

Separating the effects of prey size and speed on the kinematics of prey capture in the omnivorous lizard *Gerrhosaurus major*

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Abstract Feeding behavior is known to be modulated as prey properties change. During prey capture, external prey properties, including size and mobility, are likely some of the most important components in predator–prey interactions. Whereas prey size has been demonstrated to elicit modulation of jaw movements during capture, how prey speed affects the approach and capture of prey remains unknown. We quantified the kinematics associated with movements of both the feeding and locomotor systems during prey capture in a lizard, *Gerrhosaurus major*, while facing prey differing in size and mobility (newborn mice, grasshoppers, and mealworms). Our data show that the feeding and locomotor systems were recruited differently in response to changes in the size or speed of the prey. The timing of jaw movements and of the positioning of the head are affected by changes in prey size—and speed, to a lesser extent. Changes in prey speed resulted in concomitant changes in the speed of strike and an early and greater elevation of the neck. External prey properties, and prey mobility in particular, are relevant in predator–prey

interactions and elicit specific responses in different functional systems.

Keywords Capture · Prey · Speed · Size · Lizard

Introduction

The acquisition of food and nutrients is essential to the survival of all living beings (Schwenk 2000). Whereas predators have evolved a wide array of morphological specializations allowing them to capture and process food, potential food items are in turn characterized by a variety of defensive structures and behaviors (e.g. chemical defenses, display behavior) that allow them to minimize the potential for predation. In general, adaptations of predators can involve modifications of elements of the jaw system (e.g. tongue papillary; Schwenk 1985; Iwasaki 1990, 2002; Toubeau et al. 1994), the digestive system (Herrel et al. 2008) or may involve the development of distinct behavioral strategies (e.g. foraging mode; see Reilly et al. 2007).

Given the variety of anti-predatory and escape strategies of prey, it is imperative that predators are able to adjust the movements of the musculoskeletal elements involved in the food acquisition process (i.e. the trophic and locomotor systems; Higham 2007). The degree of modulation observed in predators is often variable and may lead to an actual behavioral switch from one strategy to another as is observed for the prey approach strategy in *Anolis carolinensis* (Moermond 1981; Montuelle et al. 2008) or may involve a switch between prey prehension modes as observed in some cordyliform and scincid lizards (Reilly and McBrayer 2007; Montuelle et al. 2009a). Given the importance of modulation in response to prey escape and defensive strategies (Lappin and German 2005), the ability to modulate the

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movements of the feeding system in response to prey properties is essential and often considered a basal trait of vertebrates (Agrawal et al. 1998; Lucas 2004; Popowics and Herring 2006; Ross et al. 2007).

In the context of feeding, two classes of prey properties are likely relevant: internal properties such as food toughness and elasticity, and external properties including the size, mass, and mobility of the prey (Agrawal et al. 1998; Lucas 2004). Whereas internal properties are relevant to food mastication, transport, and swallowing (Lucas 2004), external properties may be more relevant to the success of the capture of prey (Schaerlaeken et al. 2007). Although a considerable body of work has been devoted to the study of modulation of feeding movements and the underlying muscle recruitment patterns, these studies have often been hampered by a lack of quantification of prey properties (e.g. Delheusy and Bels 1992; Smith et al. 1999; Elias et al. 2000; but see Vincent et al. 2006; Schaerlaeken et al. 2007). Exceptions are studies on food breakdown in mammals where modulation of the jaws during prey processing has been shown to be determined by food texture, toughness and the modulus of elasticity (Lucas 2004).

Typically, studies of predator–prey interactions are based on a classification of prey into different arbitrary types or categories that typically aim to capture some aspect of the food properties relevant to the predator, e.g. large versus small prey, fast versus slow prey, etc., (e.g. Vanhooydonck et al. 2007; Kohlsdorf et al. 2008). However, the classification of prey into a set of discrete types is obviously a simplification of reality. In essence, any given food item can be described quantitatively by a combination of the different external and internal properties. These properties are elements likely relevant to the predator and may allow the discrimination of potential food items. Prey discrimination by a predator may involve, amongst others, different sensory modalities including vision (Kaufman et al. 1996; Ott et al. 2004), smell (Schwenk 1993; Cooper and Perez-Melado 2001), chemoreception (Schwenk 1995), mechanoreception (Berkhoudt 1979), or a combination thereof. Interestingly, although the modulation of movements of the predator in accordance to prey type has been demonstrated in several amphibians and reptiles (Delheusy and Bels 1992; Anderson 1993; Anderson and Nishikawa 1993; Urbani and Bels 1995; Deban 1997; Smith et al. 1999; Schwenk 2000; Schaerlaeken et al. 2007), surprisingly little is known about which aspects of a prey precisely trigger modulation.

Two major external prey properties that are likely relevant to prey capture are prey size and prey speed. Prey size, for example, has been demonstrated to affect cranial and postcranial movements in snakes (Vincent et al. 2006), but it can also be expected to directly affect jaw movements and the positioning of the head during capture. Indeed, prey size

has been shown to affect the prey capture strategy (use of tongue or jaws) and the degree of involvement of the locomotor system during prey capture in frogs (Anderson 1993; Anderson and Nishikawa 1993; Valdez and Nishikawa 1997). Prey speed, on the other hand, represents an indicator of prey activity or prey mobility and likely also correlates with prey evasiveness (Vanhooydonck et al. 2007). Consequently, prey speed is expected to affect the movements of both the postcranial and cranial systems, as faster prey will likely require a more rapid attack and faster jaw closure. However, understanding which external prey properties may be driving modulation of feeding behavior may be difficult as these often co-vary.

