RESEARCH ARTICLE

Flexibility in locomotor–feeding integration during prey capture in varanid lizards: effects of prey size and velocity

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SUMMARY

Feeding movements are adjusted in response to food properties, and this flexibility is essential for omnivorous predators as food properties vary routinely. In most lizards, prey capture is no longer considered to solely rely on the movements of the feeding structures (jaws, hyolingual apparatus) but instead is understood to require the integration of the feeding system with the locomotor system (i.e. coordination of movements). Here, we investigated flexibility in the coordination pattern between jaw, neck and forelimb movements in omnivorous varanid lizards feeding on four prey types varying in length and mobility: grasshoppers, live newborn mice, adult mice and dead adult mice. We tested for bivariate correlations between 3D locomotor and feeding kinematics, and compared the jaw–neck–forelimb coordination patterns across prey types. Our results reveal that locomotor–feeding integration is essential for the capture of evasive prey, and that different jaw–neck–forelimb coordination patterns are used to capture different prey types. Jaw–neck–forelimb coordination is indeed significantly altered by the length and speed of the prey, indicating that a similar coordination pattern can be finely tuned in response to prey stimuli. These results suggest feed-forward as well as feed-back modulation of the control of locomotor–feeding integration. As varanids are considered to be specialized in the capture of evasive prey (although they retain their ability to feed on a wide variety of prey items), flexibility in locomotor–feeding integration in response to prey mobility is proposed to be a key component in their dietary specialization.

Key words: integration, flexibility, prey properties, Varanus, kinematics, jaw prehension.

INTRODUCTION

In many vertebrate lineages, the function and morphology of the feeding structures are influenced by the adaptive pressures that stem from diet. The effects include adaptation of the jaw apparatus (e.g. Rodriguez-Robles et al., 1999; Ferry-Graham et al., 2002; Van Cakenberghe et al., 2002; Metzger and Herrel, 2005; Santana et al., 2010; Hampton, 2011; Perry et al., 2011), teeth (e.g. Hotton, 1955; Herrel et al., 1997; Herrel et al., 2004; Santana et al., 2011; Kupczik and Stynder, 2012), hyolingual apparatus (e.g. Bels et al., 1994; Schwenk, 2000; Bels, 2003; Meyers and Herrel, 2005; Schwenk and Rubega, 2005; Herrel et al., 2009) and digestive track (O'Grady et al., 2005; Herrel et al., 2008; Griffen and Mosblack, 2011). From a functional perspective, feeding movements vary (i.e. are flexible) (*sensu* Wainwright et al., 2008) in response to the physical, textural and mechanical properties of the ingested food item in many vertebrates (e.g. Deban, 1997; Nemeth, 1997; Valdez and Nishikawa, 1997; Ferry-Graham, 1998; Dumont, 1999; Ferry-Graham et al., 2001; Vincent et al., 2006; Reed and Ross, 2010; Monroy and Nishikawa, 2011). Such variability in feeding movements has been documented extensively in squamate lizards during both the capture and intra-oral transport and processing of food (e.g. Bels and Baltus, 1988; Herrel et al., 1996; Herrel et al., 1999; Smith et al., 1999; Schaerlaeken et al., 2007; Schaerlaeken et al., 2008; Sherbrooke and Schwenk, 2008; Metzger, 2009; Montuelle et al., 2010; Schaerlaeken et al., 2011).

Organisms that feed on a particular food item (i.e. dietary specialists) face a specific set of physical, mechanical and textural properties. Consequently, in such organisms, the form and function as well as the behavioral capabilities of the feeding system are known to be specialized for handling the particular characteristics of their diet (e.g. Herrel et al., 1997; Ralston and Wainwright, 1997; Korzoun et al. 2001; Korzoun et al., 2003; Aguirre et al., 2003; Homberger, 2003; Meyers and Herrel, 2005; Herrel and De Vree, 2009). In contrast, organisms that typically feed on a wide variety of food items (i.e. dietary generalists) routinely face variability in food properties. Thus, in dietary generalists such as omnivorous predators, flexibility of feeding movements is a key aspect of feeding behavior (e.g. Liem, 1978; Herrel et al., 1999). Flexibility is defined as the 'ability of an organism to alter its behavior' in response to changes in the applied stimulus (i.e. 'across experimental treatments' in functional and behavioral studies) (*sensu* Wainwright et al., 2008). From a neurological perspective, flexibility is based on the ability to modulate the motor pattern dictating movements (e.g. Deban et al., 2001). Here, because we used kinematic data, our study focused on the flexibility of the movements involved during prey capture; complementary electromyographic data are required to understand the modulation of the neuromotor control of prey capture. To date, flexibility of the feeding movements involved during prey capture has been documented in response to changes in prey size (e.g. Deban, 1997; Ferry-Graham, 1998; Delheusy and Bels, 1999; Vincent et

al., 2006; Freeman and Lemen, 2007; Schaerlaeken et al., 2007) and prey mobility (e.g. Ferry-Graham, 1998; Ferry-Graham et al., 2001; Montuelle et al., 2010; Monroy and Nishikawa, 2011) in a wide array of vertebrates.

Recently, prey-capture behavior has been demonstrated to not be solely based on the movements of the feeding elements (e.g. the jaws, the hyolingual apparatus) but, rather, to involve the integration of the feeding and locomotor elements (e.g. Higham, 2007a; Higham, 2007b; Montuelle et al., 2009a; Kane and Higham, 2011; Montuelle et al., 2012). Integration is defined as the coordination of the movements of two or more body parts (Wainwright et al., 2008). It is thought to be based on a complex motor control which ensures that their respective movements are coordinated in time (e.g. synchronized) and space (i.e. position) (Wainwright et al., 2008). Locomotor–feeding integration has been observed in fishes, with the movements of the jaw and hyoid (e.g. jaw opening, expansion of the buccal cavity through the ventral depression of the hyoid) being coordinated with those of the fins (Rice and Westneat, 2005; Higham, 2007a). In terrestrial tetrapods, although fewer data are available, locomotor–feeding integration has been demonstrated in snakes (e.g. Frazzetta, 1966; Janoo and Gasc, 1992; Kardong and Bels, 1998; Cundall and Deufel, 1999; Alfaro, 2003; Young, 2010; Herrel et al., 2011) and lizards (Montuelle et al., 2009a; Montuelle et al., 2012). Interestingly, in one omnivorous lizard, *Gerrhosaurus major*, both feeding and locomotor movements are observed to be flexible in response to prey size and mobility (Montuelle et al., 2010). However, flexibility in locomotor–feeding integration in response to prey properties itself has yet to be investigated. Knowing whether integrated movements can be flexible is thus of interest for our understanding of the mechanisms that drive complex behaviors like feeding.

Similar to some other cordyliform lizards, the prey-capture behavior in *G. major* is characterized by a switch between tongue prehension and jaw prehension depending on prey type (Urbani and Bels, 1995; Smith et al., 1999; Reilly and McBrayer, 2007; Montuelle et al., 2009a). From a motor control perspective, each prey prehension mode stems from two different integrative motor patterns that coordinate feeding movements (i.e. tongue and jaw movements) with those of the locomotor elements (e.g. neck and forelimb movements) (Montuelle et al., 2009a). Therefore, in *G. major*, flexibility in locomotor–feeding integration allows the use of two different prey prehension modes, each being used for capturing prey of different size: jaw prehension is used to capture large prey, whereas tongue prehension is used for relatively small prey (Montuelle et al., 2009a). Thus, flexibility in locomotor–feeding integration in response to prey properties may be a key adaptation for animals with an omnivorous diet.

Here, we examined flexibility in locomotor–feeding integration in organisms that only use a single prey prehension mode. Varanid lizards were chosen because they are omnivorous predators that use jaw prehension for catching different types of prey (Schwenk, 2000; Vitt et al., 2003; Vitt and Pianka, 2005; Montuelle et al., 2012). Because the success of jaw prehension lies in the positioning of the skull on the prey, the movements of the anterior elements of the locomotor system (the forelimbs and the cervical region of the vertebral column) are expected to be coordinated with jaw movements, and locomotor–feeding integration is thus likely a key functional component of jaw prehension (Montuelle et al., 2012). Our hypothesis was that because jaw prehension is utilized successfully and efficiently to capture different prey types, locomotor–feeding integration may be flexible to respond to changes in prey properties. Alternatively, if locomotor–feeding integration

during jaw prehension is found to be inflexible in response to variability in prey properties, the motor control of locomotor–feeding integration may be independent from dietary constraints.

