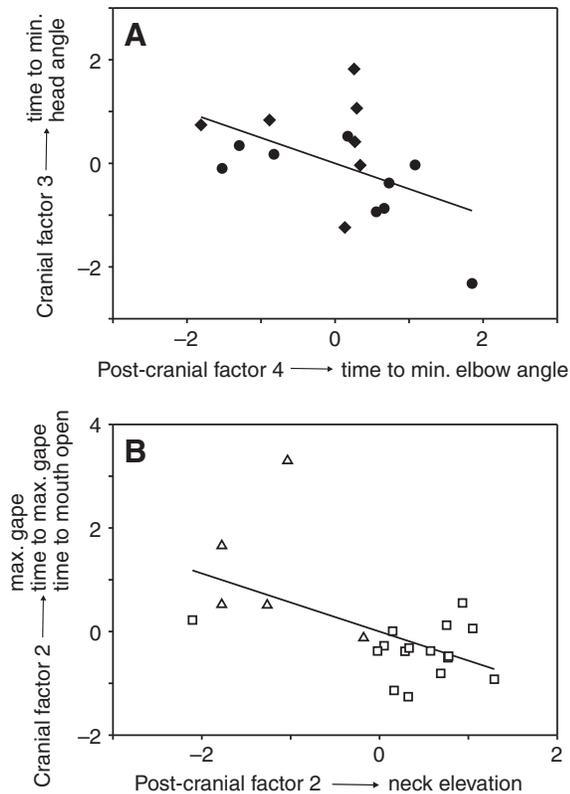


Fig. 4. Correlations between multivariate indicators of the kinematics of cranial and post-cranial systems associated with prey capture in *Gerrhosaurus major*. (A) During jaw prehension events, a significant negative correlation was observed between post-cranial factor 4 and cranial factor 3 ($P=0.05$). This indicates the timing of flexion of the head and the elbow are coupled. Note that correlations are independent of prey type. (B) During tongue prehension, a significant negative correlation was observed between post-cranial factor 2 and cranial factor 2 ($P<0.01$). This indicates a greater elevation of the neck is associated with a faster strike, and thus reflects the functional coupling between the jaw and locomotor systems. Squares represent capture events on mealworms, triangles represent the capture of banana, circles represent the capture of grasshoppers and diamonds represent the capture of newborn mice. Variables with loading greater than 0.70 are indicated on the factor axes.

tongue prehension for mealworms and fruit. The selection pattern is clear and involves movements of both the cranial system (jaws and tongue) and the locomotor system (vertebral axis and forelimbs). The strike of jaw prehension differs from the strike of tongue prehension in that it is faster and induced further from the prey. We suggest the predator is slower and closer when using tongue prehension because the capture efficiency is based on tongue mobility. The two capture modes display specific kinematic features associated with the movement of the jaws, with jaw prehension involving a greater gape angle and quicker mouth opening, as previously observed (Bels and Goosse, 1990). Tongue prehension, on the other hand is slower and is characterized by a tongue protrusion–retraction cycle and tongue deformation similar to that observed for iguanian, scincid and gerrhosaurid lizards (Schwenk and Throckmorton, 1989; Kraklau, 1991; Herrel et al., 1995; Urbani and Bels, 1995; Smith et al., 1999; Meyers and Nishikawa, 2000; Schwenk, 2000). Indeed, in most species using tongue prehension, the tongue deforms and contacts the prey with its dorsal surface (Delheusy et al., 1994) (but see Meyers and Herrel, 2005). The

initialization of the strike is also highly different between tongue and jaw prehension: when using its jaws to capture prey *G. major* extends its forelimbs and raises its head and neck to position its jaws dorsal to the prey, which is crucial for the jaws to be able to grasp the prey (Frazzetta, 1983; Delheusy et al., 1995). During tongue prehension, on the other hand, the head is kept in a more horizontal position and elbow extension is much smaller.

Head positioning is thus largely dependent on the movements of the elements of the locomotor system. The most important component of the locomotor system included in our data set was the angular change at the elbow. A greater elbow extension during the initial positioning allows rapid extension of the head during jaw prehension, providing a higher acceleration and ultimately a greater strike velocity, which is likely to be crucial in determining prey capture success. In support of this statement is the observation that jaw prehension was associated with the capture of active and mobile prey (grasshoppers, newborn mice) where speed of capture may make the difference between a successful or failed strike. Moreover, tongue-based capture of mealworms involved a greater elevation of the neck and was associated with a more rapid strike compared with the capture of banana. Consequently, neck elevation may be associated with the capture of more evasive prey, regardless of the prehension mode used. The extension of the forelimbs during jaw prehension also resulted in a change in the bending of the vertebral axis and differences in the elevation of the neck. In summary, both prey capture modes are kinematically well characterized by cranial and post-cranial movements and are strongly discriminated by the timing of kinematic events.

