RAPID COMMUNICATION

Comparative Kinematic Analysis of Prey Capture in *Anolis carolinensis* (Iguania) and *Lacerta viridis* (Scleroglossa)

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ABSTRACT   The kinematic profiles of jaw movements are described for *Anolis carolinensis* and *Lacerta viridis* feeding on the same prey item (maggot). *A. carolinensis* is an iguanian (typified by lingual prey capture) and *L. viridis* is a scleroglossan (typified by prey capture using jaws alone). *A. carolinensis*, however, catches maggots by using only the jaws. In so doing, it exhibits the four stages of gape profile considered typical for lizards (slow open, fast open, fast close, slow close). Gape cycle in *L. viridis* shows a hyperbolic curve (no slow open). Two hypotheses concerning the relationship between the two gape cycles are discussed.

The movement of the tongue and hyoid is one of the dominant components of food manipulation in tetrapods (Bramble and Wake, '85; Hiiemae and Crompton, '85). The relation between movements of the hyo-lingual complex and the jaws during feeding phases (e.g., ingestion or food capture, intra-oral manipulation, and deglutition) have been described for a great number of primitive terrestrial tetrapods. Most analyses concern amphibians (Thexton et al., '77; Bemis et al., '83; Larsen and Guthrie, '75; Lauder and Shaffer, '85, '88; Dockx and de Vree, '86; Larsen and Beneski, '88; Reilly and Lauder, '89; Larsen et al., '89). Among Lacertilia, the kinematic profiles of gape and the hyo-lingual complex have been described for only a few lizards (Gnanamuthu, '37; Frazzetta, '84; Bels and Baltus, '87, '89; Bels, '89; Schwenk and Throckmorton, '89).

Recently, Schwenk ('87) emphasized that the primary cladistic dichotomy (Iguania and Scleroglossa) of the Lacertilia reflects a functional segregation in the means of food capture. Iguanians use the tongue as a prehensile organ while scleroglossans take food with the jaws only. Frazzetta ('84) provided a first kinematic profile of prey capture in scleroglossan lizards in his study of *Gerrhonotus multicarinatus*. He showed that the mandible and the upper jaw do not approach the prey with equal accuracy. The movements of the jaws of *G. multicarinatus* were compared with the grasping operation of a human hand and

it was postulated that cranial kinesis permits the upper jaw to approach the prey without the requirement for a large change in the posture and movement of the head and trunk. Goosse and Bels ('89) reported an initial description of the kinematic profiles of the gape in *Lacerta viridis* during prey capture. Such profiles do not show the four phases described for other lizards (Smith, '84; Bels and Baltus, '87). *Trachydosaurus rugosus*, a scleroglossan lizard, contacts food items with the tongue before capture with the jaws, but does not use the tongue as a prehensile organ (Gans et al., '85). No kinematic profiles are described for this scleroglossan lizard, however. In their description of kinematic profiles in terrestrial agamids and iguanids, Schwenk and Throckmorton ('89) report that lingual prehension seems to be the primitive mode of food capture, and is correlated with a "fleshy" protrusible tongue. This situation is limited to the Iguania (Agamidae, Iguanidae, and Chamaeleontidae).

Several iguanids catch prey items with the jaws as well (i.e., *Polychrus acurostris*, Vitt and Lacher, '81). We have observed that *Anolis carolinensis* catches maggots by employing the jaws alone. These observations provided the opportunity to compare the mode of jaw-based food prehension in both sister groups of the Lacertiformes, since *Lacerta viridis* also captures mag-

gots with the jaws (Goosse and Bels, '89). To be able to discuss the evolution of tongue-hyoid movements in relation to gape in Lacertilia, it is necessary to compare the kinematic profiles of capture of a similar food item in the two sister groups of the Lacertiformes: the Scleroglossa and the Iguania. To enable this comparison, high-speed cinematography was employed to obtain images of prey capture of both species. These images were used to provide details of the capture kinematics. Our analysis provides a part of the data necessary to enable discussion of the evolution of motor pattern employed during food ingestion in vertebrates.

