

## KINEMATICS OF PREY CAPTURE IN IGUANID LIZARDS : COMPARISON BETWEEN *ANOLIS EQUESTRIS* (ANOLINAE) AND *OPLURUS CUVIERI* (OPLURINAE)

by

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### SUMMARY

Prey capture in *Anolis equestris* MERREM, 1820 and *Oplurus cuvieri* (GRAY, 1831) involves tongue prehension. Prey capture is a complex motor pattern involving displacements of the body and the head toward the prey related to the gape-tongue cycle. At short distances between the lizard and the prey ( $\leq 15$  cm), the gape cycle begins prior to or simultaneously with the lizard's displacement toward the prey. At long distances ( $\geq 15$  cm), the jaws are always opened after displacement of the lizard toward the prey. The role of the tongue is (1) pressing the prey onto the substratum and (2) retracting the prey into the buccal cavity. Retraction of the tongue is short (about 0.03 s). The gape cycle is divided into four stages : slow opening I (SO I), slow opening II (SO II), fast opening (FO), and fast closing (FC) in both iguanids. In *O. cuvieri*, SO II is shorter for short prey-lizard distance, and often absent in *A. equestris*.

*Key words* : prey capture, kinematics, Iguanidae, Reptilia.

### INTRODUCTION

In general, prey capture of lizards has been classified into lingual prehension for iguanians (Agamidae, Chameleontidae, Iguanidae) and jaw prehension for scleroglossans (other families). Kinematics of lingual prehension has been studied in agamids (SCHWENK and THROCKMORTON, 1989 ; KRAKLAU, 1991), chameleontids (BELS and BALTUS, 1987 ; BELL, 1990 ; WAINWRIGHT *et al.*, 1991) and a few iguanids (SCHWENK and THROCKMORTON, 1989 ; BELS, 1990). The iguanians share several plesiomorphic characters in the displacements of the jaws and the tongue (SCHWENK, 1988 ; SCHWENK and BELL, 1988 ; SCHWENK and THROCKMORTON, 1989 ; REILLY and LAUDER, 1990). For instance, the pattern of gape cycle is similar for terrestrial insectivorous and herbivorous species. It involves a slow opening stage divided into opening *per se* (SO I) and a stationary stage (SO II) prior to the

fast opening stage (FO). FO corresponds to a sudden increase of the gape angle as soon as the tongue contacts the prey. This stage is followed by a fast closing (FC) of the jaws.

SCHWENK (1988) assumes that tongue morphology is phylogenetically related and states « Hence, phylogeny is better predictor of tongue morphology than is ecology ». In iguanians, SCHWENK and THROCKMORTON (1989) describe an inter-familiar difference between agamids and iguanids for the tongue shape within the buccal cavity prior to protrusion. If tongue prehension is plesiomorphic for iguanians, kinematics of its displacements and intrinsic deformations prior to prey contact may be functionally adapted. Body, head, jaw and tongue displacements may be related to the diet characteristics (size, volume, etc.) or the species-specific foraging strategies (*i.e.*, sit-and-wait, and active foraging).

Comparison of kinematics in prey capture provides a very useful example to test the major evolutionary adjustments to environmental contingencies of the feeding behaviour in iguanid lizards. In the present study, we examine body, head, jaw and tongue displacements toward large prey (relative to the size of the lizards), by using a high speed cinematographic analysis, in one terrestrial (*Oplurus cuvieri* (GRAY, 1831)) and one arboreal (*Anolis equestris* MERREM, 1820) iguanid. The prey items were placed at variable distances from *O. cuvieri* for analyzing the timing relationship between gape opening, tongue protrusion, and locomotor pattern.

## MATERIALS AND METHODS

Four adult male *A. equestris* (133-164 mm snout-vent length) were filmed at 200 frames per second and eight adult male *O. cuvieri* ( $117 \pm 23$  mm snout-vent length) were filmed at 100 frames per second (*O. cuvieri*) with Eastman Ektachrome high speed 7250 Tungsten 16 mm film, using a Photosonic 1 PL camera. The lizards were filmed under three 1000-watt tungsten photoflood lights. Each lizard was isolated in a vivarium two or three weeks before filming. Anoline lizards were conditioned to feed while perched on a branch (100 mm diameter). Food consisted of live adult locusts *Locusta migratoria* (length : 49-65 mm) placed near the branch. *A. equestris* did not take prey at distances over 10 cm. *O. cuvieri* were conditioned to capture the food (live adult crickets *Acheta domesticus* of almost same size ( $24 \pm 3$  mm)) on the ground. The crickets were placed at different distances (range : 230-10 mm) for analyzing the relationship between gape opening and body displacements toward the prey.