Our primary objective was to compare the jaw–neck–forelimb coordination patterns associated with the capture of prey varying in two properties: size and mobility, the effects of these two properties on feeding movements being well documented in lizards (e.g. Bels and Baltus, 1988; Herrel et al., 1996; Delheusy and Bels, 1999; Herrel et al., 1999; Schaerlaeken et al., 2007; Schaerlaeken et al., 2008; Metzger, 2009; Montuelle et al., 2009b; Montuelle et al., 2010; Schaerlaeken et al., 2011). Regarding prey size (here represented by prey length), we expected that the larger the prey, the higher the cranio-cervical system would have to rise. Consequently, we expected the capture of large prey to be characterized by a wider gape to accommodate the size of the prey item to be ingested, and a higher neck elevation, coupled with greater extension of the forelimbs, to lift the cranio-cervical system of the predator above the prey. In contrast, we expected the capture of small prey to be characterized by small maximum gape, as well as a reduced elevation of the neck (i.e. the neck would remain close to its rest position) and flexion of the forelimbs so that the head drops down to the ground to pick up the prey.

Regarding prey mobility, we hypothesized that the quicker the prey, the quicker the predator would strike. Thus, we expected jaw movements to be quicker when feeding on evasive prey, i.e. jaw opening to occur late and maximum gape angle to occur just before or at the same time as predator–prey contact. Additionally, we predicted that maximum gape would be greater for the capture of evasive prey. Indeed, evasive prey change position in space constantly and in an unpredictable manner; therefore, wider jaw opening is necessary to encompass the range of potential prey positioning during the strike. According to recent data on prey capture in lizards (Montuelle et al., 2012), quick strikes are based on a jaw–neck coordination pattern that supports a lunge onto the prey; thus, maximum neck elevation would occur just before or at the same time as jaw opening (i.e. at the start of the strike), and the neck would subsequently lower as the predator lunges on its prey. In contrast, the capture of immobile prey may not need a quick strike; thus, we would expect maximum neck elevation to occur later in the jaw-opening phase, i.e. closer to maximum gape and predator–prey contact. Alternatively, because a quick strike is not required, feeding on immobile prey may not require the precise coordination of jaw movements with those of the neck and forelimbs, which might lead to variability in the timing of neck elevation and forelimb flexion–extension with respect to jaw opening. Finally, we expected the forelimbs to support the strike by extending during jaw opening to thrust the head forward onto the evasive prey. For the capture of immobile prey, the extension of the forelimb may not be as great as it merely supports the elevation of the cranio-cervical system.

MATERIALS AND METHODS
Animal husbandry

Two adult individuals of *Varanus ornatus* (Daudin 1803) and one adult individual of *Varanus niloticus* (Linnaeus 1758) (snout–vent length 480±11mm) were purchased from a commercial animal dealer. *Varanus niloticus* and *V. ornatus* are closely related (Böhme, 2003) and used to be considered different subspecies (e.g. Luiselli et al., 1999). Because their feeding morphology and behavior are similar, individuals of both species were grouped in the analysis. They were maintained individually in large vivaria (1.5m long×1.5m deep×30cm high) on a 12h:12h light/dark cycle.

Temperature was set at 24–30°C during the day, with a basking spot at the higher temperature, and a temperature of no lower than 24°C during the night. Water was available *ad libitum* and the lizards were fed mice and grasshoppers twice a week.

Experimental set-up

A trackway (420×60 cm) covered with non-slip green plastic flooring was used for the experiments. At one end, a wooden box (60×60×60 cm) with a sliding door provided the animal with a place to rest between trials. A heating lamp provided a basking spot in front of the box. At the other end, a Plexiglas box (60×60×60 cm) covered the area filmed by the cameras. Each individual was maintained for 1 week, during which recording sessions were organized daily. After enough data were recorded for the first individual, the second individual was brought in for 1 week and subjected to daily recording sessions, followed by the third. The trackway was cleaned between trials. At the beginning of each recording session, the individual was allowed to walk along the trackway to become familiar with the experimental set-up. Between trials, the individual was kept in the wooden box with the door shut. During trials, the prey item was placed in the area covered by the cameras. All prey items were oriented with their long axis perpendicular to the long axis of the predator's head. For mobile prey, as their orientation varied during the approach of the predator, only strikes on perpendicularly oriented prey were analyzed. The door of the box was subsequently opened and we then waited for the animal to spontaneously initiate foraging along the trackway and strike on the prey item.

Prey capture was recorded at 200 frames s^{-1} using four synchronized high-speed cameras (Prosilica GE680, Allied Vision Technologies GmbH, Stadtroda, Germany). Two cameras were set up in dorsal view, filming through the Plexiglas sheet above the trackway. One camera was set up in oblique frontal view, filming through the Plexiglas sheet placed at the end of the trackway. The fourth camera was installed in lateral view. In this way, the anatomical points of interest were visible in at least three of the four views during the whole sequence recorded. Cameras were calibrated and scaled using a DLT routine based on the digitization of a black-and-white checkerboard composed of ten by ten 1×1 cm squares.

Data set

Four prey types were offered during the recording session: grasshoppers (*Locusta migratoria*, 44±1 mm), live newborn mice (*Mus musculus*, 39±1 mm), adult mice (*M. musculus*, 90±1 mm) and dead adult mice (*M. musculus*, 87±3 mm). The length of every prey item was measured using a pair of calipers before being offered. To quantify prey mobility, the maximum speed of the prey during the approach of the predator was extracted from the displacement of the prey point over time. These four prey types were chosen as they represent prey of different length and mobility (Fig. 1): grasshoppers are small and evasive prey, newborn mice are small prey with reduced mobility, adult mice are large and mobile prey, and dead adult mice are large and immobile prey. This allowed us to assess the effect of prey length in mobile (grasshoppers *versus* adult mice) and immobile prey (newborn mice *versus* dead adult mice), and the effect of mobility in two length categories (small prey: grasshoppers *versus* newborn mice; large prey: adult mice *versus* dead adult mice).

Twenty sequences representing the successful capture of grasshoppers were analyzed (eight, seven and five sequences for each individual, respectively; Fig. 2A), seven sequences for newborn
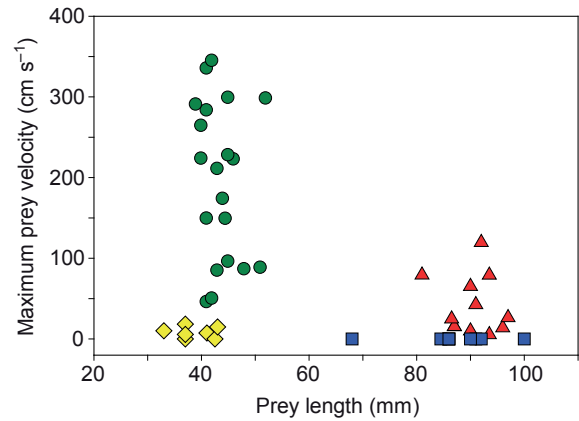

Fig. 1. Prey properties of the four prey types tested in this study. The length of each prey item was measured prior to being offered using a digital caliper. Prey mobility is represented by the maximum velocity of the prey item during the predator's approach. Maximum prey velocity was extracted from the 3D displacement of the point digitized at the insertion of the head of the prey on the prothorax or the trunk, during the predator's approach. Prey types are represented by different colored symbols: grasshoppers, green circles; newborn mice, yellow diamonds; adult mice, red triangles; and dead adult mice, blue squares.

mice (four and three sequences for the two *V. ornatus* individuals only; Fig. 2B), 12 sequences for adult mice (five, four and three for each individual, respectively; Fig. 2C), and nine sequences for dead adult mice (three for each individual; Fig. 2D). Note that during the recording sessions, prey types were offered in random order to avoid learning effects.

Kinematic analysis

Seven markers were painted on the body: the tip of the lower and upper jaws, the corner of the mouth, on a point halfway between the occipital and the pectoral girdle, and on the shoulder, the elbow and the wrist joints (Fig. 2). These markers were digitized on each frame for each camera view. Screen coordinates of the digitized markers were extracted for each of the four camera views and their position in 3D over time was calculated using the calibration. The position of the prey (point at the insertion of the head on the prothorax or the trunk) and the position of the eye of the predator were also digitized to quantify movements of the predator relative to the prey during the strike. Quantifying movements of skeletal elements based on external markers must be performed carefully because of the movements of the skin, but here we believe that potential error is reduced because of the small amount of soft tissue between the skin and the actual skeletal elements of interest. We acknowledge this as a limitation in our study. Additionally, although we recognize that the hindlimbs are important for propulsion during the lunge, our study focuses on the movements of the forelimbs and the cervical portion of the vertebral column because the requirements for sufficient resolution in reconstructing movements in 3D based on a multiple-camera set-up constrained the field of view.