In the present study, we specifically investigate the contribution of two external prey properties, size, and speed, to the modulation of the kinematics of the feeding and locomotor systems during prey capture in a lizard (*Gerrhosaurus major*). *Gerrhosaurus major* was selected because of its omnivorous diet which enables us to test for a wide range of different prey sizes and speeds by using newborn mice, grasshoppers, and mealworms. We aim to explicitly separate the roles of prey size and speed on the kinematics of prey capture, and thus identify the functional response of the predator to each of these external prey properties. To do so, we test for correlations between prey size and the speed of the prey during the actual capture event, and several multivariate indicators describing the kinematics of the feeding and locomotor systems.

Materials and methods

Experimental protocol and animals

The experimental procedure is identical to the one presented previously and will be described only briefly here (Montuelle et al. 2009a). A 2 m long and 30 cm wide trackway was covered with a nonslip green plastic carpet. On one side of the track, three synchronized high-speed cameras AVT Pike F-032B (Allied Vision Technologies, Stadroda, Germany) set at 200 fps were used to film prey capture behavior in *Gerrhosaurus major*. One camera was set in frontal view, a second one in lateral view and the third one tilted down in an oblique dorsal view; all three being centered on the prey item. The overlapping set-up of the cameras enabled us to retrieve three-dimensional movements of both prey and predator.

Five male adult *Gerrhosaurus major* of similar size were used (snout-vent length: 208.6 ± 8.0 mm, cranial length: 39.0 ± 1.2 mm, mass: 235.6 ± 22.3 g). During the recording sessions, the animals were placed at the side of the track opposite to the prey and we waited for them to detect and approach spontaneously. Three prey items were offered:

newborn mice (*Mus musculus*; length: 29.8 ± 3.6 mm), grasshoppers (*Locusta migratoria*; length: 45.0 ± 1.3 mm), and mealworms (*Tenebrio molitor*; length: 36.8 ± 7.5 mm). The prey items were selected because they reflect natural omnivorous diet of *Gerrhosaurus major* and represent a wide range of prey sizes and degree of mobility. Overall, 32 sequences were recorded: seven capture events of newborn mice (representing three of the five individuals: three, zero, one, zero and three sequences, respectively), nine capture events of grasshoppers (representing four of the five individuals: zero, two, three, three and one sequences, respectively), and 16 capture events of mealworms (representing the five individuals: one, two, four, four and five sequences, respectively).

Quantification of prey properties

Two prey properties were quantified. Firstly, the size of each prey item was measured prior to the onset of the recording session using digital calipers. Secondly, the position of the prey (P) was digitized and the screen-coordinates were calculated on the three synchronized views using a custom Matlab routine (Loco 2.8). The three sets of two-dimensional screen-coordinates (one set per camera) were used to calculate the three-dimensional coordinates of prey position using a DLT-routine (Hartley and Sturm 1997). The three-dimensional reconstruction of the movements of the prey enabled us to calculate prey velocity as the derivative of the three-dimensional coordinates of the position over time, and allowed us to quantify the changes in prey velocity while approached by the predator. From this profile, we extracted the peak velocity of the prey during the approach of the predator. Interestingly, the peak prey velocity was independent of prey size (Fig. 1).

Three-dimensional kinematics data set

Markers were painted on the body and the head with non-toxic white paint (Fig. 2). Representing the cranial system, the tip of the upper jaw (UJ) and of the lower jaw (LJ), the corner of the mouth (CM), the anterior corner of the eye (EY), the mid-sagittal point between both eyes (H) and the back of the parietal bones (O) were digitized. For the vertebral axis were digitized the pectoral girdle (SG), the neck (NE) as the mid-way point between the back of the parietal bones (O) and the pectoral girdle (SG), the pelvic girdle (PG), and one marker (V) which has been placed so that the pectoral girdle point (SG) is the middle of the NE-V line (Fig. 2). To quantify the movements of the forelimbs, the left shoulder (SH), the left elbow (EL), and the left wrist (W) were digitized. Similarly to the prey position, the position of the 13 landmarks was digitized on the three synchronized views and the three-dimensional coordinates were

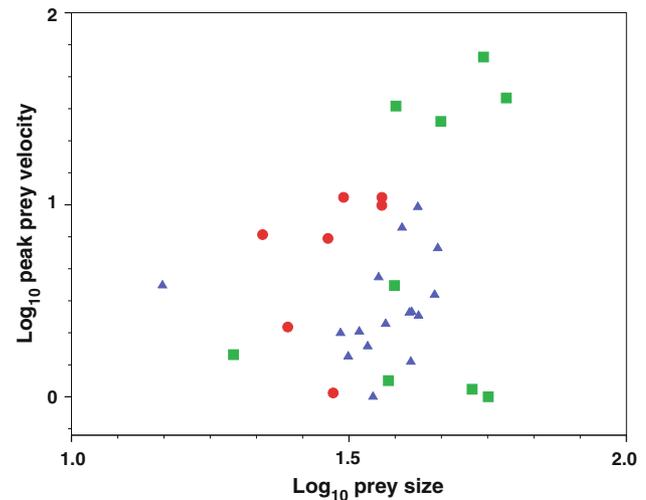


Fig. 1 Independence between prey properties used in this study. Log_{10} -transformed prey size is not correlated to log_{10} -transformed prey peak velocity ($r = 0.25$; $P = 0.17$). Circles represent the capture of newborn mice, squares represent the capture of grasshopper, and triangles represent the capture of mealworms

calculated from the three sets of two-dimensional screen-coordinates.

The movements of the cranial system (jaw and head positioning; Fig. 3), of the postcranial system (forelimb and body axis; Fig. 4), and features associated with the actual strike (distances and peak velocities) were considered separately. 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 (Figs. 3, 4).

For the cranial system, five variables were extracted from two kinematical profiles (Fig. 3). First, the gape angle is defined as the angle subtended by the upper jaw, the corner of the mouth and the lower jaw (angle UJ-C-LJ; Fig. 3a). The time to mouth opening, the maximal gape angle, and the time to maximal gape were extracted (Table 1). Second, the head angle is calculated as the angle between the long axis of the head (line O-H) and the long axis of the neck (line V-NE) (Fig. 3b). The minimal head angle (describing the most ventrally flexed position of the head), and the time to the minimal head angle were extracted (Table 1).