A total of 14 capture cycles for *A. equestris*, and 14 for *O. cuvieri* were filmed. In seven capture cycles for *O. cuvieri* and 10 for *A. equestris*, the prey items were captured with almost no lateral head displacements (eye-snout distance did not change on the successive frames). These sequences were projected onto a graphic table (AGMEE, ULg) using a NAC motion analyzer connected to a Copam AT microcomputer. Each sequence of frames was analyzed by digitizing a combination of points on the body, the head, the tongue, and the prey for selected frames.

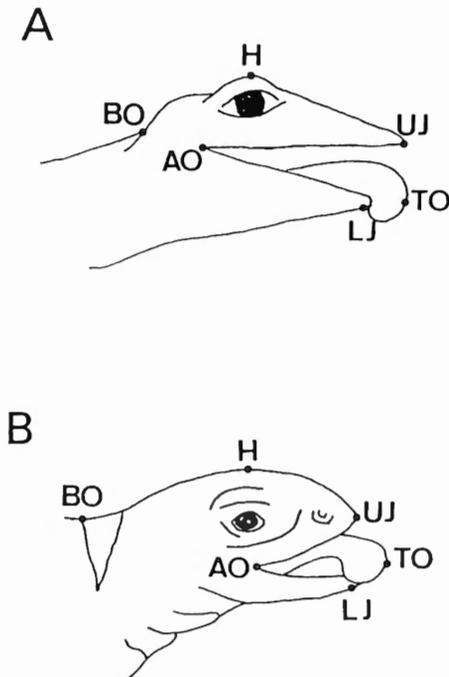


Fig. 1. — Points digitized from high speed films in *Anolis equestris* (A) and *Oplurus cuvieri* (B). AO, angulus oris; BO, body; H, head; LJ, lower jaw; TO, tongue; UJ, upper jaw.

Vertical (Y) and horizontal (X) coordinates were recorded for each digitized point (Fig. 1). The data were stored in data files as tables of bipolar (X and Y) coordinates. The files were then analyzed using a computer set of programs developed by P. Theate, and V. Bels. Frame 1 for each gape cycle was arbitrarily chosen to occur at the beginning of the slow opening (SO) stage. Kinematic graphs were plotted by using Lotus 123.

The kinematic profiles illustrate the displacements of the tongue, the jaws, and the head of the lizard. The X- and Y-coordinates of the points of the jaws (LJ and UJ), and the tongue (TO) were calculated relative to the X- and Y-coordinates of the body point (BO) for deleting the effects of its displacements (transformed coordinates). The following kinematic variables were measured: (1) the *gape angle* is the angle between the tip of the snout (UJ), the angulus oris (AO) and the most anterior point on the mandible (LJ); (2) *tongue protrusion* is the horizontal distance (X-coordinates) between the anterior-most points of the tongue (TO) and the mandible (LJ): this distance is positive as soon as the tongue is protruded beyond the mandibular tip; (3) *displacement of the lizard* is the horizontal distance (X-coordinates) between the tip of the snout (UJ) and the prey (P); (4) *displacements*