Three kinematic profiles were constructed and variables were extracted to quantify movements of the jaws, neck and forelimbs. In these profiles, time was set at *t*=0 at the instant of predator–prey contact so that events occurring before contact are characterized by negative time values, and events occurring after are characterized by positive values. First, gape angle was calculated between the tip of the upper jaw, the corner of the mouth and the tip of the lower jaw (Fig. 3A). From this profile, we extracted the time of the start
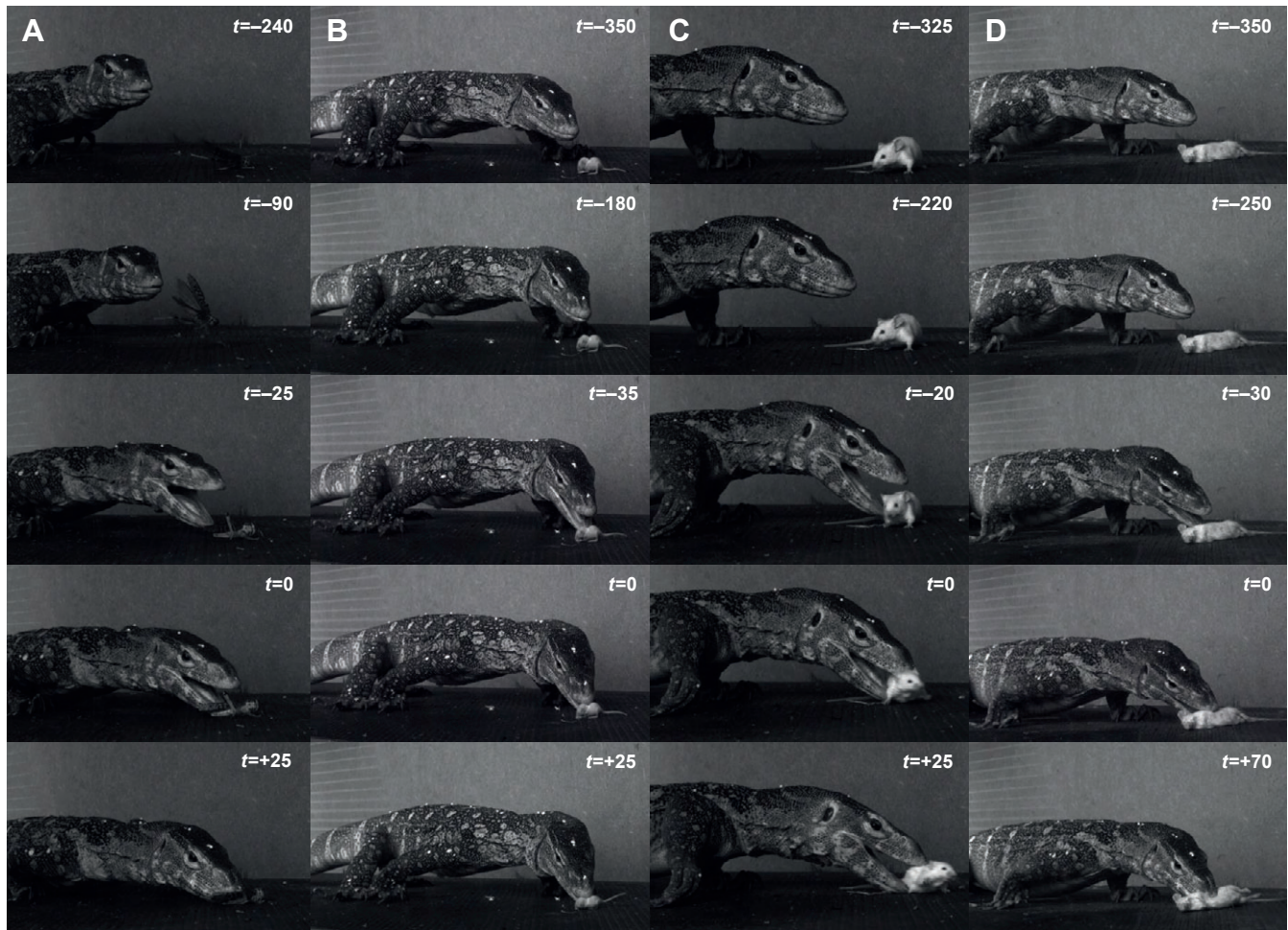
Fig. 2. Frame sequences illustrating prey-capture behavior in *Varanus ornatus* feeding on four prey items varying in length and mobility: grasshoppers (small/mobile; A), newborn mice (small/immobile; B), live adult mice (large/mobile; C) and dead adult mice (large/immobile; D). Each frame corresponds to an event of interest, from top to bottom: preparation for the strike, start of jaw opening, instant of maximum gape, predator–prey contact, bite. Time values are indicated, with time t=0 being set at the instant of predator–prey contact.

of jaw opening, the time of maximum gape angle, and the amplitude of maximum gape angle (Table 1). Second, neck elevation was calculated as the difference in the Z-coordinate of the point on the neck with respect to its position at rest (Fig. 3B). Maximum neck elevation and the time to maximum neck elevation were extracted (Table 1). Variation of neck height between the instant of jaw opening and the instant of predator–prey contact was also calculated, with negative values representing the neck being lowered during the strike and positive values representing neck elevation. Finally, elbow angle was calculated between the shoulder point, the elbow point and the wrist point (Fig. 3C). From this profile, four variables were extracted: maximum elbow angle (representing maximum extension of the forelimb at the elbow joint), minimum elbow angle (representing maximum flexion of the forelimb at the elbow joint), and the timing of both (Table 1). Variation of elbow flexion between the instant of jaw opening and the instant of predator–prey contact was also calculated, with negative values indicating forelimb flexing during the strike and positive values indicating forelimb extension.

Additionally, the distance between the predator and the prey was calculated as the difference in position between the predator's eye and the position of the prey. From this, we extracted the predator–prey distance at the onset of jaw opening to quantify how far from the prey the predator initiates the strike (Table 1). Finally,

based on the displacement of the eye of the predator over time, we calculated the speed of the head during the strike, and extracted maximum head velocity (Table 1).

To estimate integration among jaw–neck–forelimb movements at the functional level, we calculated the latency of maximum neck elevation, maximum forelimb extension and maximum forelimb flexion with respect to jaw opening. Latency was defined as the difference between the time of occurrence of one event of interest (i.e. maximum neck elevation, minimum and maximum elbow angle) and the time to jaw opening (Fig. 4). A latency value close to 0 represents a movement being synchronized with jaw opening (Fig. 4A). A negative latency value represents a movement occurring before the start of jaw opening (Fig. 4B), whereas a positive value represents a movement occurring after jaw opening (Fig. 4C).

Statistical analysis

Normality was verified using histograms of frequency of observations and Shapiro–Wilk's tests for each variable. First, ANOVA coupled to univariate F-tests considering the effects of prey type (fixed factor) and individual (random factor), and the corresponding interaction effects, were performed on the speed of the head during the strike, as well as on the predator–prey distance at the onset of jaw opening to identify significant differences in the
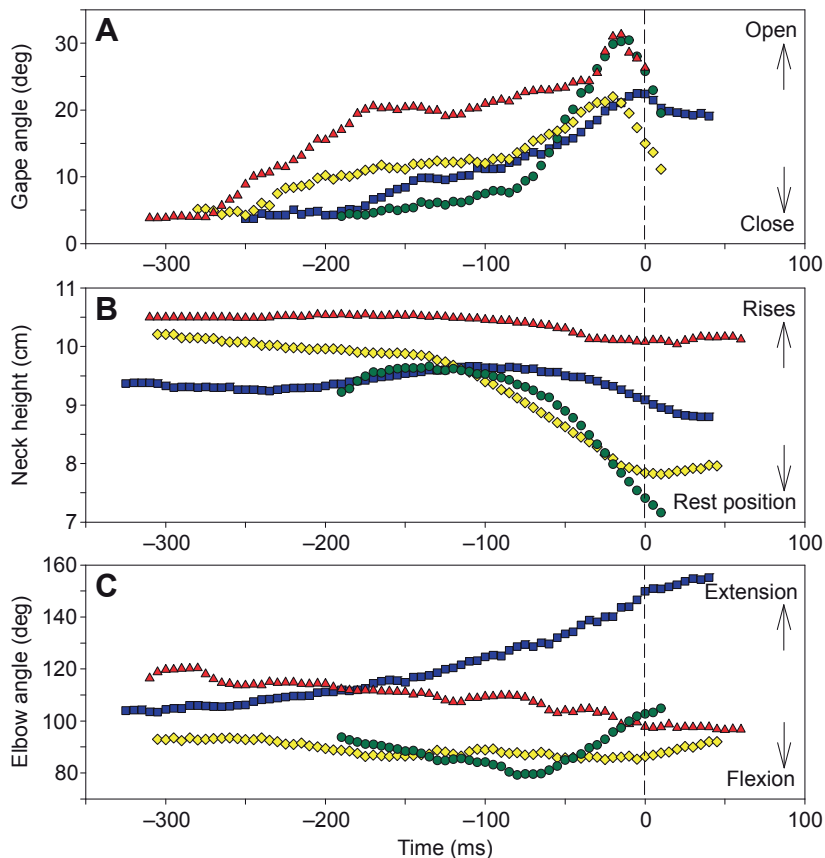
Fig. 3. Representative kinematic profiles associated with the movement of the feeding (jaws) and locomotor (vertebral column and forelimb) systems during prey capture in *Varanus niloticus* and *V. ornatus*. (A) Gape angle is calculated as the angle between the upper and lower jaw, representing the opening–closing movements of the jaw. (B) Neck height is extracted from the *Z*-coordinate of the point digitized on the neck, illustrating the rise of the neck above the ground with respect to its rest position. (C) Elbow angle is calculated as the angle between the shoulder point, the elbow point and the wrist point, quantifying the flexion–extension movements of the forelimb. Time *t*=0 was set at the instant of predator–prey contact (dashed line) so that negative time values represent events occurring before predator–prey contact, whereas positive time values represents events occurring afterwards. Prey types are represented by colored symbols: grasshoppers, green circles; newborn mice, yellow diamonds; adult mice, red triangles; and dead adult mice, blue squares.

characteristics of the strike itself. Note that non-significant interaction effects were removed from the final design of the ANOVA. Bonferroni *post hoc* tests were used to test differences among the four prey-types tested, and among the three individuals.