As predicted, correlations between movements of the jaws and those associated with the locomotor system exist, indicating a functional coupling between the two anatomical systems as observed previously for other vertebrates (for a review, see Higham, 2007b). However, note the factors summarizing neck elevation and head positioning were not correlated, suggesting the head movements are decoupled from the movements of the neck and the rest of the vertebral axis. Besides, and in support of our prediction, the cranial–post-cranial coupling is expressed differently depending on the prehension mode used. During jaw capture, the timings of the head and elbow actions are correlated, suggesting quick head positioning is associated with late movements of the elbow. In contrast to our prediction, however, tongue prehension in *G. major* also involved integration between the jaw and locomotor systems. Indeed, the timing of jaw movements during tongue prehension is dependent on neck elevation, with faster jaw movements and lower gape angles being associated with greater elevation of the neck. Yet, our data also suggest that this coupling may be dependent on prey type (Fig. 3B), with more mobile prey eliciting faster jaw movements and a faster strike, in turn facilitated by movements of the post-cranial system.

Previous studies on tongue-based prey capture in other tetrapods suggest that tongue actions may be decoupled from the locomotor system, especially in systems characterized by extreme protrusion and projection (Wainwright et al., 1991; Deban et al., 1997; Nishikawa, 1999; Nishikawa, 2000). Consequently, tongue prehension may require less integration between the two anatomical systems but this may come at the cost of a reduced attack speed. Although tongue protrusion in *G. major* is qualitatively similar to that observed in other lizards using their tongue to capture prey, our data suggest that these movements are clearly coupled to the movements of the locomotor system. Although this appears to be in contrast to what has been observed for lizards using lingual prehension (e.g. iguanian lizards like chameleons or *Anolis* lizards),

Table 4. Results of a factor analysis performed on the kinematics of cranial and post-cranial movements during tongue prehension in *Gerrhosaurus major*

	Factor 1	Factor 2	Factor 3
Cranial kinematics			
Eigenvalues	3.67	1.80	
% of variance explained (cumulative %)	42.58	35.53 (78.11)	
Time to mouth opening	0.07	0.84	
Maximal gape	0.28	0.78	
Time to maximal gape	0.28	0.90	
Head angle at mouth opening	0.91	0.29	
Head angle at prey contact	0.94	0.29	
Minimal head angle	0.98	-0.00	
Time to minimal head angle	-0.38	0.45	
Post-cranial kinematics			
Eigenvalues	4.92	2.76	1.19
% of variance explained (cumulative %)	38.15	28.76 (66.91)	13.76 (80.67)
Elevation of the neck at mouth opening	0.21	0.91	-0.05
Elevation of the neck at prey contact	0.11	0.97	-0.01
Maximal elevation of the neck	0.05	0.91	0.07
Time to maximal elevation of the neck	-0.66	-0.37	-0.07
Angle of elbow at mouth opening	0.95	0.27	0.05
Angle of elbow at prey contact	0.95	0.13	0.23
Maximal elbow angle	0.91	-0.10	0.30
Time to maximal elbow angle	-0.18	-0.35	0.09
Minimal elbow angle	0.91	0.28	-0.16
Time to minimal elbow angle	-0.03	-0.09	-0.92
Total variation of elbow angle	0.47	-0.36	0.69

Values in bold represent loadings greater than 0.70.

tongue prehension in *G. major* is slow and consequently may allow feedback between jaw and locomotor systems. As a true comparative database is still lacking, it remains difficult to generalize these observations. One notable feature that may be associated with the difference in coupling between the jaw and locomotor systems between these different lizards using tongue prehension is that *G. major* is a more active forager (Cooper and Steele, 1999) than the iguanian lizards studied previously. Indeed, iguanians are typically dedicated ambush foragers that use a 'sit and wait' strategy and wait for the prey to come within strike distance and rely on a rapid strike (Reilly et al., 2007). Consequently, there may not be enough time for on-line integration between the jaw and locomotor systems and thus modulation of the strike in ambush foragers may be largely feedforward.

Cordyliform lizards would be an ideal system in which to further investigate the coupling of jaw and locomotor systems during prey capture as this clade contains both sit-and-wait (*Cordylus*) and active foragers [*Platysaurus*, *Gerrhosaurus* (Cooper and Steele, 1999; Whiting, 2007)]. Moreover, the clade is characterized by species using both prehension modes like members of the genera *Gerrhosaurus* (this study) or *Zonosaurus* (Urban and Bels, 1995) as well as species that use jaw prehension exclusively like lizards of the genus *Platysaurus* (A.H., unpublished observations), thus allowing us to test for jaw and locomotor coupling in species differing in foraging mode and prey capture strategy while minimizing historical effects. Further studies investigating jaw and locomotor coupling in dedicated active foragers like *Varanus* or *Tupinambis* and dedicated ambush foragers like *Pogona* are needed, however, to evaluate these patterns in a broad comparative framework.

In summary, our data show how the integration of jaw and locomotor systems is not reduced to a simple mechanical link. The

observed co-variation between the kinematics of the jaw and locomotor system during prey capture suggests the existence of neural pathways between the two systems allowing feedback, which is crucial to ensure an integration and synchronization between the movements of the elements associated with the two systems.

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