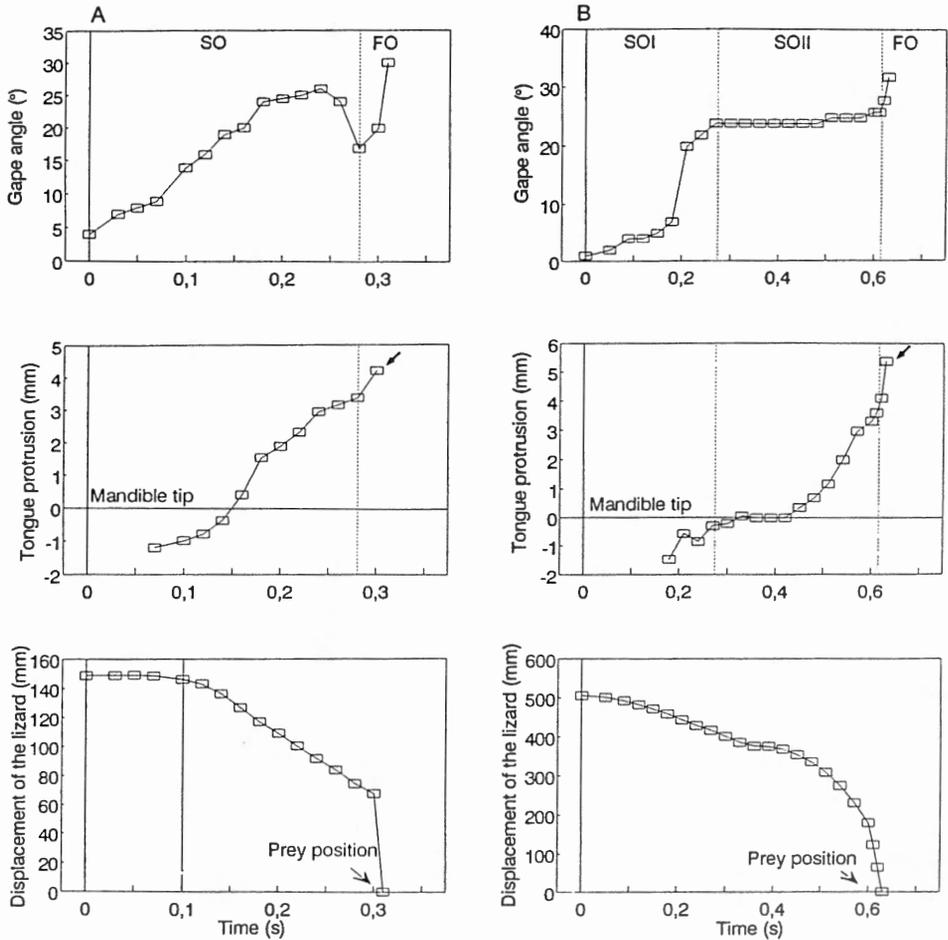


Fig. 2. — Representative kinematic profiles of prey capture by *Opturus cuvieri*. A. The distance between the lizard and the prey is short ( $\leq 15$  cm). The solid vertical line in the lower graphs indicates the beginning of lizard displacement. B. The distance between the lizard and the prey is long ( $\geq 15$  cm). The arrow in the second graphs indicates tongue-prey contact. FO, fast opening stage; SO I, slow opening I stage, and SO II, slow opening II stage.

of the prey : horizontal and vertical displacements (X- and Y-coordinates) of point P against time from the first frame of tongue-prey contact ; (5) *displacements of the tongue* : transformed X- and Y-coordinates of point TO against time ; (6) *displacements of the head* : horizontal and vertical displacements (X- and Y-coordinates) of point H against time. The displacements of the point H are appropriated to describe the displacements and the rotation of the head of the lizard toward the prey. The coordinates of this point used in the graphs were not transformed relative to point BO. Durations of the successive stages (slow opening, fast opening, fast closing), maximal gape angle, duration of the tongue retraction and time to tongue-

prey contact were measured from 6-7 cycles in *O. cuvieri* (1-2 cycles/individual) and 10 cycles in *A. equestris* (1-2 cycles/individual). Time to tongue-prey contact was calculated as the time between the first frame in which the tongue touched the prey and the frame corresponding to maximal gape angle at the end of the fast opening stage.

The coefficient of variation (CV) was measured for some of the variables depicting the gape cycle : duration of slow opening (SO) and fast opening (FO) stages. The regression line between prey-lizard distance and the beginning of gape opening was calculated for *O. cuvieri*. The first frame involving horizontal displacement of the body of the lizard toward the prey refers to time 0. The timing difference between this frame and the first frame involving opening of the mouth was then computed. When the mouth opened prior to body displacement, this timing was thus considered negative.