Factor analyses were performed on jaw variables, neck variables and forelimb variables separately to reduce the dimensionality of the data set. Multivariate factors with eigenvalues greater than 1 were retained for the rest of the analysis. Jaw factors, neck factors and forelimb factors were submitted to ANOVA coupled to univariate *F*-tests with prey type entered as a fixed factor, and individual as a random factor. Non-significant interaction terms were removed from the final model, and Bonferroni *post hoc* tests were used to test differences among the four prey types tested. To determine the pattern of coordination between jaw, neck and forelimb movements, the bivariate correlations between the jaw factors with the neck factors and with the forelimb factors were tested for each prey type separately. To assess the flexibility of the jaw–neck–forelimb coordination pattern in response to prey types, the characteristics of the significant correlations (i.e. the Pearson's coefficient *r*, the slope and the intercept) were compared between prey types. The Pearson's correlation coefficients were compared between prey types using Fisher's *z*-test (Fisher, 1921), whereas the slopes and the intercepts were compared using Student's *t*-tests.

To investigate the flexibility of jaw–neck–forelimb synchronization, the latency of neck elevation, forelimb flexion and forelimb extension with respect to jaw opening were submitted to ANOVA coupled to univariate *F*-tests. Prey type was entered as a fixed factor and individuals as a random factor, and non-significant interaction terms were removed from the final model. Bonferroni *post hoc* tests were performed on the prey-type factor to test which prey type differs from the others. To quantify the extent to which

synchronization between jaws and neck movements is altered in response to prey size, bivariate correlations between the latency of neck elevation with respect to jaw opening and prey size were tested for each of the four prey types separately. Similarly, bivariate correlations between the latency of neck elevation with respect to jaw opening and the maximum velocity of the prey during the predator's approach was tested for mobile prey (i.e. grasshoppers and mice) to determine the effect of prey mobility on jaw–neck synchronization. Latency of forelimb flexion and of forelimb extension were submitted to the same procedure. The characteristics of the significant correlations were compared between prey types: the Pearson's correlation coefficients using Fisher's *z*-test (Fisher, 1921), the slopes and the intercepts using Student's *t*-tests.

RESULTS
Prey-capture behavior in varanid lizards

Similar to other varanid lizards, *V. ornatus* and *V. niloticus* make use of extensive tongue-flicking while approaching prey, suggesting that chemoreception is used to detect and locate different prey items (see Cooper, 1989; Kaufman et al., 1996; Cooper and Habegger, 2001). Typically, *V. ornatus* and *V. niloticus* stop between 7 and 12 cm from the prey (see Table 1), then the jaws open and the strike is initiated (see Montuelle et al., 2012). As expected, jaw prehension was always used during prey capture (Schwenk, 2000; Vitt et al., 2003; Vitt and Pianka, 2005; Montuelle et al., 2012). For both types of evasive prey, the successful/missed trials ratio was greater than 50%: 30 successful captures of live grasshoppers out of the 51 sequences observed (63.8% of success), 11 successful captures of adult mice out of the 16 sequences observed (68.8% of success); no missed trial was observed when feeding on immobile prey (i.e. newborn mice and dead adult mice).

Table 1. Summary of the kinematic variables associated with jaw movements, neck elevation and forelimb flexion–extension at the elbow joint during prey capture behavior of *Varanus niloticus* and *Varanus ornatus*

	Grasshopper N=20	Newborn mice N=7	Adult mice N=12	Dead adult mice N=9
Prey				
Length (cm)	4.37±0.79	3.86±1.37	9.04±1.30	87.06±2.86
Length category	Small	Small	Large	Large
Maximum speed (cm s^{-1})	195.9±21.8	1.7±1.5	41.5±10.5	0
Mobility category	Mobile	Immobile	Mobile	Immobile
Jaw movements				
Time of the start of jaw opening (ms)	−176±15	−226±26	−195±27	−288±30
Maximum gape angle (deg)	32.8±0.7	19.6±1.5	28.3±1.0	24.4±1.1
Time of maximum gape angle (ms)	−23±4	−35±7	−28±4	−12±7
Neck movements				
Maximum neck elevation (cm)	4.74±0.39	5.44±0.13	5.68±0.58	4.68±0.56
Time of maximum neck elevation (ms)	−154±18	−244±34	−163±34	−154±31
Latency of maximum neck elevation (ms)*	22±15	−19±40	32±29	133±32
Variation of neck elevation during the strike (cm)	−2.22±0.23	−1.28±0.26	−0.87±0.19	−0.59±0.17
Forelimb movements				
Minimum elbow angle (deg)	82.9±1.6	113.2±6.6	105.9±6.9	91.2±8.1
Time of minimum elbow angle (ms)	−102±27	−97±49	−67±32	−291±48
Latency of minimum elbow angle (ms)*	74±32	128±67	128±46	−3±36
Maximum elbow angle (deg)	108.0±3.0	127.2±8.2	124.4±6.6	112.6±10.0
Time of maximum elbow angle (ms)	−72±27	−208±49	−128±40	−64±26
Latency of maximum elbow angle (ms)*	104±28	18±37	68±31	223±43
Variation of elbow angle during the strike (deg)	0.9±3	−2.6±2.6	−4.2±3.4	6.8±7.1
Strike performance				
Predator–prey distance at jaw opening (cm)	12.84±1.39	7.68±0.32	9.05±0.78	8.52±0.62
Maximum head velocity during the strike (cm s^{-1})	103.3±8.9	61.4±8.0	101.7±11.8	47.0±6.0

The capture of four different prey types varying in length and mobility was recorded (see Fig. 2).
N represents the number of sequences analyzed. Table entries are means ± s.e.m.
*Standardized with respect to jaw opening.

The strike consists of a lunge on the prey with the jaws opened. Maximum gape occurs shortly before predator–prey contact (Fig. 3A), suggesting that jaw closing is initiated without any sensory feedback from the prey. The lunge on the prey is characterized by the neck height dropping down during the strike, but the neck movements involved during prey capture vary between the prey types investigated here (Fig. 3B). The neck remains high above its resting position all along the strike when feeding on large prey items (adult mice; Fig. 2C, Fig. 3B), whereas the neck is lowered further to bring the skull closer to the ground so that the jaws can pick up small prey items such as grasshoppers and newborn mice (Fig. 2A,B, Fig. 3B). Similarly, the forelimb angular configuration at the elbow joint is different between prey types (Fig. 3C). During the capture of dead adult mice, the forelimb extends continuously while the jaws open (Fig. 2D, Fig. 3C). In contrast, the forelimb flexes during jaw opening when feeding on adult mice (Fig. 2C, Fig. 3C). Forelimb flexion also occurs early in the strike on grasshoppers, but the forelimb extends quickly during jaw opening (Fig. 2A, Fig. 3C). Finally, forelimb movements are limited during the capture of small motionless prey like newborn mice (Fig. 2B, Fig. 3C).

Varability in strike in response to prey type

Maximum velocity of the head during the strike is also significantly different among prey types ($F_{3,42}$=13.339, $P<0.001$; see Table 1). *Post hoc* tests demonstrate that strikes on grasshoppers are significantly quicker than on newborn mice (P=0.006) and dead adult mice ($P<0.001$). Strikes on live adult mice are also significantly quicker than on newborn mice (P=0.021) and dead adult mice ($P<0.001$). These results show that strikes are faster when feeding on evasive prey. Head velocity is different among individuals ($F_{2,42}$=15.800, $P<0.001$), indicating that the strikes of both

individuals of *V. ornatus* are quicker than those of the one individual of *V. niloticus* ($P<0.001$ for both *post hoc* tests between individuals). Prey type × individual interaction effects are not significant.

Predator–prey distance at the onset of jaw opening is significantly different among the four prey types ($F_{3,42}$=7.264, $P<0.001$), and *post hoc* tests reveal that jaw opening is initiated at a greater distance from the prey when striking on grasshoppers (see Fig. 2A, Table 1) than when striking on newborn mice (P=0.013; Fig. 2B, Table 1), adult mice (P=0.036; Fig. 2C, Table 1) or dead adult mice (P=0.027; Fig. 2D, Table 1). This suggests that varanids stop further away from the prey when preparing a strike on small evasive prey like grasshoppers, probably to avoid eliciting anti-predator behavior from the prey. Significant individual differences are also observed in the predator–prey distance at the onset of jaw opening ($F_{2,42}$=12.108, $P<0.001$), with *post hoc* tests indicating that the one individual of *V. niloticus* moves closer to the prey before initiating a strike compared with the two individuals of *V. ornatus* ($P<0.001$ and P=0.004, respectively). Prey type × individual interaction effects are not significant.

