Inertial feeding in the teiid lizard *Tupinambis merianae*: the effect of prey size on the movements of hyolingual apparatus and the cranio-cervical system

Stéphane J. Montuelle[1,*], Anthony Herrel[2], Vicky Schaerlaeken[3], Keith A. Metzger[4], Alexandre Mutuyeyezu[1] and Vincent L. Bels[1]

[1]UMR 7179 'Mécanismes Adaptatifs: des Organismes aux Communautés', Muséum National d'Histoire Naturelle, équipe 'Diversité Fonctionnelle et Adaptations', Département EGB Ecologie et Gestion de la Biodiversité, 57, rue Cuvier bp55, F-75231 Paris cedex 5, France, [2]Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA, [3]Department of Biology, University of Antwerp, Universiteitsplein 1,B-2610 Antwerpen, Belgium and [4]Hofstra University, School of Medicine, 145 Hofstra University, East Library Wing, Hempstead, NY 11549-1010, USA

*Author for correspondence (e-mail: montuelle@mnhn.fr)

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SUMMARY

In most terrestrial tetrapods, the transport of prey through the oral cavity is accomplished by movements of the hyolingual apparatus. Morphological specializations of the tongue in some lizard taxa are thought to be associated with the evolution of vomerolfaction as the main prey detection mode. Moreover, specializations of the tongue are hypothesized to compromise the efficiency of the tongue during transport; thus, driving the evolution of inertial transport. Here we use a large teiid lizard, *Tupinambis merianae*, as a model system to test the mechanical link between prey size and the use of inertial feeding. We hypothesize that an increase in prey size will lead to the increased recruitment of the cranio-cervical system for prey transport and a reduced involvement of the tongue and the hyolingual apparatus. Discriminant analyses of the kinematics of the cranio-cervical, jaw and hyolingual systems show that the transport of large prey is indeed associated with a greater utilization of the cranio-cervical system (i.e. neck and head positioning). The tongue retains a kinematic pattern characteristic of lingual transport in other lizards but only when processing small prey. Our data provide evidence for an integration of the hyolingual and cranio-cervical systems; thus, providing partial support for an evolutionary scenario whereby the specialization of the tongue for chemoreception has resulted in the evolution of inertial transport strategies.

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INTRODUCTION

Food acquisition is an important activity that is directly linked to the survival and fitness of an individual. Feeding is a highly complex behavior that is dependent on both the locomotor and cranio-cervical systems in order to detect, find, capture, kill, transport and swallow prey (Higham, 2007; Montuelle et al., 2008; Montuelle et al., 2009). The feeding system itself is also highly complex and depends on the integration of the jaw, the hyolingual and cervical systems (Bels et al., 1994; Schwenk, 2000; Herrel et al., 2001; Bels, 2003; Vincent et al., 2006; Ross et al., 2007). The control mechanisms involved in feeding are intricate as well and may, for example, involve feedback pathways between the jaws and the tongue to coordinate extremely rapid and ballistic movements in frogs (Nishikawa, 1999). Because of its integrated nature, the feeding system has been suggested to be constrained, and evolutionary specialization of individual components of the system may be limited (Bramble and Wake, 1985; Herrel et al., 2009). Consequently, duplication and decoupling events have been proposed as major evolutionary pathways, allowing morphological and functional specialization (Galis, 1996; Galis and Drucker, 1996; Schaefer and Lauder, 1996). For example, the decoupling of the hyobranchial system from its ancestral function during respiration in plethodontid salamanders allowed it to become a highly specialized ballistic tongue projection system (Wake and Deban, 2000).