## RESULTS

Prey capture in *A. equestris* and *O. cuvieri* was effected by displacements of the body, jaws and tongue. This behaviour in both species can be divided into preparatory, lunge, and retraction phases. The preparatory phase mainly involved orientation of the head toward the prey when the lizard was not in line with the prey. The lunge phase involved locomotor behavioural patterns toward the prey and one gape cycle. *A. equestris* captured prey when the distance between the lizard and the prey did not exceed 10 cm. In *O. cuvieri*, lunge phases were observed even

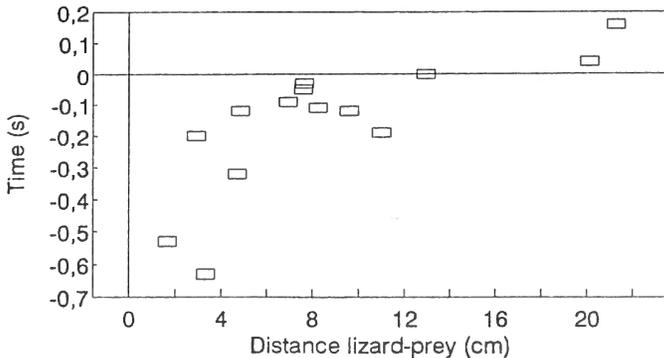


Fig. 3. — The time between beginning of the gape cycle and beginning of body displacement of *Oplurus cuvieri* is positively correlated to prey-lizard distance. Beginning of gape cycle refers to the first frame of increasing gape angle. The first frame involving body displacement is arbitrarily selected as time 0. When the gape cycle begins after body displacement, the time is positive. When the gape cycle begins prior to body displacement, the time is negative.