Variability in jaw, neck and forelimb movements in response to prey types

One multivariate factor was defined by the factor analysis, representing 50.9% of the variance of jaw kinematics. The jaw factor is correlated with time to jaw opening and maximum gape angle (Table 2). In the ANOVA of jaw factor, the prey type × individual interaction term is significant, indicating individuals respond differently to changes in prey type. Prey-type effect is significant for each individual ($F_{3,16}$=8.546, P=0.001; $F_{3,13}$=14.481, $P<0.001$; $F_{2,8}$=4.921, P=0.04); see Table 3 for the individual results of the *post hoc* tests.
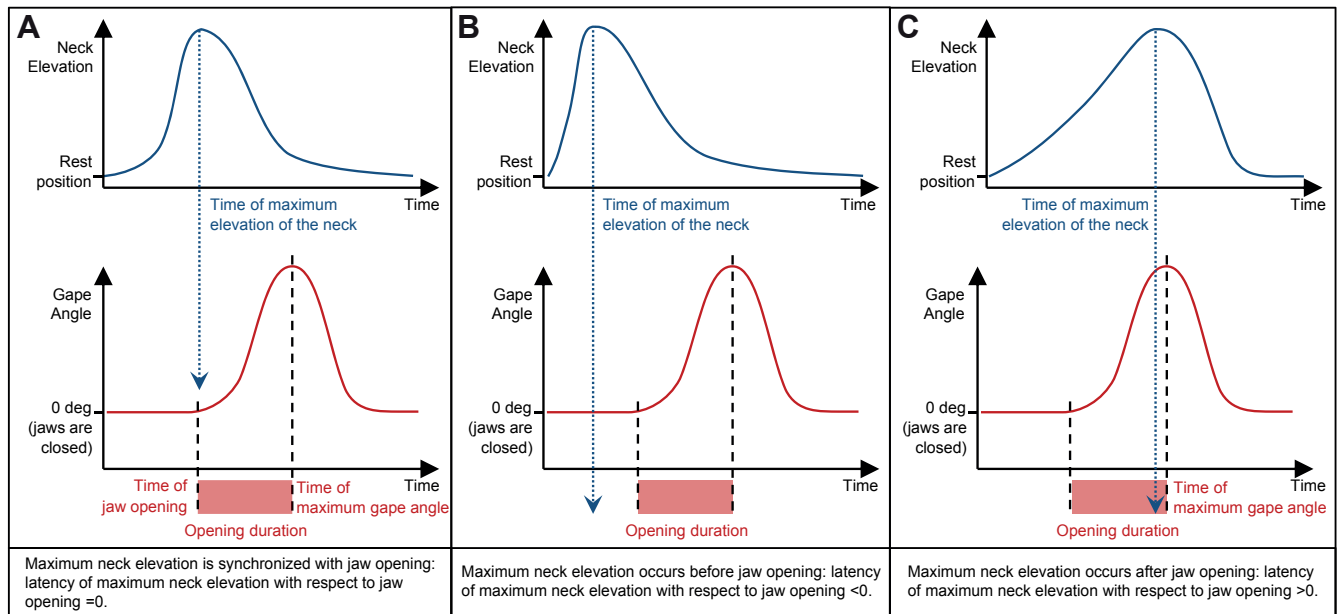
Fig. 4. Schematic diagrams illustrating the calculation of latency of maximum neck elevation with respect to jaw opening, which is used to determine the jaw–neck coordination pattern. First, both neck elevation (top) and gape angle (bottom) profiles are synchronized in time according to t=0 at the instant of predator–prey contact. Then, the difference in time between maximum neck elevation (blue dotted arrow) and jaw opening (black dashed line) is calculated. Three cases are illustrated. (A) Maximum neck elevation is synchronized with jaw opening: latency with respect to jaw opening is zero. (B) Maximum neck elevation occurs before jaw opening: latency with respect to jaw opening is represented by a negative value. (C) Maximum neck elevation occurs later in the jaw-opening phase (e.g. close to maximum gape angle): latency with respect to jaw opening is represented by a positive value. Latency of forelimb flexion at the elbow joint and latency of forelimb extension at the elbow joint were calculated using the same procedure (modified from Montuelle et al., 2012).

Two multivariate factors represent 71.8% of the total variance of the kinematics associated with neck elevation. Neck factor 1 represents 37.7% of the total variance and is correlated with maximum neck elevation (positively) and variation in neck height during the strike (negatively; Table 2). ANOVA reveals that prey-type effects are significant on neck factor 1 ($F_{3,42}$=5.285, P=0.003) with neck lowering when striking on grasshoppers, whereas it is kept at rest position during the capture of dead mice (P=0.001; Fig. 5A, Table 1). Individual differences are also significant ($F_{2,42}$=33.841, P<0.001) revealing that the neck of both individuals of *V. ornatus* elevates higher than in the one individual of *V. niloticus*. Neck factor 2 represents 34.1% of the total variance and is correlated with the time to maximum elevation of the neck (Table 2). No prey-type or individual effects are found on neck factor 2.

Two multivariate factors represent 85.1% of the total variance of the kinematics describing forelimb movements at the elbow joint. Elbow factor 1 represents 48.3% and is correlated positively with variation of elbow angle during the strike and the time to maximum elbow angle, and negatively with the time to minimum elbow angle (Table 2). Prey-type effects approach significance on elbow factor 1 ($F_{3,42}$=2.769, P=0.053; Fig. 5B), but individual effects are not significant. Elbow factor 2 represents 36.8% and is correlated with

Table 2. Summary of the factor analysis performed on the kinematic variables associated with jaw movements, neck elevation and forelimb flexion–extension at the elbow joint during prey-capture behavior of *Varanus niloticus* and *Varanus ornatus*

	Jaw factor (50.85%)	
Time to jaw opening	**0.865**	
Maximum gape angle	**0.845**	
Time to maximum gape angle	0.251	
	Neck factor 1 (37.71%)	Neck factor 2 (34.08%)
Maximum neck elevation	**0.776**	0.304
Time to maximum elevation of the neck	−0.001	**0.934**
Variation of neck height during the strike	**−0.724**	0.304
	Elbow factor 1 (48.27%)	Elbow factor 2 (36.82%)
Minimum elbow angle	−0.24	**0.969**
Time to minimum elbow angle	**−0.883**	−0.045
Maximum elbow angle	0.098	**0.965**
Time to maximum elbow angle	**0.876**	−0.072
Variation of elbow angle during the strike	**0.895**	0.135

Values in bold are loadings greater than 0.70 (Velicer and Fava, 1998).

Table 3. Summary of the prey-type effects on jaw and forelimb kinematics for each individual

	Individual no. 1 *Varanus ornatus*	Individual no. 2 *Varanus ornatus*	Individual no. 3 *Varanus niloticus*
Jaw factor	Newborn mice<grasshoppers (*P*=0.002) Newborn mice<dead mice (*P*=0.007)	Newborn mice<grasshoppers (*P*=0.004) Dead mice<grasshoppers (*P*<0.001) Dead mice<mice (*P*=0.016)	Grasshoppers>mice (*P*=0.042)
Elbow factor 2	Grasshoppers<mice (*P*=0.008) Newborn mice>grasshoppers (*P*=0.002) Newborn mice>dead mice (*P*=0.025)	Grasshoppers<mice (*P*=0.026)	

ANOVA performed on the multivariate factors (see Table 2) reveal that the prey type × individual interaction term is significant on the jaw factor and on elbow factor 2, indicating different prey-type effects in each individual. Consequently, prey-type effects were tested for each individual separately, and the significant Bonferroni *post hoc* tests are reported here to identify which prey type differs from the others.

minimum and maximum elbow angle (Table 2). The prey type × individual interaction term is significant on elbow factor 2, so prey-type effects were tested for each individual separately. Prey-type effects are significant in the two *V. ornatus* individuals ($F_{3,16}$=9.675, *P*=0.001 and $F_{3,16}$=5.124, *P*=0.015, respectively), but not in the *V. niloticus* individual. Specifically, in both individuals of *V. ornatus*, the elbow joint is more extended during the capture of mice than during the capture of grasshoppers (Table 3).