For the postcranial system, seven variables were extracted from two kinematical profiles (Fig. 4). First, the elevation of the neck is calculated as the difference between the Z-coordinate of the neck point (NE) with the Z-coordinate of the neck at rest position (Fig. 4a). The maximal elevation of the neck, and the time to the maximal elevation of the neck were extracted (Table 1). Second, the elbow angle is defined as the angle subtended by the shoulder, the elbow, and wrist markers (angle SH-EL-W; Fig. 4b). The

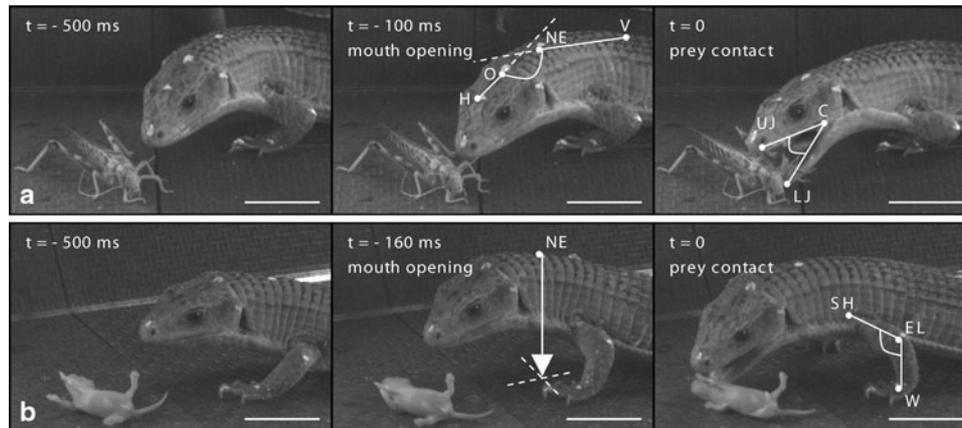


Fig. 2 Representative sequences of prey capture behavior in *Gerrhosaurus major* when facing a grasshopper (**a**) and a newborn mouse (**b**), recorded at 200 frames per second. **a** Illustration of the markers digitized to quantify movements of the cranial system: the mid-sagittal point between both eyes (*H*), the back of the occipital bones (*O*), the mid-way point between *O* and the pectoral girdle (*NE*), the mirror point of *NE* relative to the pectoral girdle point (*V*), the upper jaw (*UJ*), the lower jaw (*LJ*) and the corner of the mouth (*C*). Construction of the

kinematic variables is illustrated: head angle is the angle between the lines *O-H* and *V-NE*, and gape angle is the angle *UJ-C-LJ*. **b** Illustration of the markers digitized to quantify movements of the postcranial system: the mid-way point between the occipital bones *O* and the pectoral girdle (*NE*), the shoulder (*SH*), the elbow (*EL*) and the wrist (*W*). Construction of the kinematic variables is illustrated: neck elevation is the *Z*-coordinate of *NE*, and elbow angle is the angle *SH-EL-W*. See “Materials and methods” for details. Scale bar = 2 cm

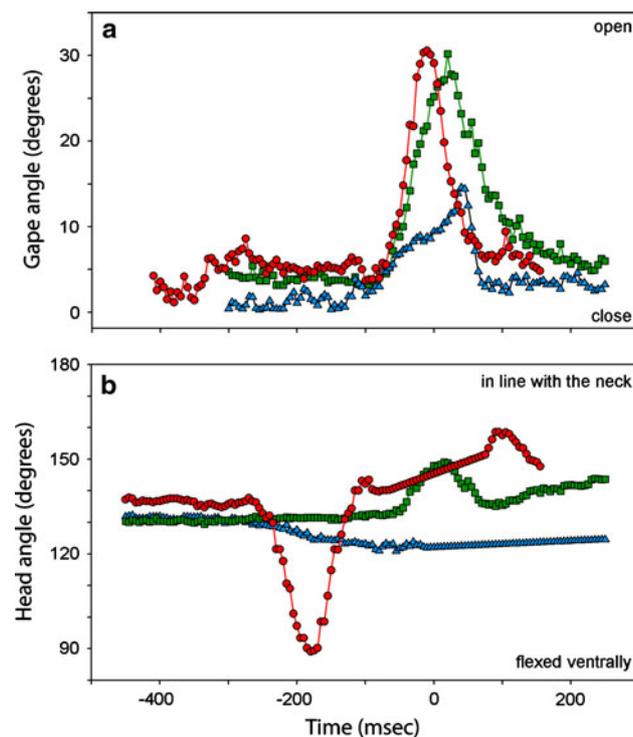


Fig. 3 Kinematic profiles of the movements of the cranial system during capture of three different prey types by *Gerrhosaurus major*: changes in gape angle (**a**) and positioning of the head relative to the neck over time (head angle; **b**). On both profiles, each curve illustrates one prey type: circles represent the capture of newborn mice, squares represent the capture of grasshopper, and triangles represent the capture of mealworms

minimal and maximal elbow angles were extracted, along with their respective times (Table 1).

Three strike features were calculated from the predator–prey distance profile over time (distance *EY-P* over time). The total strike distance was retained. Additionally, the peak strike velocity and the time to the peak strike velocity were calculated as the normed derivative of the three-dimensional coordinates of the predator eye (*EY*) through time.

Statistical analysis

SPSS 15.0 for Windows (SPSS Inc., Chicago, IL, USA) was used for all statistical analyses. Prior to analysis, kinematic data were \log_{10} -transformed to fulfill assumptions of normality and homoscedasticity. Similarly, prey size and peak prey velocity were also \log_{10} -transformed. Initially, a MANCOVA was performed on the complete data set (cranial, postcranial and strike variables) to test for an effect of the size of the predator on the kinematics of prey capture. Since predator size effects were not significant they were not considered in subsequent analyses.