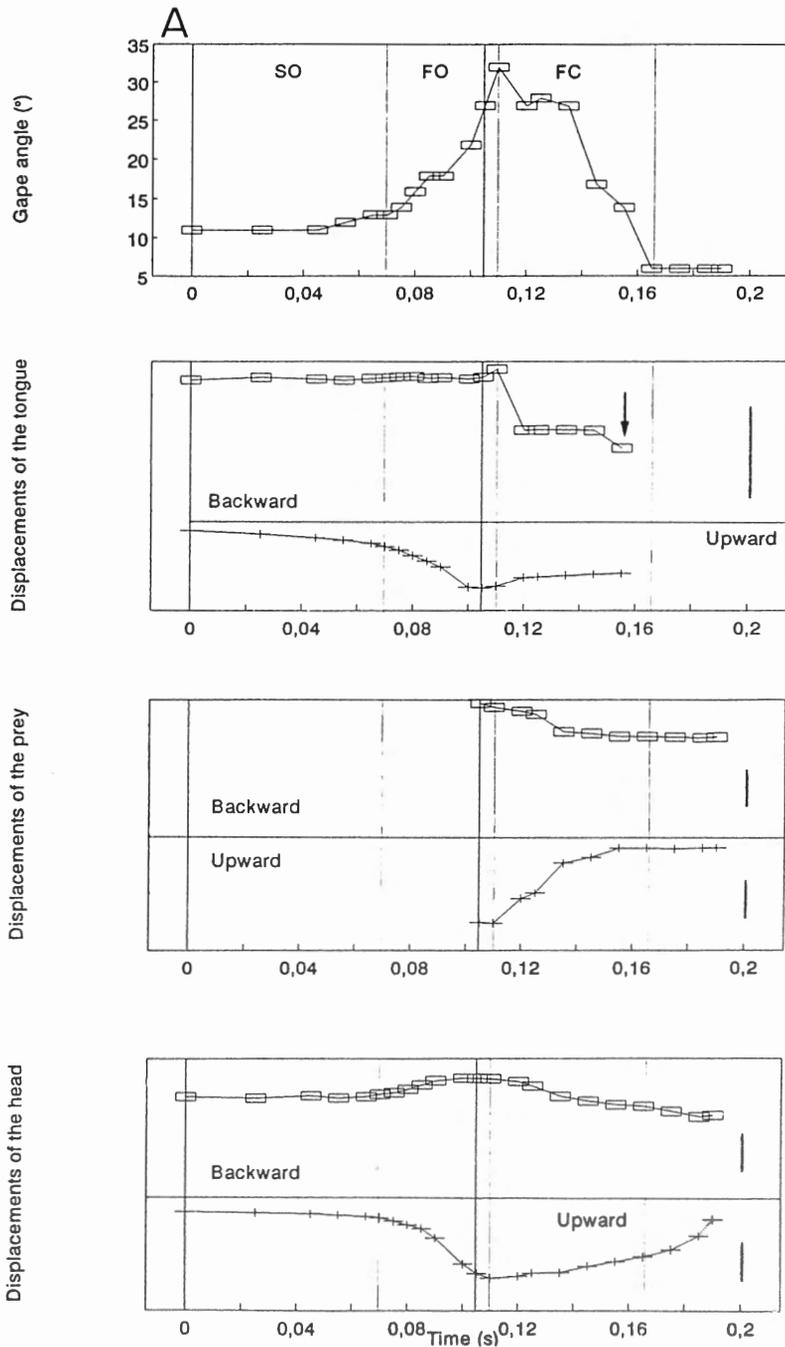
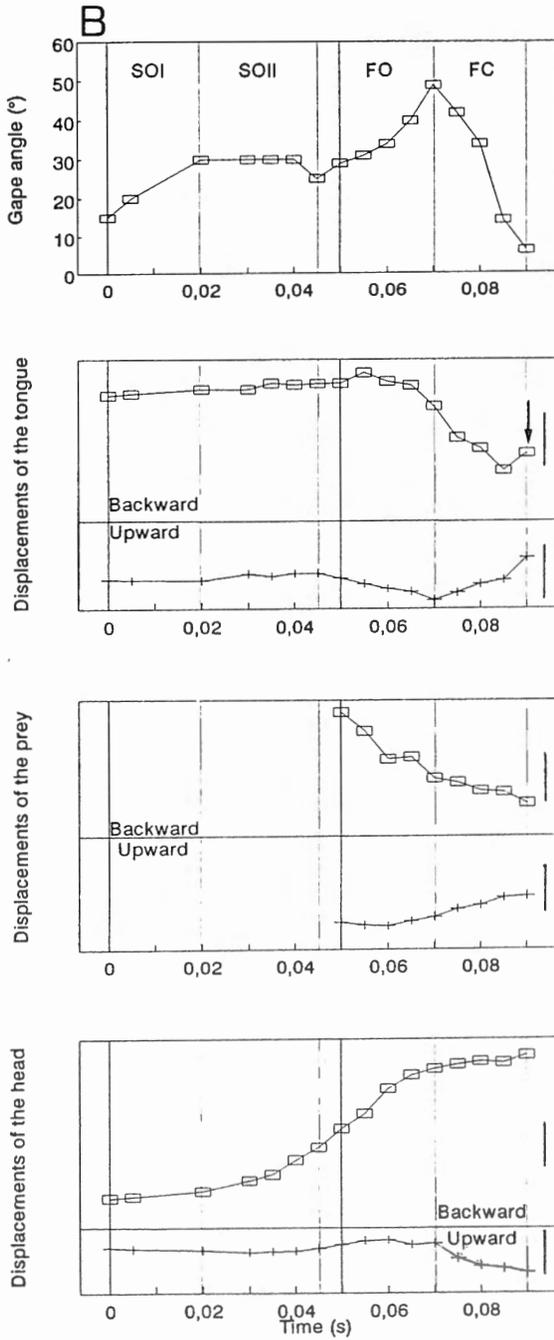


Fig. 4. — Representative kinematic profiles of prey capture by *Anolis equestris* (A) and *Opturus cuvieri* (B) at short prey distances. The solid vertical line indicates tongue-prey contact. The vertical bars correspond to



10 mm. In the second graph (displacements of the tongue), the arrow indicates the last frame in which the tongue was visible for digitizing. (□), horizontal displacement; (+), vertical displacement.

when distances between the lizard and the prey were about 50 cm. In *A. equestris*, the gape cycle began simultaneously or immediately prior to the rotation of the forebody onto the elbow. In *O. cuvieri*, at long distances ( $\geq 15$  cm), the locomotor behaviour began prior to or simultaneously with gape opening (Fig. 2). At short distances ( $\leq 15$  cm), the mouth opened prior to or simultaneously with locomotion toward the prey as in *A. equestris* (Fig. 3). The timing between beginning of gape opening (first frame of SO stage) and the beginning of body displacements was significantly related (Timing =  $-0.39 + 0.027 X$ ;  $r = 0.56$ ) to the prey-lizard distance.