In lizards, specialization of elements of the feeding system is also relatively common as exemplified by, for example, the tongue of chameleons (Bell, 1989; Wainwright et al., 1991; Herrel et al., 2000) or the jaw system in durophagous lizards (Dalrymple, 1979; Pregill, 1984; Herrel and Holanova, 2008). However, one of the most striking functional specializations in squamates involves the sensory modalities used to locate prey (Bels et al., 1994; Schwenk, 2000; Bels, 2003). Whereas geckoes, the basalmost squamates (Townsend et al., 2004; Vidal and Hedges, 2004), rely predominantly on olfaction and vision to detect prey (Dial and Schwenk, 1996), several groups of squamates have independently evolved a more active foraging style that is highly dependent on the use of vomerolfaction (Vitt et al., 2003). This shift in behavior and performance was associated with distinct morphological changes of the tongue. Indeed, the evolutionary development of vomerolfaction is suggested to have gone hand-in-hand with (i) the evolution of a long, bifurcated tongue used to sample chemical stimuli from the environment (Schwenk, 1993; Cooper, 2007) (Fig. 1), and (ii) modifications in the papillary morphology of the tongue (Schwenk, 1988; Toubeau et al., 1994; Schwenk, 2000; Iwasaki, 2002). Because the mechanisms that generate adhesion between the tongue and prey are surface area-dependent phenomena (Emerson and Diehl, 1980; Bramble and Wake, 1985; Schwenk, 2000), the ability of the tongue to generate adhesion and friction is strongly reduced in these lizards. As the ancestral use of the tongue was clearly
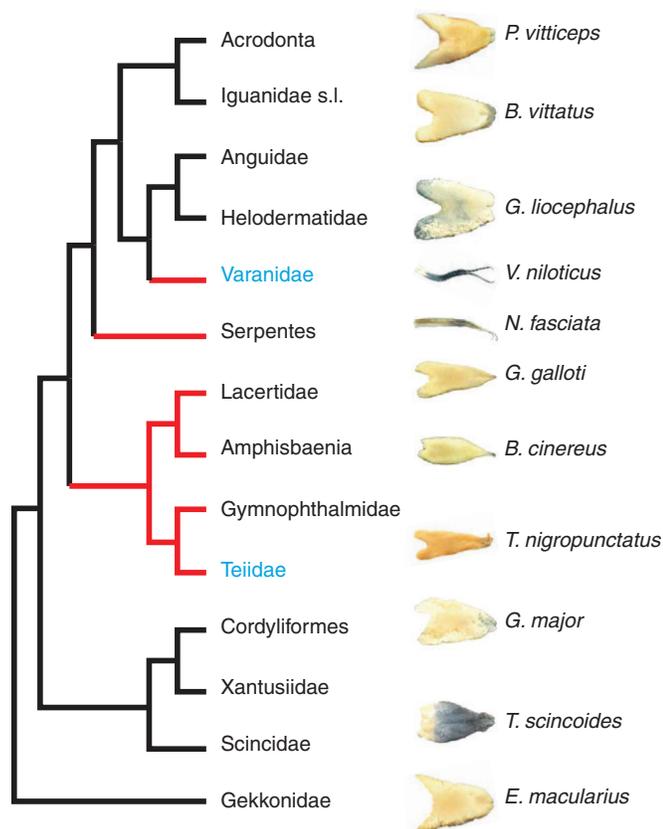
Fig. 1. Phylogenetic relationships of the Squamata (Townsend et al., 2004). For each genus, a picture of the dorsal side of the tongue of a representative species is shown to the right to illustrate the differences in tongue shape among different squamate groups. Branches indicated in red are those where significant tongue elongation has occurred. Clade names indicated in blue are those in which species have been reported to use kinetic inertial prey transport. *P. vitticeps* = *Pogona vitticeps*; *B. vittatus* = *Basiliscus vittatus*; *G. liocephalus* = *Gerrhonotus liocephalus*; *V. niloticus* = *Varanus niloticus*; *N. fasciata* = *Nerodia fasciata*; *G. galloti* = *Gallotia galloti*; *B. cinereus* = *Blanus cinereus*; *T. nigropunctatus* = *Tupinambis nigropunctatus*; *G. major* = *Gerrhosaurus major*; *T. scincoides* = *Tiliqua scincoides*; *E. macularius* = *Eublepharis macularius*.

associated with prey transport, this specialization of the tongue for chemoreceptive purposes has been suggested to compromise the ability of long-tongued lizards to transport large prey (Smith, 1986; Schwenk, 1995; Schwenk, 2000).

Although specializing on small clumped prey such as ants or termites could be a way out of this conundrum, several of the highly specialized clades such as varanids (characterized by extreme elongation of the tongue) or teiids have become active foragers specializing in relatively large prey, including vertebrates (Losos and Greene, 1988). Consequently, these lizards probably cannot use lingual prey transport and must rely on an alternative transport mechanism (Gans, 1969; Smith, 1982; Smith, 1986; Metzger, 2005). Indeed, varanids and large teiids that eat large and heavy prey use an inertial prey transport mechanism whereby a rapid movement of the cranio-cervical system is used to accelerate the prey posteriorly, similar to that observed in many archosaurs (Smith, 1982; Smith, 1986; Cleuren and De Vree, 1992). Once the cranio-cervical system is set into motion, the jaws are opened rapidly and the movement of the head is reversed, resulting in a net posterior displacement of the prey relative to the jaw (Cleuren and De Vree,

1992). Given the observed specialization of the tongue for chemoreceptive purposes in lizards using inertial feeding, it has been hypothesized that inertial feeding and specialization of the tongue have evolved in concert (Smith, 1986).