Next, our kinematic data set was divided into three matrices representing movements of the cranial system (jaws and head), movements of the postcranial system (forelimb and vertebral axis) and the strike features (distance and velocity). All variables were introduced into a correlation matrix together with \log_{10} -transformed prey size and peak prey velocity. This correlation matrix tests for

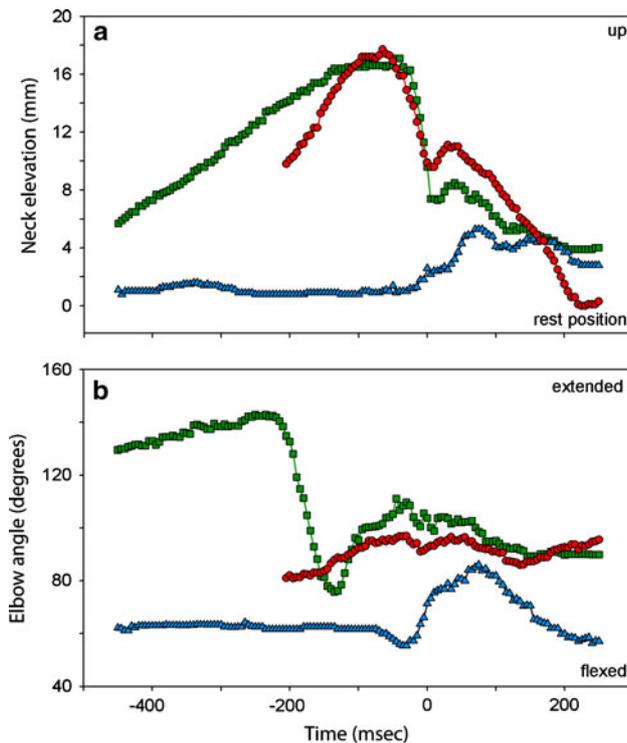


Fig. 4 Representative kinematic profiles of the movements of the postcranial system during capture of three different prey types by *Gerrhosaurus major*: changes in neck elevation (a) and elbow angle over time (b). On both profiles, each curve illustrates one prey type: circles represent the capture of newborn mice, squares represent the capture of grasshopper, and triangles represent the capture of mealworms

co-variation of predator kinematics with external prey properties and thus evaluates predator–prey interactions.

Results

Prey capture behavior

Gerrhosaurus major uses two different prehension modes to capture food items: jaw prehension for newborn mice (78.6%) and grasshoppers (91.3%), and tongue prehension for mealworms (100%) and banana (92.9%). Modulation of the kinematics of the predator associated with different prehension modes have been described previously (Montuelle et al. 2009a) and will not be discussed here.

The approach is initiated from up to almost 20 cm away from the prey and the animals engage in the actual strike at distances varying from 2 to 10 cm. When strike initiation distance is reached, the predator pauses to configure its body and strikes at a speed around 50 cm s^{-1} (Table 1). During the strike, the jaws open and close with a typical gape cycle as has been observed in other lizards (Fig. 3a; Table 1; Schwenk 2000). During the strike the position of

the head relative to that of the neck changes and involves a dorsad rotation at the craniocervical joint (Fig. 3b; Table 1) as has been observed during prey capture in other lizard species (head-up capture strategy in *Anolis carolinensis*; Montuelle et al. 2008). The limbs of the predator are also active during the strike and the elbow joint is extended to accelerate the head towards the prey (Fig. 4a; Table 1). Note that the elbow joint may flex prior to the strike such that the total extension is greater during the actual strike. The vertebral axis and especially the neck are actively involved during the strike as well, as the neck may rise up to 3 cm from its rest position prior to the strike (Fig. 4b; Table 1).

Predator–prey interactions

Our data demonstrate significant correlations between the movements of the predator and specific external properties, i.e. prey size and peak prey velocity during the predator approach (Figs. 5, 6). Prey size is correlated with two cranial variables (Fig. 5a, c): the time to maximal gape angle ($r = -0.38$; $P = 0.03$; Fig. 5a) and the time to minimal head angle, which represents the most flexed position of the head ($r = -0.36$; $P = 0.04$; Fig. 5c). This indicates that the movements of the predator are modulated according to prey size (in accordance with), especially the timing of the movements of the cranial elements. As prey gets larger, the maximal opening of the jaws occurs earlier in the prey capture event. Jointly, the head achieves its most flexed position earlier. Consequently, in comparison with the capture of small preys, the capture of large preys involves movements resulting in the early preparation of the cranial elements.

Interestingly, the variables correlated with prey size tend to be associated with peak prey velocity too. Indeed, peak prey velocity shows a tendency towards correlation with the time to maximal gape angle ($r = -0.30$; $P = 0.09$; Fig. 5b) and the time to minimal head angle ($r = -0.34$; $P = 0.06$; Fig. 5d). This suggests the timing of movements of the cranial elements may be modulated in response to prey mobility, with the capture of fast thus evasive preys being associated with the early maximal opening of the jaws and the early positioning of the head.