The gape cycle was divided into four successive stages: slow opening (SO) divided into slow opening I (SO I) and slow opening II (SO II), fast opening (FO), and closing (FC). The duration of the SO I stage was rather stereotyped (CV in *A. equestris*: 37.5; CV in *O. cuvieri*: 47.1). The duration of SO II stage in *O. cuvieri* was highly variable (CV: 84.0). The SO II stage was often absent (more than 80% of gape cycles) in *A. equestris* feeding on prey at close distance, and ranged from 0 to 0.03 s in 20% of the cycles. The duration of FO stage in both iguanids was rather similar (Table 1). In both lizards, the velocity of mouth closure (fast closing stage or FC) was also similar (Fig. 4), and this stage can not be divided into fast and slow steps. Gape amplitude was larger in *O. cuvieri* than in *A. equestris* (Table 1).

The tongue was protruded and deformed simultaneously as illustrated for *O. cuvieri* (Fig. 5). The anterior-most point of the tongue moved downward until it contacted the prey. Anteriorly, two lateral masses were separated by a central concavity as soon as the tongue was beyond the jaw margins (Fig. 5). When the tongue contacted the prey, it expanded and then retracted with the prey. At the same time, the jaws surrounded the prey.

During SO and early FO, the tongue was protruded beyond the mandibular symphysis (Figs 2 and 5). However, in both lizards the maximal extension of the tongue tip beyond the mandibular symphysis was slight: 7-9 mm ( $N = 14$ ) in *O. cuvieri* and 6-7 mm ( $N = 10$ ) in *A. equestris*. The tongue contacted the prey during FO (Fig. 4) and always before maximal gape. In both species, tongue-prey contact occurred variably in the FO stage (0.04-0.02 s before maximal gape, see also BELS, 1990 and DELHEUSY and BELS, 1992). Retraction of the tongue with the adhering prey always began during the FO stage and continued until the end of the FC stage. Tongue retraction in *O. cuvieri* and *A. equestris* were rather similar for prey items of different weights, crickets and locusts respectively (Table 1).

After tongue-prey contact, the head of *O. cuvieri* continued to move forward and the widely opening jaws completely surrounded the prey (Figs 4 and 5), which started to be retracted into the mouth by the tongue. The prey was thus brought into the buccal cavity by tongue retraction, but also by forward shift of the lower and upper jaws around the prey item. Whereas the forward movement of the jaws (head, body) continued during FC in *O. cuvieri*, in *A. equestris* in contrast this movement was reversed at the transition between FO and FC (Fig. 4).

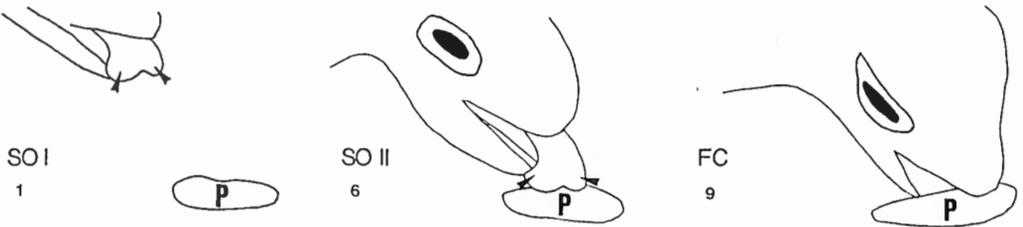


Fig. 5. — Tracings from three typical frames of *Oplurus cuvieri* capturing a cricket. The arrows indicate deformations of the foretongue. Time is indicated in frames, and time between two successive frames is 0.01 s. See figure 2 for abbreviations ; P, prey.