Variability in jaw–neck–forelimb integration in response to prey types

To investigate jaw–neck–forelimb integration, correlations between jaw factor and the neck and elbow factors were tested for each prey type separately. No correlations were significant during the capture of newborn mice and of dead adult mice. In contrast, the jaw factor is positively correlated with neck factor 2 during the capture of grasshoppers and adult mice (*r*=0.639, *P*=0.002 and *r*=0.658, *P*=0.02, respectively; Fig. 6A) illustrating the integration of jaw opening with neck elevation during the capture of evasive prey. This shows that during the capture of grasshoppers and adult mice, the later and wider the jaws open (i.e. the closer to predator–prey contact; Fig. 2A,C), the later maximum elevation of the neck occurs (i.e. closer to predator–prey contact), showing that jaw movements and neck movements are delayed concomitantly during the capture of evasive prey, demonstrating their integration. The capture of adult mice is also characterized by the correlation of the jaw factor with neck factor 1 (*r*=0.754, *P*=0.005; Fig. 6B) as well as with elbow factor 2 (*r*=0.599, *P*=0.040; Fig. 6C), indicating that the later and wider the jaws open, the higher the neck rises and the greater the extension of the forelimb at the elbow joint.

To investigate flexibility in jaw–neck–forelimb integration, we compared the correlation coefficients between prey types. Only the correlation between the jaw factor and neck factor 2 is common to the capture of two different prey types (i.e. grasshoppers and adult mice; Fig. 6A). The Pearson's correlation coefficients are not significantly different (*z*=–0.080, *P*=0.468), and the slope of the correlation is not significantly different either (*t*=–0.409, *P*=0.343). However, the intercept differs between the capture of grasshoppers and adult mice (*t*=–2.347, *P*=0.013), showing that maximum neck elevation is achieved closer to predator–prey contact during the capture of larger prey (i.e. adult mice) so that the head is raised over the prey item. This indicates that the jaw–neck integration pattern characterizing evasive prey is flexible in response to prey length.

Variability in the synchronization of jaw, neck and forelimb movements in response to prey properties

Synchronization of neck and forelimb movements with jaw opening is also altered in response to prey type (Fig. 7). The analysis of variance performed on the latency of neck elevation with respect to jaw opening reveals that prey-type effects are significant ($F_{3,42}$=4.121, *P*=0.012), with maximum neck elevation occurring significantly later in the jaw-opening phase during the capture of dead mice (Fig. 2D, Fig. 4C, Fig. 7D, Table 1) than during the capture of newborn mice (*post hoc* test *P*=0.008; Fig. 2B, Fig. 4B, Fig. 7B, Table 1) and grasshoppers (*post hoc* test *P*=0.017; Fig. 2A, Fig. 4A, Fig. 7A, Table 1). This indicates that maximum neck elevation is synchronized with the instant of jaw opening during the capture of small prey, whereas it is delayed in the jaw-opening phase during the capture of large immobile prey. Latency
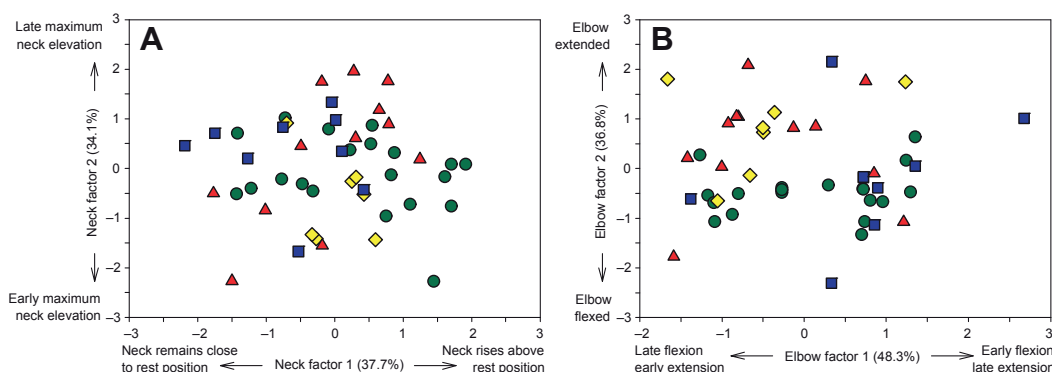

Fig. 5. Multivariate spaces representing variation in the kinematics associated with neck elevation (A) and elbow configuration (B) during prey-capture behavior in *V. ornatus* and *V. niloticus* feeding on different prey types. For each factor, the percentage of variance explained is indicated, as are the kinematic variables loading on each factor (see Table 2 for the complete composition of the multivariate factors). Prey types are represented by colored symbols: grasshoppers, green circles; newborn mice, yellow diamonds; adult mice, red triangles; and dead adult mice, blue squares.
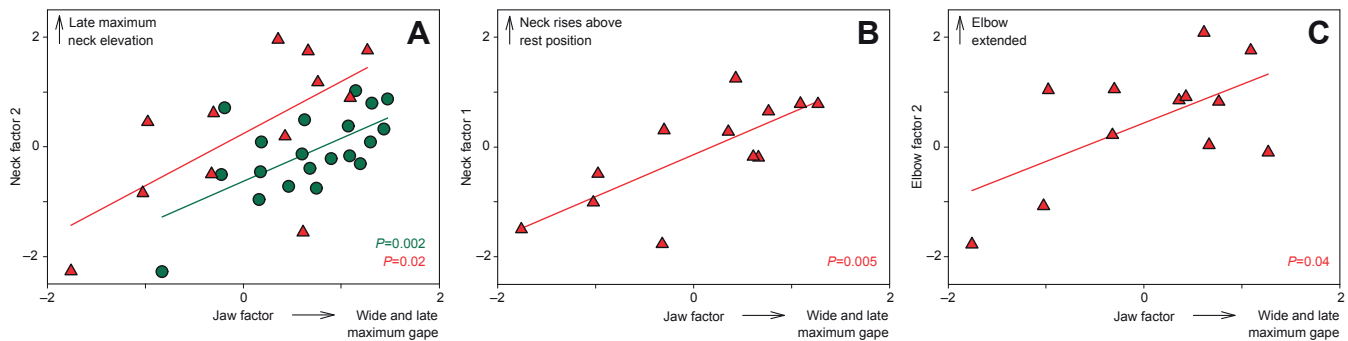
Fig. 6. Bivariate correlations between the multivariate factors representing jaw movements and those representing neck and forelimb movements, illustrating jaw–neck–forelimb integration during prey-capture behavior in *V. ornatus* and *V. niloticus*. Jaw factor is correlated with neck factor 2 during the capture of grasshoppers and adult mice (A), indicating the timing of neck elevation is associated with the time and amplitude of maximum gape during the capture of evasive prey. Jaw factor is also correlated with neck factor 1 (B) and elbow factor 2 (C) during the capture of adult mice, indicating the amplitude of maximum neck elevation and the amplitude of elbow angle are both associated with the time and amplitude of maximum gape. The kinematic variables loading on each factor are indicated (see Table 2 for the complete composition of the factors). Prey types are represented by colored symbols: grasshoppers, green circles; and adult mice, red triangles. Only the significant correlations are presented: note, no bivariate correlation was found to be significant for immobile prey (i.e. newborn mice, dead adult mice).

of maximum elbow angle is also affected by prey type ($F_{3,42}$=4.045, P=0.013). Forelimb extension at the elbow joint is achieved later in the jaw-opening phase (i.e. closer to predator–prey contact) during the capture of dead mice (Fig. 2D, Fig. 4C, Fig. 7D) than during the capture of newborn mice (*post hoc* test P=0.009; Fig. 2B, Fig. 4A, Fig. 7B) and adult mice (*post hoc* test P=0.031; Fig. 2C, Fig. 4A, Fig. 7C). This reveals that maximum extension of the forelimb at the elbow joint is synchronized with the instant of jaw opening for the capture of newborn and adult mice, whereas it is synchronized with maximum gape for the capture of dead adult mice. No effects of prey type are significant on the latency of minimum elbow angle. Finally, there are no significant individual differences in the latency of neck elevation or on the latency of minimum and maximum elbow angle.

The effects of prey length and prey mobility on the latency of neck and forelimb movements with respect to jaw opening were analyzed for each prey type separately. Prey length has no effect on the latency of neck elevation, the latency of minimum elbow angle or the latency of maximum angle in any of the four prey types tested in our analysis. In contrast, prey mobility, described by the maximum velocity of the prey during the approach of the predator, is correlated with the latency of minimum elbow angle in grasshoppers and adult mice (r=0.512, P=0.021 and r=0.600, P=0.039, respectively; Fig. 8A). This shows that forelimb flexion is delayed closer to maximum gape and predator–prey contact for the capture of quick prey (see Fig. 4C). This late flexion of the forelimb may be used to counter the inertia created by the body during the strike, reducing the speed of the head as predator–prey contact approaches. The Pearson's correlation coefficients associated with each correlation are significantly similar (z=–0.312, P=0.378), as are their intercepts (t=–0.915, P=0.184). However, the difference between the slopes of the correlation associated with each prey approaches significance (t=–1.640, P=0.056), suggesting that the latency of elbow flexion is more sensitive to changes in prey velocity in adult mice than in grasshoppers (Fig. 8A). This shows that the effects of prey mobility on jaw–forelimb coordination are altered in response to the length of the prey. The maximum velocity of grasshoppers is also correlated with latency of maximum elbow angle (r=–0.482, P=0.032; Fig. 8B), indicating that the capture of small and quick prey is characterized by the earlier extension of the forelimb at the elbow joint.