Peak velocity of the prey during the approach of the predator is significantly associated with two variables, and tends to be with a third one (Fig. 6). Peak prey velocity is positively correlated with peak strike velocity of the predator ($r = 0.43$; $P = 0.01$; Fig. 6a) indicating the strike is quicker on evasive preys. Peak prey velocity is also correlated with the time to maximal elevation of the neck ($r = -0.37$; $P = 0.04$; Fig. 6c). This link between the timing of movements of the neck and the prey velocity demonstrates that the capture of evasive preys involves the early

Table 1 Summary of the prey properties, the kinematics associated with the movements of the cranial and postcranial systems, and the characteristics of the strike during prey capture behavior in *Gerrhosaurus major*

	Newborn mice (<i>N</i> = 7)	Grasshoppers (<i>N</i> = 9)	Mealworms (<i>N</i> = 16)
Prey properties			
Size (mm)	29.8 ± 2.0	45.0 ± 4.3	36.8 ± 1.9
Peak velocity (cm s ⁻¹)	6.0 ± 1.5	17.1 ± 7.1	2.5 ± 0.6
Cranial kinematics			
Time to mouth opening (ms)	-241 ± 53	-116 ± 7	-92 ± 6
Maximal gape angle (°)	29.5 ± 1.5	26.6 ± 2.1	18.6 ± 0.7
Time to maximal gape angle (ms)	-4 ± 5	7 ± 14	71 ± 7
Minimal head angle (°)	124.0 ± 8.2	114.5 ± 4.1	119.9 ± 2.4
Time to minimal head angle (ms)	-41 ± 72	-300 ± 45	-52 ± 42
Postcranial kinematics			
Maximal elevation of the neck (mm)	20.7 ± 2.4	20.2 ± 3.8	16.3 ± 1.1
Time to maximal elevation of the neck (ms)	-101 ± 27	-82 ± 86	85 ± 34
Maximal elbow angle (°)	105.8 ± 8.8	102.2 ± 10.5	89.7 ± 5.4
Time to maximal elbow angle (ms)	126 ± 44	-92 ± 53	120 ± 40
Minimal elbow angle (°)	65.8 ± 8.0	66.4 ± 7.2	68.9 ± 4.2
Time to minimal elbow angle (ms)	-204 ± 90	-88 ± 87	-209 ± 54
Strike kinematics			
Strike distance (mm)	43.0 ± 6.0	47.2 ± 6.7	33.2 ± 1.5
Speed of strike (cm s ⁻¹)	116.7 ± 59.6	72.4 ± 7.1	21.6 ± 2.4
Time to maximal speed of strike (ms)	-8 ± 6	-12 ± 6	-3 ± 6

Table entries are means ± the standard error of the mean. See “Material and methods” for details

positioning of the anterior region of the vertebral axis. Additionally, the correlation of peak prey velocity with the maximal elevation of the neck approaches significance ($r = 0.34$; $P = 0.06$; Fig. 6e). This suggests the positioning of the neck is modulated according to prey mobility, being set higher when facing evasive preys.

Interestingly, the variables significantly associated with prey mobility are independent of prey size (Fig. 6b, d, f). This indicates that prey mobility has specific effects on the prey capture behavior of *Gerrhosaurus major*, contrary to prey size.

Discussion

Our data show that the kinematics of prey capture are modulated with respect to both prey type and prey speed in the lizard *Gerrhosaurus major*. These observations are in accordance with previous studies that have tested for a prey type effect on kinematic features of both prey capture and transport in squamates (Herrel et al. 1996, 1999; Montuelle et al. 2009a, b) and emphasize the relevance of predator–prey interactions in the study of the evolution of feeding behavior. Our observations complete our understanding of the prey properties effects on feeding behavior by presenting the modulation of the movements of the postcranial elements (see also Vincent et al. 2006).

Although feeding behavior has been demonstrated to be modulated in response to prey type in tetrapods in general (Lucas 2004; Popowics and Herring 2006; Ross et al. 2007), the actual quantification of prey properties and explicit tests of their effect on feeding kinematics have been largely restricted to studies quantifying the effects of internal prey properties (e.g. toughness, modulus of elasticity) on the modulation of chewing in mammals (Agrawal et al. 1998; Lucas 2004; Popowics and Herring 2006). In most other previous studies, variation in prey has been categorized rather than quantified. Observed effects include behavioral shifts (Reilly and McBrayer 2007; Montuelle et al. 2009a), the modulation of the movements of the feeding system (Schaerlaeken et al. 2007), and also those of the postcranial system (Vincent et al. 2006).

In this study, we specifically quantified two external prey properties, i.e. prey size and speed, as we hypothesized that these are among the principal sources of information collected by the predator, allowing it to adjust its feeding movements accordingly. Indeed, although chemical discrimination is used by squamate predators in general (Cooper 1990, 1994; Halpern and Martinez-Marcos 2003) and has been demonstrated to be important for *Gerrhosaurus* species (*G. nigrolineatus* in Cooper 1992; *G. validus* in Cooper and Steele 1999), sight is likely to be the main sensory mode used to identify the prey during capture. Support for this statement comes from observations where a