## DISCUSSION

Kinematic profiles of jaw and tongue displacements during prey prehension in one terrestrial (*O. cuvieri*) and one arboreal (*A. equestris*) insectivorous lizard do not differ from the previously described capture kinematics in terrestrial iguanids (SCHWENK and THROCKMORTON, 1989) and agamids (SCHWENK and THROCKMORTON, 1989; KRAKLAU, 1991). However, high speed cinematographic data in *A. equestris* and *O. cuvieri* show that the duration of tongue retraction is lesser in these iguanids (range : 0.03-0.04 s, Table 1) than those data reported by SCHWENK and THROCKMORTON (1989) for iguanids (range : 0.049-0.180 s). Prey retraction in the buccal cavity in *A. equestris* and *O. cuvieri* is produced by simultaneous forward displacements of the jaws around the prey and tongue retraction (Fig. 5) as in the previously described agamids and iguanids (SCHWENK and THROCKMORTON, 1989). For calculating the duration of tongue retraction, we thus only measure the time of the X-displacement of the tongue tip relative to the tip of the mandible. The speed of filming and method of calculation may explain the discrepancy with the data of SCHWENK and THROCKMORTON (1989). Except in Chamaeleontidae which do not move the head toward the prey (WAINWRIGHT *et al.*, 1991), the jaws in iguanians play a major role for prey capturing. In two iguanids using different habitats, the jaw-tongue displacements toward the prey are similar (Fig. 4). The displacement of the jaws in *A. equestris* is mainly produced by a rotation of the body on the elbow (Fig. 1 in BELS, 1990) whereas the displacement of the jaws in *O. cuvieri* is a by-product of the running movement of the lizard toward the prey. Such a running movement should be unfavourable in *A. equestris* because this lizard moves on rather round substrates such as branches with variable diameters. The fixation of this lizard by the subdigital lamellae that contact strongly the surface of the substratum when the lizard is at about 10 cm of the prey (BELS, 1990) is highly favourable for approaching the head toward the prey and capturing it firmly.

Tongue shape in the buccal cavity resembles that described for other iguanids (SCHWENK and THROCKMORTON, 1989). The tongue may have two functional roles : (1) hold the prey onto the substratum, and (2) help to enter the prey into the buccal

TABLE 1

Summary statistics for eight kinematic variables describing the capture cycles in *Anolis equestris* and *Oplurus cuvieri*. FC, fast closing; FO, fast opening; SO I, slow opening I; SO II, slow opening II. (\*) refers to DELHEUSY and BELS (1992) and (\*\*) to BELS (1990). N corresponds to the number of digitized cycles.

| Variables                         | N  | <i>Anolis equestris</i> | N | <i>Oplurus cuvieri</i> |
|-----------------------------------|----|-------------------------|---|------------------------|
| Duration of SO I (s)              | 10 | 0.15 ± 0.10 **          | 7 | 0.17 ± 0.10 *          |
| Duration of SO II (s)             | 10 | 0.02 ± 0.01 **          | 7 | 0.25 ± 0.21 *          |
| Duration of FO (s)                | 10 | 0.04 ± 0.01 **          | 7 | 0.04 ± 0.01 *          |
| Duration of FC (s)                | 10 | 0.04 ± 0.01 **          | 7 | 0.04 ± 0.02 *          |
| Maximal gape angle (°)            | 10 | 30 ± 5 **               | 7 | 35 ± 17 *              |
| Duration of tongue retraction (s) | 10 | 0.03 ± 0.01 **          | 7 | 0.04 ± 0.01 *          |
| Time to tongue-prey contact (s)   | 10 | 0.02 ± 0.01 **          | 6 | 0.02 ± 0.01 *          |

cavity. Except in chameleontids (BELL, 1990; WAINWRIGHT *et al.*, 1991; So *et al.*, 1992) and perhaps some agamids such as *Phrynocephalus helioscopus* (SCHWENK and BELL, 1988; SCHWENK and THROCKMORTON, 1989), the main role of the tongue should be maintaining the prey in position when the jaws are moving forward around the prey. But, retraction of the prey off the substratum is necessary to allow the mandible to slide underneath the prey. In lizards which do not use tongue prehension, the head positioning is completely different (BELS and GOOSSE, 1990; GOOSSE and BELS, 1992). Kinematics of head displacement during retraction of the prey may thus depend on the mechanism used for prey prehension. It also seems to depend on the species-specific adaptation. In a terrestrial species such as *O. cuvieri*, that runs fast toward the prey (Fig. 2), the head elevation occurs after the complete capture cycle (DELHEUSY and BELS, 1992). *A. equestris* moves the head posteriorly during the mouth closure by a backward rotation on the elbow (BELS, 1990). Both displacements of the head may help to prevent the escape of the prey because the prey loses its contact with the substratum.