MATERIALS AND METHODS

A total of eight feeding sequences in both *Anolis carolinensis* and *Lacerta viridis* were filmed at 100 frames/second using a 1PL Photosonic 16 mm camera fitted with an Angenieux zoom lens. A 1,000 W photoflood was used for illumination. All sequences were shot from the lateral aspect and allowed us to obtain good kinematic profiles. Three adult male *A. carolinensis* (SVL: 55.3 +/− 4.7 mm, x̄ +/− s.d.) and three young *L. viridis* (SVL: 30.2 +/− 2.4 mm, x̄ +/− s.d.) were filmed. The food items used were blow fly maggots (+/− 10 mm length). *A. carolinensis* were filmed together in a 100*50*50 cm glass cage and *L. viridis* singly in 30*18*15 cm glass cages. All recorded sequences were projected frame by frame onto a graphic table by using an Old Delft projector. They were analyzed by digitizing selected points on the head of each lizard (tip of the upper and lower jaws, eye). Each point was characterized by its vertical (Y) and horizontal (X) coordinates. All the coordinates were stored in a dedicated Copam AT microcomputer in the form of a frame by frame table. Frame one was arbitrarily chosen to represent a stage just prior to increase of the vertical distance between the upper and lower jaws. Gape profiles refer to the linear separation of the jaws (Fig. 1) or to the gape angle (Fig. 2). (A comparison of gape angle for various types of food will be provided in a subsequent paper.) Since the lizards took the maggots directly from the substratum, the jaw displacements have two components: 1) displacement of the head and 2) displacements of the jaws themselves. To avoid the effect of head displacement, the jaw displacements were calculated relative to the displacement of the eye. All distances are thus expressed in relative units (no parameters) and plotted against time since the emphasis of this paper is on the comparison of the profiles.
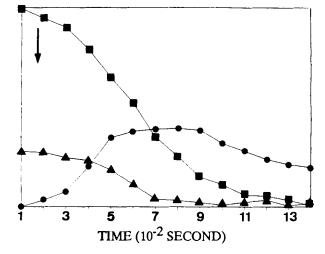

Fig 1. Kinematic profiles of selected cranial components during capture of a maggot by *Lacerta viridis.*(●), gape (▲), horizontal displacement of the head (■), vertical displacement of the head. The arrow under this profile indicates the forward direction.

RESULTS AND DISCUSSION

A generalized model of the feeding cycle in tetrapods was presented by Bramble and Wake ('85). This was characterized by the following four stages: 1) a slow opening of the jaws (SO) immediately followed by 2) a fast opening phase (FO), 3) a fast closing (FC), and finally 4) a slow closing of the jaws (SC). Except in the case of some amphibians (Lauder and Shaffer, '85, '88), results gained from tetrapods seem to support this model. Data presented by Schwenk and Throckmorton ('89) for some Iguanidae and Agamidae corroborate the model well. Since Regal ('66) and Ozeti and Wake ('69) hypothesized that prey capture via tongue projection may be derived from the movements of the tongue during intra-oral food manipulation, it is pertinent to compare the kinematic profiles of capture to Bramble and Wake's generalized model. The kinematic profiles of prey capture by *Lacerta viridis* (Scleroglossa) differ significantly from the model (Figs. 1, 2). The overall gape cycle appears to follow a hyperbolic curve. The SO stage is not present. As in other lizards (Bels and Baltus, '89; Schwenk and Throckmorton, '89), jaw closing is divided into two stages (FC and SC), but the SC stage is not easily distinguished. The duration of the gape cycle may vary greatly even for the same prey type (Fig. 2). Displacement of the prey (e.g., slipping on the substratum) appears to be correlated with this observed variability. During maggot capture the head is strongly inclined downward (Fig. 3). Forward movement begins simultaneously with
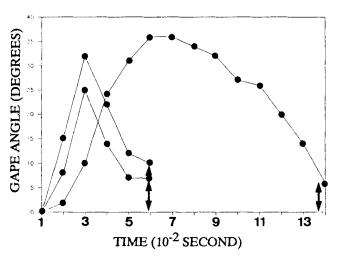
Fig 2. Comparison of the gape during three typical captures of a maggot by *Lacerta viridis*. The arrows represent the thickness of the prey.

Fig 3. Drawings of four steps of capture of a maggot by *Lacerta viridis*. The total duration of the sequence is 0.08 sec.

jaw opening (Fig. 1). *Anolis carolinensis* (Fig. 4A) captures maggots by using its jaws alone and this mode of prehension accords well with the descriptions presented by Schwenk and Throckmorton ('89) for *Iguana iguana* and with Bramble and Wake's model ('85). The SO and FO stages are easily distinguishable for the lower jaw. The upper jaw moves upward during the FO stage (Fig. 4A). In *L. viridis*, the gape cycle is effected only by displacement of the lower jaw (Fig. 4B).