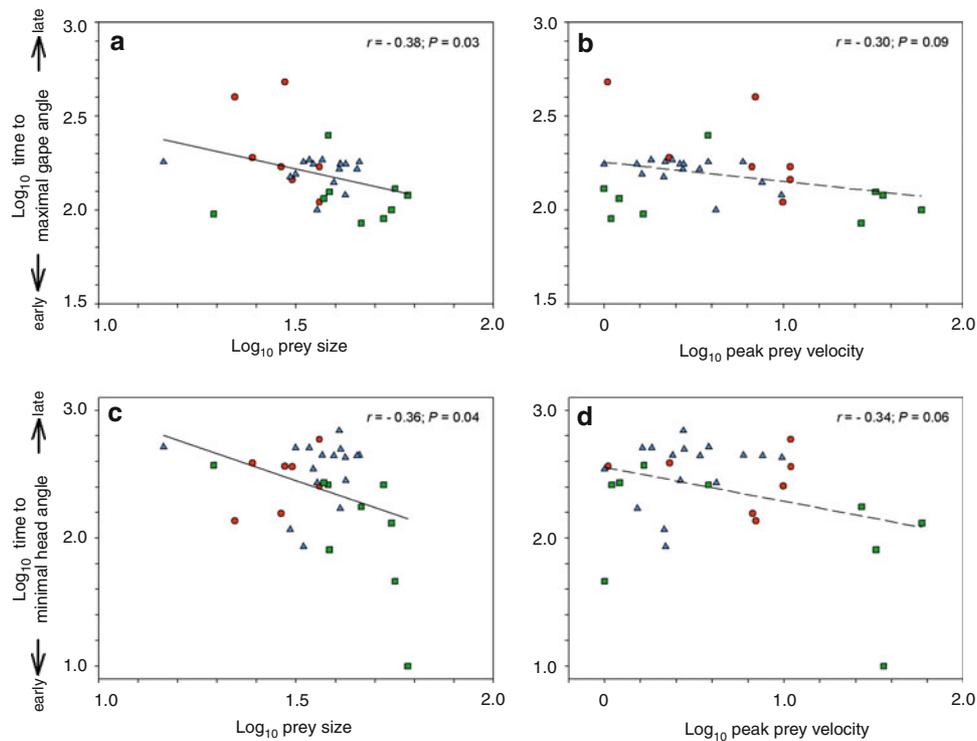


Fig. 5 Correlations between \log_{10} transformed prey size and the kinematics associated with the cranial and postcranial movements involved in prey capture behavior in *Gerrhosaurus major* (on the left; **a**, **c**). In order to compare the effects of prey size and mobility, the kinematic variables correlated with prey size were also plotted with peak prey velocity (on the right; **b**, **d**). **a** Prey size is negatively correlated with time to maximal gape angle ($r = -0.38$; $P = 0.03$), indicating maximal gape angle occurs earlier when catching large preys. **b** Similarly, note time to maximal gape angle tends to be correlated to peak prey velocity

($r = -0.30$; $P = 0.09$). **c** Prey size is negatively correlated with time to minimal head angle ($r = -0.36$; $P = 0.04$), indicating the most ventrally flexed position of the head is achieved earlier when catching large preys. **d** Similarly, note time to minimal head angle tends to be correlated to peak prey velocity ($r = -0.34$; $P = 0.06$). These scatter plots illustrate how prey size strongly affect cranial kinematics, and how prey size effects are concomitant with prey mobility effects. *Circles* represent the capture of newborn mice, *squares* represent the capture of grasshopper, and *triangles* represent the capture of mealworms

spontaneous movement of the prey instantaneously triggers the strike of the predator without eliciting any prior interest (pers. obs.; see also Kaufman et al. 1996). Our data demonstrate modulation of movements involved in prey capture in the lizard *G. major* in response to both prey size and mobility. This response involves both the cranial and postcranial kinematics as well as behavioral changes involved in the actual strike event (e.g. speed of strike; see Fig. 6). This observation provides additional support for the importance and role of the locomotor system during feeding (Vincent et al. 2006; Higham 2007; Montuelle et al. 2008, 2009a).

The two external prey properties studied here have different effects on the kinematics of the movements of the two functional systems involved in predatory behavior of *Gerrhosaurus major*. Indeed, the predator response to prey size largely involves a modulation of the movements of the feeding apparatus (in accordance with Anderson 1993 and Schaerlaeken et al. 2007). In contrast, the role of the entire body is adjusted and enhanced, particularly the movements of the anterior region of the vertebral axis, in order to produce greater speeds of strike in response to changes in prey mobility. These observations indicate a strong functional

integration of the feeding and locomotor systems during prey capture as observed previously in other vertebrates (Higham 2007). This integration allows the predator to specifically respond to the changes in external prey properties, thus likely improving its capture success. Our results emphasize the importance for a predator to collect and integrate the appropriate prey stimuli in order to successfully discriminate and identify the food items. Consequently, both the prey detection and foraging mode of a predator may affect predator–prey interactions and are likely crucial in providing an individual with a selective advantage during prey capture.

Interestingly, prey mobility appears to be a more relevant properties for the predator, than prey size. Indeed, changes in prey mobility are correlated with changes in specific postcranial variables (i.e. neck movements) which are not linked to changes in prey size (Figs. 6c, e vs. 6d, f). In contrast, the cranial kinematics that answer changes in prey size (i.e. timing of jaw movements and head positioning) tend to be associated with prey mobility too (Figs. 5a, c vs. 5b, d). Consequently, in *Gerrhosaurus major*, prey size effects seem to be concomitant with prey mobility