In *Agama agama* (KRAKLAU, 1991), the beginning of the lunge phase involving the locomotor behaviour is the « committed » step of the prey capture (= strike, in KRAKLAU, 1991) for two reasons; (1) the tongue may retract at any time of the preparatory phase, and (2) the lunge phase is always completed and the lizard moves along the original trajectory without any modulation. Prey capture is thus a complex motor pattern that involves locomotor and jaw muscles (Fig. 4; see also BELS, 1990). In *O. cuvieri*, gape opening is initiated prior to or after the displacement of the lizard toward the prey depending on prey distance (Figs 2 and 3). At

short distances (range : 1-15 cm), the gape cycle always begins prior or simultaneously to displacements of the body or the head toward the prey. This is also the case for *A. equestris*. At long distances (range : 16- 22 cm), the gape cycle in *O. cuvieri* often begins after the displacement of the lizard (Figs 2 and 3). The duration of the SO II stage is related to the distance between the lizard and the prey, whereas duration of SO I is more stereotyped. For prey captures recorded in this study, the SO II stage was short or absent at short distance, but increased at long distance (Fig. 2). BELS (1990) emphasized that the SO II stage may be completely absent in *A. equestris*. The duration of the SO II stage may be affected by different prey characteristics such as mobility, velocity and shape which are not considered in this study, but also by the distance between the lizard and the prey. When the prey is close to its snout ( $\leq 15$  cm for *O. cuvieri*), the lizard might « evaluate » the distance for opening the gape which is necessary for tongue protrusion. The predator thus reduces the duration of the SO II, and begins body displacement toward the prey after the beginning of gape opening. When the prey is at long distances, this « evaluation » might occur during displacements of the lizard toward the prey.

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#### REFERENCES

- BELL, D.A. (1990) — Kinematics of prey capture in the Chameleon. *Zool. Jb. Anat.*, **94** : 247-260.
- BELS, V.L. (1990) — Quantitative analysis of prey-capture kinematics in *Anolis equestris* (Reptilia : Iguanidae). *Can. J. Zool.*, **68** : 2192-2198.
- BELS, V.L. and I. BALTUS (1987) — First analysis of the feeding sequence of *Chameleo dilepis*. In : *Proc. Fourth Ord. Gen. Meet. S.E.H. Nijmegen*. VAN GELDER, J.J., H. STRIJBOSCH and P.J.M. BERGERS (Eds.). Nijmegen : 67-70.
- BELS, V.L. and V. GOOSSE (1990) — Comparative kinematic analysis of prey capture in *Anolis carolinensis* (Iguania) and *Lacerta viridis* (Scleroglossa). *J. Exp. Zool.*, **255** : 120-124.
- DELHEUSY, V. and V.L. BELS (1992) — Kinematics of feeding behaviour in *Oplurus cuvieri*. *J. exp. Biol.*, **170** : 155-186.
- GOOSSE, V. and V.L. BELS (1992) — Kinematic and functional analysis of feeding behaviour in *Lacerta viridis*. *Zool. Jb. Anat.*, **122** : 187-202.
- KRAKLAU, D.M. (1991) — Kinematics of prey capture and chewing in the lizard *Agama agama* (Squamata : Agamidae). *J. Morphol.*, **210** : 195-212.
- REILLY, S.M. and G.V. LAUDER (1990) — The evolution of tetrapod feeding behavior : kinematic homologies in prey transport. *Evolution*, **44** (6) : 1542-1557.

- SCHWENK, K. (1988) — Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. In : *Phylogenetic relationships of the lizard families*. ESTES, R. and G. PREGILL (Eds.). Stanford University Press, Stanford, California : 569-604.
- SCHWENK, K. and D.A. BELL (1988) — A cryptic intermediate in the evolution of Chameleon tongue projection. *Experientia (Basel)*, **44** : 697-700.
- SCHWENK, K. and G. THROCKMORTON (1989) — Functional and evolutionary morphology of lingual feeding in squamate reptiles : phylogenetics and kinematics. *J. Zool. (Lond.)*, **219** : 153-175.
- SO, K-K.J., P.C. WAINWRIGHT and A.F. BENNETT (1992) — Kinematics of prey processing in *Chamaeleo jacksonii* : conservation of function with morphological specialization. *J. Zool. (Lond.)*, **226** : 47-64.
- WAINWRIGHT, P.C., D.M. KRAKLAU and A.F. BENNETT (1991) — Kinematics of tongue projection in *Chamaeleo oustaleti*. *J. exp. Biol.*, **159** : 109-133.