It is clear that the kinematic profiles for the capture of the same prey type are very different in the two species which represent both sister groups of the Lacertilia. Kinematic profiles of the jaws in *Anolis carolinensis*, which catches prey by use of the jaws alone, are similar to the kinematic profiles characteristic of prey capture in *Anolis* when the tongue is used (Bels and Baltus, '89; Bels, '90), and to kinematic profiles of other iguanians (Schwenk and Throckmorton, '89). Tongue displacement was not clearly visible in *A. carolinensis* when catching maggots by using only the jaws. In *A. carolinensis*, both jaws contact the prey at the same time, whereas the lower jaw touches the prey first in *Lacerta viridis*, as it does in *Gerrhonotus multicarinatus* (Frazzetta, '84). The variability of the gape profile in *G. multicarinatus* is extreme (Frazzeta, '84). Prey capture from the substratum seems to be rather different from capture above the substratum (in the air), but presence of an SO stage is difficult to ascertain (Figs. 10, 11, and 13 in Frazzetta, '84).

Schwenk and Throckmorton ('89) hypothesize that in scleroglossans, prehension using the jaws is a derived feature when compared with the primitive state of lingually based capture. The
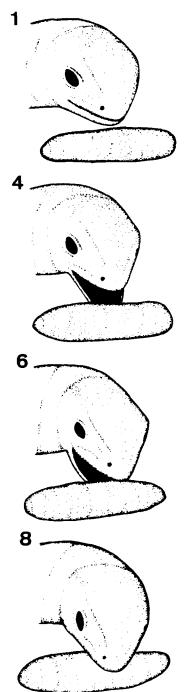
former represents a loss of lingual prehension associated with a dramatic modification of the foretongue, which is used in different behavioral pattern (i.e., flicking). In the Scleroglossa, kinematic profiles of the gape and jaws reveal a loss of the SO stage (Fig. 4B), which corresponds to a slight advance of the tongue at the symphysis of the jaws (Bels and Baltus, '87; Schwenk and Bell, '88; Schwenk and Throckmorton, '89). In
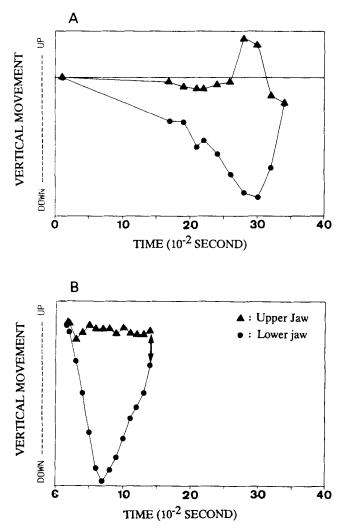
Fig 4. Vertical displacement of the upper and lower jaws during capture of a maggot by (A) *Anolis carolinensis* and (B) *Lacerta viridis*. Young *Lacerta viridis* cannot reduce the prey as *A. carolinensis* after closing. The arrow represents the thickness of the prey.

An alternate hypothesis could be that the kinematic profiles in the Lacertidae (Scleroglossa) may have been derived directly from a more primitive kinematic profile which lacked an SO stage, rather similar to that of certain amphibians (Bemis and Findeis, '86; Lauder and Shaffer, '85, '88). *Sphenodon punctatus* is known to catch crickets with the tongue and mice with the jaws only (Gorniak et al., '82) but no kinematic profiles are available. They should, however, be very useful in determining whether this more primitive Squamate (cladogram based on tongue morphology by Schwenk, '88) has a gape cycle similar to that of the Lacertidae and some amphibians, or to that of the Iguanidae. If it accords with the first case the more primitive kinematic profile of lepidosaurians could be viewed as being directly derived from one lacking the SO stage. If, however, it agrees with the situation seen in the Iguanidae and Agamidae (Bels and Baltus, '89; Schwenk and Throckmorton, '89; this paper) then our last hypothesis will not be confirmed.

ACKNOWLEDGMENTS

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Lacerta viridis, it is clear that the tongue does not touch the prey at any time during capture of maggots, but it does act during intra-oral food manipulation (Goosse and Bels, pers. obs.). We hypothesize that the loss of lingual prehension could be part of a set of modifications in increasing the velocity of gape opening (loss of the SO stage). The mean duration of maggot capture in *L. viridis* (98 +/− 32 ms; x̄ +/− s.d.) is significantly shorter (ANOVA, $P < 0.05$) than that in *Anolis carolinensis* (233 +/− 70 ms; x̄ +/− s.d.) (Fig. 4A,B). Closing is rather similar in both species. When it is present, the SO stage of the kinematic profiles described for *Gerrhonotus multicarinatus* (Frazzetta, '84) is relatively short and generally encompasses less than 25% of the total duration of jaw opening (Figs. 10–13 in Frazzetta, '84).

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