DISCUSSION

In accordance with our predictions, our data show that varanid lizards use a specific jaw–neck coordination pattern for the capture of different prey items that vary in length and mobility (Figs 3, 7). Strikes on grasshoppers (small evasive prey) have more in common with the strikes on live adult mice (large evasive prey) than with the strikes on newborn mice (motionless prey of similar size), suggesting that the effects of prey mobility overcome those of prey size. Indeed, in addition to the fact that strikes on grasshoppers and live adult mice are quick strikes (Table 1), strikes on all sizes of evasive prey are similar in that they are characterized by a strong link between jaw movements and neck elevation: if one is delayed, then the other is delayed concomitantly (Fig. 6A). The capture of grasshoppers is significantly quicker and is initiated further from the prey, likely to avoid eliciting an anti-predator response (Table 1). The neck rises above its rest position to reach its maximum elevation before jaw opening (Fig. 3B, Fig. 7A), and lowers quickly after jaw opening as the predator lunges forward (Fig. 2A, Fig. 3B). Finally, forelimbs flex and then quickly extend during the strike, like a spring, likely contributing to the lunge by thrusting the cranio-cervical complex forward towards the prey (Fig. 2A, Fig. 3C, Fig. 7A). During the strike on live adult mice, the neck rises similar to the strikes on grasshoppers but does not lower as much as during the strike on small prey (immobile or evasive ones; Fig. 3B). Flexion of the forelimbs is also observed during the strikes on live adult mice, although it is not followed by a quick extension (Fig. 3C, Fig. 7C). In this case, forelimb flexion is suggested to contribute to the immobilization of large evasive prey by pinning the prey on the ground, limiting the potential for prey escape after the strike.

To capture small motionless prey like newborn mice, the strike is different in that it is initiated close to the prey. The strike on newborn mice consists of the neck rising, supported by the extension of the forelimb at the elbow joint (Fig. 3B,C, Fig. 7B). During the jaw-opening phase, the neck lowers and the forelimbs flex to drop the head down to the ground to pick up the prey item (Fig. 2B, Fig. 3B,C, Fig. 7B). The strike on dead adult mice is the most singular among the strike strategies observed here. Strikes on large immobile prey are the slowest and are initiated close to the position of the prey (Table 1). The neck rises slightly during jaw opening, remaining close to its rest position, with maximum elevation being achieved late in the jaw-opening phase. This indicates that neck elevation is
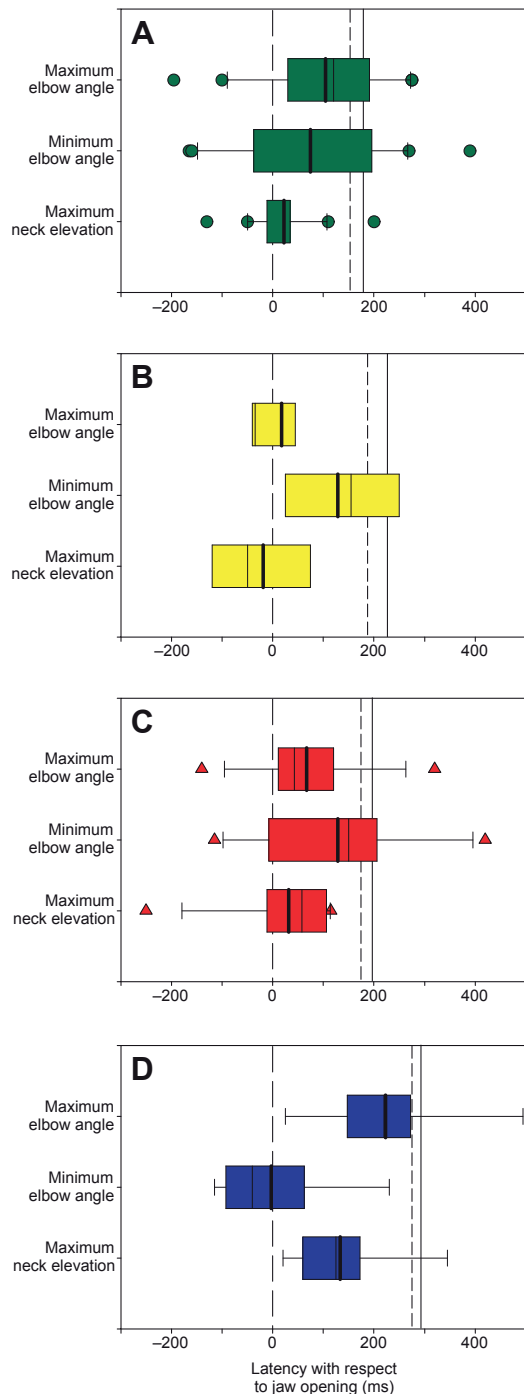
Fig. 7. Flexibility of jaw–neck–forelimb coordination in response to prey type during prey-capture behavior in *V. ornatus* and *V. niloticus* feeding on different prey types. Latency (i.e. time difference) of maximum neck elevation, maximum elbow angle and minimum elbow angle with respect to jaw opening were calculated for each prey type: grasshoppers (A), newborn mice (B), adult mice (C) and dead mice (D). Low latency values indicate events occurring close to the start of jaw opening, whereas high latency values indicate events occurring later in the jaw-opening phase (i.e. closer to maximum gape and predator–prey contact; see Materials and methods). Long-dash lines represent the start of jaw opening (at latency=0; see Fig. 4A), short-dash line represents the instant of maximum gape, and solid lines represent the instant of predator–prey contact. Colored symbols represent outliers: grasshoppers, green circles; adult mice, red triangles.

always initiated before jaw opening (Fig. 3B, Fig. 7A–C), but that its duration is extended for the capture of large immobile prey to allow the positioning of the head above the prey item. Finally, the forelimbs extend slowly during the strike on dead adult mice in order to bring the head of the predator above and forward towards the prey item.

Within this repertoire of strike strategies, the jaw–neck–forelimb coordination pattern is demonstrated to be flexible in response to prey properties. Between the two prey properties tested here, prey mobility appears to be a defining parameter, over and above the size of the prey for instance, in dictating what coordination pattern will be used. On the one hand, predator–prey distance at which the predator stops before initiating the strike (i.e. before opening the jaws) is greater for both types of evasive prey than for any type of immobile prey (see Table 1). This indicates that varanid lizards are able to ascertain the difference between evasive and immobile prey during the approach, and choose the appropriate strike strategy accordingly: stop far away and trigger a quick strike if targeting an evasive prey, or keep approaching the target as long as no movement is displayed (Fig. 9). This demonstrates how prey mobility is key information for the success of prey-capture behavior in varanid lizards. By extension, it illustrates the importance of sensory feedback from visual cues and chemoreception during the approach of varanid lizards in order to assess the risk of prey escape (Cooper, 1989; Garrett et al., 1996; Kaufman et al., 1996; Cooper and Habegger, 2001; Chiszar et al., 2009; Gaalema, 2011).

On the other hand, our data demonstrate how flexibility of jaw–neck–forelimb integration is an important component of the capture of evasive prey in varanid lizards (Figs 6, 8). Indeed, consistent jaw–neck integration patterns are observed during the capture of both types of evasive prey (Fig. 6A). However, despite the consistency of this integration pattern (i.e. statistically similar slope of bivariate correlations across experimental treatments), prey length affects jaw–neck integration as the neck is raised higher during the capture of large evasive prey. Such variability in the jaw–neck integration pattern indicates that the jaw–neck integration pattern characterizing the capture of evasive prey is flexible in response to prey size (here represented by the length of the prey item). This shows that prey-capture behavior in omnivorous predators like varanid lizards is not solely based on the flexibility of feeding movements but, rather, involves the flexibility of the integration pattern coupling the feeding and locomotor movements. This suggests that the motor control responsible for the integration of multiple structures across different anatomical systems might be modulated, although the neurological dimension of this hypothesis remains to be investigated.