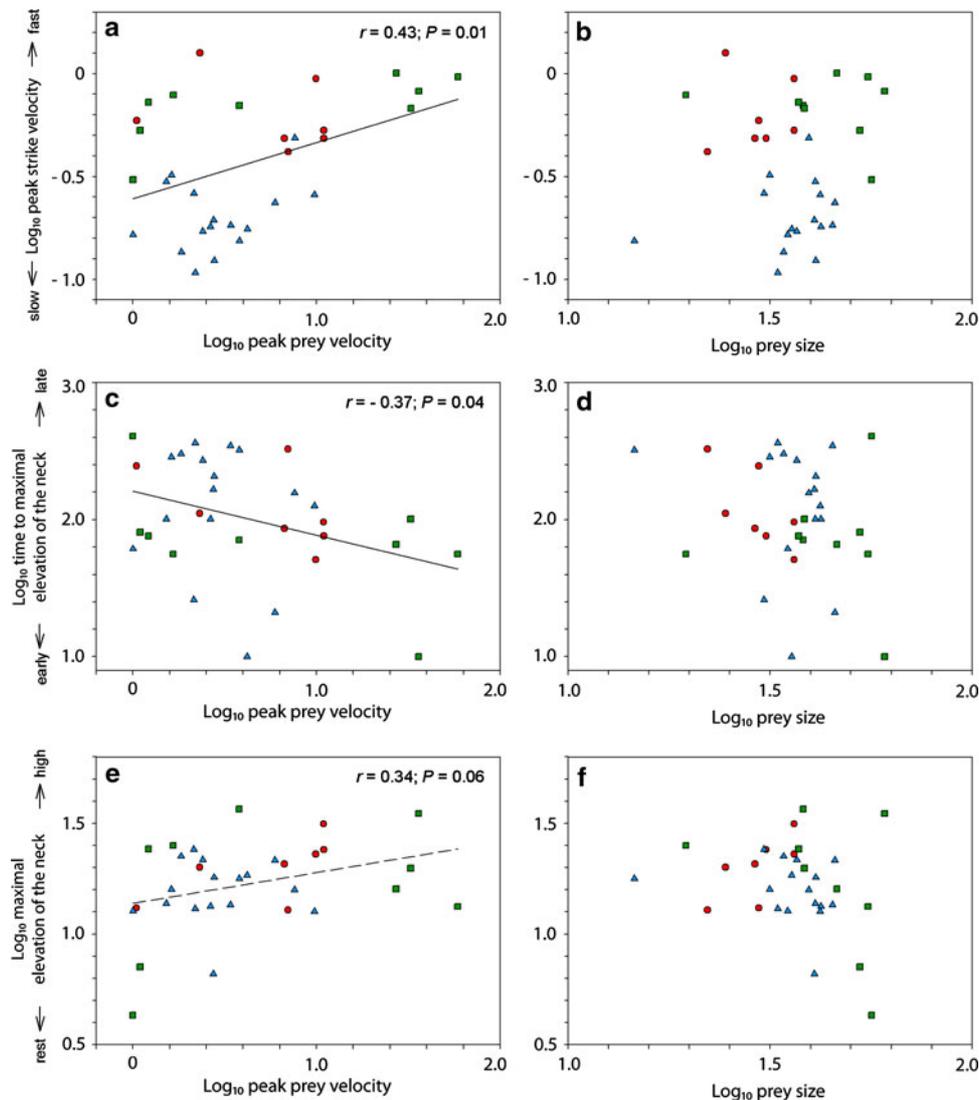


Fig. 6 Correlations between \log_{10} -transformed peak prey velocity and the kinematics associated with the cranial and postcranial movements involved in prey capture behavior in *Gerrhosaurus major* (on the left; **a**, **c**, **e**). In order to compare the effects of prey mobility and size, the kinematic variables correlated with peak prey velocity were also plotted with prey size (on the right; **b**, **d**, **f**). **a** Peak prey velocity is positively correlated with peak strike velocity ($r = 0.43$; $P = 0.01$), indicating strike is quicker on mobile preys. **b** Note peak strike velocity is independent from prey size ($r = -0.01$; $P = 0.96$). **c** Peak prey velocity is negatively correlated with time to maximal elevation of the neck ($r = -0.37$; $P = 0.04$), indicating the most elevated position of the neck

occurs earlier when catching mobile preys. **d** Note time to maximal elevation of the neck is independent from prey size ($r = -0.26$; $P = 0.16$). **e** Peak prey velocity tends to be positively correlated with maximal elevation of the neck ($r = 0.34$; $P = 0.06$), indicating the neck raises higher when catching mobile preys. **f** Note maximal elevation of the neck is independent from prey size ($r = -0.26$; $P = 0.15$). These scatter plots illustrate how prey mobility strongly affect prey capture behavior, particularly postcranial kinematics. *Circles* represent the capture of newborn mice, *squares* represent the capture of grasshopper, and *triangles* represent the capture of mealworms

effects. Therefore, although prey size effects have been widely investigated, our data shows that the study of prey mobility effects is likely to provide interesting insights in the mechanisms of predator–prey interactions, thus in the inter-specific component of evolution.