Furthermore, our results show that jaw–forelimb integration is flexible in response to the maximum velocity of the prey during the approach of the predator (i.e. prior to the strike; Fig. 8A). When striking on very active prey, varanids alter the jaw–forelimb coordination pattern so that forelimb flexion is delayed in the jaw-opening phase (i.e. closer to maximum gape; Fig. 8A). Because the jaw–forelimb integration pattern is different during the capture of grasshoppers and adult mice (Fig. 7A,C), the flexibility in response to prey velocity yields different behavioral outputs. During the capture of adult mice, the late flexion of the forelimb at the elbow joint illustrates how forelimb flexion is delayed to occur closer to predator–prey contact (Fig. 8A), supporting our hypothesis that forelimb flexion plays a role in securing the prey after the strike. During the capture of grasshoppers, forelimb flexion occurs before
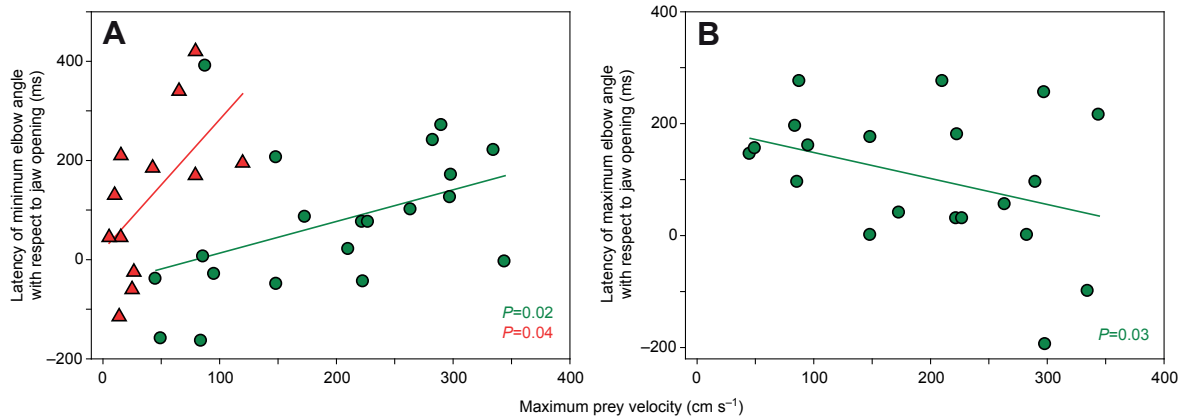
Fig. 8. Effect of prey mobility on jaw–forelimb coordination during prey-capture behavior in *V. ornatus* and *V. niloticus* feeding on evasive prey (grasshoppers and adult mice). (A) Maximum prey velocity is correlated with the latency of minimum elbow angle, indicating the capture of quick prey involves the flexion of the forelimb at the elbow joint being delayed in the jaw-opening phase. (B) Maximum prey velocity is correlated with the latency of maximum elbow angle during the capture of grasshoppers, indicating the capture of quick prey involves the extension of the forelimb at the elbow joint occurring earlier in the jaw-opening phase. Prey types are represented by colored symbols: grasshoppers, green circles; and adult mice, red triangles. Only the significant correlations are presented: note, no bivariate correlation between maximum prey velocity and the latency of maximum neck elevation with respect to jaw opening was significant.

the extension of the forelimb that thrusts the head of the predator forward onto the prey. Consequently, the delay of the flexion (Fig. 8A) coupled with the early extension (Fig. 8B) of the forelimb at the elbow joint reveals a quicker extension that is proposed to enhance head velocity during the strike.

Jaw–neck–forelimb integration during prey capture in varanid lizards is flexible in response to both the mobility and the size of

evasive prey, suggesting that the motor control responsible for the coordination of jaw, neck and forelimb movements can be modulated. Indeed, our data demonstrate that different jaw–neck–forelimb coordination patterns are used during the capture of small *versus* large prey (Fig. 6A, Fig. 7, Fig. 8A). First, because prey length is constant throughout the feeding sequence, varanids are probably able to assess the length of the prey while approaching
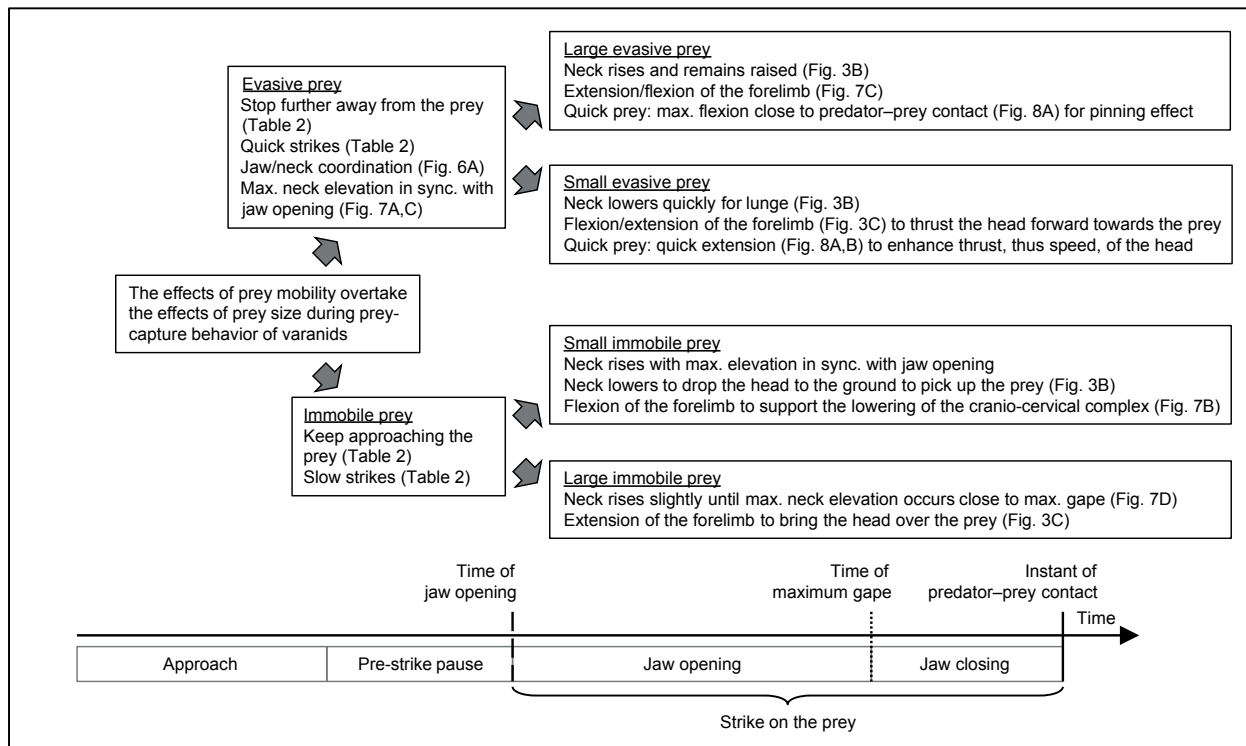

Fig. 9. Synthesis of the study. In prey-capture behavior of varanid lizards, the effects of prey mobility on the jaw, neck and forelimb movements, and on their integration, appear to supersede the effects of prey size (here quantified by prey length). The time scale (bottom), from prey approach to predator–prey contact, highlights the time dimension of the proposed decision-making process: varanids are hypothesized to assess prey mobility first as they stop further away from evasive prey to avoid eliciting an anti-predator response, then use specific strike strategies in response to the secondary properties of the prey (e.g. length). Inspired by Monroy and Nishikawa (Monroy and Nishikawa, 2011).

it and select a particular jaw–neck–forelimb integration pattern before the strike (i.e. feed-forward modulation). Most importantly, jaw–neck forelimb coordination appears to be an essential characteristic of the capture of evasive prey (Figs 6, 8, 9). Consequently, varanids first assess the mobility of the target prey (i.e. the escape risk) (see Gaalema, 2011), followed by an assessment of its size (Fig. 9). Given that prey mobility is a parameter that cannot be anticipated during a single prey-capture trial, varanids may rely on sensory-driven feedback modulation to adjust the jaw–neck–forelimb integration pattern in response to changes in prey velocity. Investigation of the neuronal pathways responsible for the sensory control of locomotor–feeding integration is a promising research direction for our understanding of feeding behavior in vertebrates.

Previously, the functional consequences of an omnivorous diet have mainly been documented as the flexibility in the movement of the feeding structures (i.e. the jaws, the tongue, the hyobranchial apparatus) (e.g. Liem, 1978; Herrel et al., 1999). Even though flexibility in the movements of locomotor structures like the forelimbs and the vertebral column (at least in the cervical region) has also been reported in an omnivorous lizard (*G. major*) (Montuelle et al., 2010), our data indicate that flexibility in locomotor–feeding integration may be a key component in the ability to feed on prey items that vary in their physical and mechanical properties, especially mobility (Fig. 9). This finding may be crucial to understanding dietary specialization. Indeed, by feeding routinely on the same food, selective pressures are imposed on the feeding structures to optimize prey-capture efficiency (e.g. Herrel et al., 1997; Ralston and Wainwright, 1997; Aguirre et al., 2003; Meyers and Herrel, 2005; Herrel and De Vree, 2009). As changes in food properties have been shown here to affect locomotor–feeding integration in lizards using jaw prehension, particular food properties are suggested to require particular locomotor–feeding integration patterns (see Fig. 9), and specialization in locomotor–feeding integration may occur in response to diet. Varanid lizards are specialized for feeding on 'hard to catch' prey (Losos and Greene, 1988). Given the strong effects of prey mobility on jaw–neck–forelimb coordination (see Figs 6, 8), flexibility of locomotor–feeding integration in response to prey mobility is proposed to be a key functional feature optimizing the capture of evasive prey, and hence may contribute to the dietary specialization of varanids. Our observations of the functional basis of jaw prehension indeed suggest that the selective pressures stemming from food properties may not be restricted to the feeding system only but, rather, act at the whole-organism level, selecting for patterns of locomotor–feeding integration flexible enough to respond to variation in prey mobility.

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