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References

- Agrawal KR, Lucas PW, Bruce IC, Prinz JF (1998) Food properties that influence neuromuscular activity during human mastication. *J Dent Res* 77:1931–1938
- Anderson CW (1993) The modulation of feeding behavior in response to prey type in the frog *Rana pipiens*. *J Exp Biol* 179:1–12
- Anderson CW, Nishikawa KC (1993) A prey-type dependent hypoglossal feedback system in the frog *Rana pipiens*. *Brain Behav Evol* 42:189–196
- Berkhoudt H (1979) The morphology and distribution of cutaneous mechanoreceptors (Herbst and Grandry corpuscles) in bill and tongue of the Mallard (*Anas Platyrhynchos* L.). *Neth J Zool* 30:1–34
- Cooper WE Jr (1990) Prey odor detection by Teiid and Lacertid lizards and the relationships of prey odor detection to foraging mode in lizard families. *Copeia* 1990:237–242
- Cooper WE Jr (1992) Prey odor discrimination and poststrike elevation in tongue flicking by a Cordylid lizard, *Gerrhosaurus nigrolineatus*. *Copeia* 1992:146–154
- Cooper WE Jr (1994) Chemical discrimination by tongue-flicking in lizards: a review with hypothesis on its origin and its ecological and phylogenetic relationships. *J Chem Ecol* 20:439–487
- Cooper WE Jr, Perez-Melado V (2001) Location of fruit using only airborne odor cues by a lizard. *Physiol Behav* 74:339–342
- Cooper WE Jr, Steele LJ (1999) Lingually mediated discriminations among prey chemicals and control stimuli in Cordyliform lizards: presence in a Gerrhosaurid and absence in two Cordylids. *Herpetologica* 55:361–368
- Deban SM (1997) Modulation of prey-capture behavior in the plethodontid salamander *Ensatina eschscholtzii*. *J Exp Biol* 200:1951–1964
- Delheusy V, Bels VL (1992) Kinematics of feeding behaviour in *Oplurus cuvieri* (Reptilia: Iguanidae). *J Exp Biol* 170:155–186
- Elias JA, McBrayer LD, Reilly SM (2000) Prey transport kinematics in *Tupinambis teguixin* and *Varanus exanthematicus*: conservation of feeding behavior in ‘chemosensory-tongued’ lizards. *J Exp Biol* 203:791–801
- Halpern M, Martinez-Marcos A (2003) Structure and function of the vomeronasal system: an update. *Prog Neurobiol* 70:245–318
- Hartley R, Sturm P (1997) Triangulation. *Comput Vis Image Underst* 68:146–157
- Herrel A, Cleuren J, De Vree F (1996) Kinematics of feeding in the lizard *Agama stellio*. *J Exp Biol* 199:1727–1742
- Herrel A, Verstappen M, De Vree F (1999) Modulatory complexity of the feeding repertoire in Scincid lizards. *J Comp Physiol* 185:501–518
- Herrel A, Huyghe K, Vanhooydonck B, Backeljau T, Breugelmanns K, Grbac I (2008) Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. *PNAS* 105:4792–4795
- Higham TE (2007) The integration of locomotion and prey capture in vertebrates: morphology, behavior and performance. *Integr Comp Biol* 47:82–95
- Iwasaki S (1990) Fine structure of the dorsal lingual epithelium of the lizard *Gekko japonicus* (Lacertilia, Gekkonidae). *Am J Anat* 187:12–20
- Iwasaki S (2002) Evolution of the structure and function of the vertebrate tongue. *J Anat* 201:1–13
- Kaufman JD, Burghardt GM, Phillips JA (1996) Sensory cues and foraging decisions in a large carnivorous lizard, *Varanus albigularis*. *Anim Behav* 52:727–736
- Kohlsdorf T, Grizante MB, Navas CA, Herrel A (2008) Head shape evolution in Tropicurinae lizards: does locomotion constrain diet? *J Evol Biol* 21:781–790
- Lappin AK, German M (2005) Feeding behavior modulation in the leopard-lizard (*Gambelia wislizenii*): effects of noxious versus innocuous prey. *Zoology* 108:287–295
- Lucas PW (2004) Dental functional morphology: how teeth work. Cambridge University Press, Cambridge
- Moermond TC (1981) Prey-attack behavior of Anolis lizards. *Z Tierpsychol* 56:128–136
- Montuelle SJ, Daghfous G, Bels VL (2008) Effects of locomotor approach on feeding kinematics in the green Anole (*Anolis carolinensis*). *J Exp Zool* 309A:563–567
- Montuelle SJ, Herrel A, Libourel P-A, Reveret L, Bels VL (2009a) Locomotor-feeding coupling during prey capture in a lizard (*Gerrhosaurus major*): effects of prehension mode. *J Exp Biol* 212:768–777
- Montuelle SJ, Herrel A, Schaerlaeken V, Metzger K, Mutuyeyezu A, Bels VL (2009b) Inertial feeding in the teiid lizard *Tupinambis merianae*: the effect of prey size on the movements of hyolingual apparatus and the cranio-cervical system. *J Exp Biol* 212:2501–2510
- Ott M, Ostheim J, Sherbrooke WC (2004) Prey snapping and visual distance estimation in Texas horned lizards, *Phrynosoma cornutum*. *J Exp Biol* 207:3067–3072
- Popowicz TE, Herring SW (2006) Teeth, jaws and muscles in mammalian mastication. In: Bels VL (ed) Feeding in domestic vertebrates: from structure to behaviour. CABI Publishing, Oxfordshire
- Reilly SM, McBrayer LD (2007) Prey-capture and processing behaviour and the evolution of lingual and sensory characteristics: divergences and convergences in lizard feeding biology. In: Reilly SM, McBrayer LD, Miles DB (eds) Lizard ecology: the evolutionary consequences of foraging mode. Cambridge University Press, New York, pp 302–333
- Reilly SM, McBrayer LD, Miles DB (2007) Lizard ecology: the evolutionary consequences of foraging mode. Cambridge University Press, New York
- Ross CF, Eckhardt A, Herrel A, Hylander WL, Metzger KA, Schaerlaeken V, Washington RL, Williams SH (2007) Modulation of intra-oral processing in mammals and lepidosaurs. *Integr Comp Biol* 47:118–136
- Schaerlaeken V, Meyers JJ, Herrel A (2007) Modulation of prey capture kinematics and the role of lingual sensory feedback in the lizard *Pogona vitticeps*. *Zoology* 110:127–138
- Schwenk K (1985) Occurrence, distribution and functional significance of taste buds in lizards. *Copeia* 1985:91–101
- Schwenk K (1993) Are Geckos olfactory specialists? *J Zool Lond* 229:289–302
- Schwenk K (1995) Of tongue and noses: chemoreception in lizards and snakes. *TREE* 10:7–12
- Schwenk K (2000) Feeding: form, function and evolution in Tetrapod vertebrates. Academic Press, New York
- Smith TL, Kardong KV, Bels VL (1999) Prey capture behavior in the blue-tongued skink, *Tiliqua scincoides*. *J Herp* 33:362–369
- Toubeau G, Cotman C, Bels VL (1994) Morphological and kinematic study of the tongue and buccal cavity in the lizard *Anguis fragilis* (Reptilia: Anguillidae). *Anat Rec* 240:423–433
- Urbani JM, Bels VL (1995) Feeding behavior in two scleroglossan lizards: *Lacerta viridis* (Lacertidae) and *Zonosaurus laticaudatus* (Cordylidae). *J Zool Lond* 236:265–290
- Valdez CM, Nishikawa KC (1997) Sensory modulation and behavioral choice during feeding in the Australian frog, *Cyclorana novae-hollandiae*. *J Comp Physiol* 180A:187–202
- Vanhooydonck B, Herrel A, Van Damme R (2007) Interactions between habitat use, behaviour and the trophic niche of Lacertid lizards. In: Reilly SM, McBrayer LD, Miles DB (eds) Lizard ecology: the evolutionary consequences of foraging mode. Cambridge University Press, New York, pp 427–449
- Vincent SE, Moon BR, Shine R, Herrel A (2006) The functional meaning of “prey size” in water snakes (*Nerodia fasciata*, Colubridae). *Oecologia* 147:204–211