Unfortunately, explicit tests of this hypothesis are extremely difficult as inertial feeding probably evolved only twice in lizards (Fig. 1). In the present study, we decided to use a representative of a lizard genus known to use both lingual and inertial transport, the teiid lizard *Tupinambis merianae* (Smith, 1984; Elias et al., 2000; Metzger, 2005), to investigate whether the transport of larger food items is indeed associated with an increased use of inertial transport. By manipulating the size and mass of the food items we experimentally reduce the relative tongue surface area in contact with food. Using videofluoroscopy, we quantify the movements of (i) the cranio-cervical system, (ii) the jaws, and (iii) the tongue and hyoid, and test whether transport kinematics during feeding on large mice are associated with inertial transport. Moreover, we use the kinematics of pharyngeal packing cycles to test whether the heavier prey items result in a greater dependence on hyoid movements due to the relative reduction of the tongue surface area as previously observed in *Varanus* (Smith, 1986). Confirmation of these hypotheses would provide indirect support for a link between the evolution of long tongues and the evolution of alternative prey transport systems like inertial feeding in lizards. Moreover, this would suggest co-evolution of different biological functions involved in predator–prey relationships (prey detection, foraging mode and prey transport), and may provide insights into the functional and evolutionary mechanisms employed to overcome trade-offs associated with morphological and functional specialization.

MATERIALS AND METHODS
Animals and husbandry

Two adult and one large subadult male *Tupinambis merianae* Duméril and Bibron 1839 [mass: 1520.7±914.6 g; snout–vent length (SVL): 317.0±72.6 mm; head length: 66.5±16.6 mm; ±s.d.] were used in the feeding experiments. Animals were housed individually in terraria placed in a temperature-controlled room set at 24°C and were provided with a basking spot at 50°C. Lizards were fed fruits, vegetables and mice twice weekly, with water available *ad libitum*. Prior to recordings, animals were fasted for 48 h. All animals were obtained through the pet trade from captive breeders and were accompanied by appropriate CITES documents upon purchase.

Videofluoroscopy

To facilitate the analysis of the videofluoroscopic images, radio-opaque markers were implanted at the front and back of the upper and lower jaws, at the front and back of the parietal and frontal bones, at the base and top of the quadrate, at the anterior, middle and posterior aspect of the tongue, and in the connective tissue sheet surrounding the cartilaginous basihyal. Note, however, that not all of these were used for the purpose of the present study. Before implantation of radio-opaque markers, animals were anaesthetized using an intramuscular injection of Ketamine (100 mg kg^{-1} body mass; ketamine hydrochloride, 50 mg ml^{-1}, Parke-Davis, Brussels, Belgium). Markers were implanted using hypodermic needles (markers in the tongue, basihyal, quadrate and neck) or by drilling small holes in the bone using a dental drill and filling these with radio-opaque material (markers in the upper and lower jaws, on the parietal and on the frontal bones). Marker placement was checked using dorso–ventral and lateral radiographs for each individual. An additional lead marker was implanted into the prey to allow quantification of the position of the prey throughout transport.

Animals were filmed in lateral view while feeding on mice of different size. Two size classes of mice were offered: newborn mice (length=31.44±4.18 mm, mass=1.74±0.46 g; ±s.d.) and adult mice (length=79.00±12.45 mm, mass=30.82±1.77 g; ±s.d.). The prey type used here was selected because small vertebrates ranging in size from small frogs and lizards to large rodents belong to the natural diet of *T. merianae*. X-rays were generated using a Philips optimus M200 X-ray generator (Philips International B.V., Amsterdam, The Netherlands) and recorded at 250 frames s^{-1} using a Philips image intensifier with a Redlake Motion Pro 2000 digital camera (Redlake MASD LLC, San Diego, CA, USA). During the recording sessions, the prey items were positioned 10–20 cm in front of the animal. No more than five trials were performed for each individual per day to avoid satiation, and all trials were conducted in the afternoon between 14:00 and 17:00 h.

Additional regular video recordings
In addition to the videofluoroscopic recordings, we also gathered an additional data set where animals were fed a wide array of mice of different size (ranging from newborns to adults) and filmed at 50 Hz using a regular video camera (JVC GR-DVL9800, JVC Corporation, Wayne, NJ, USA). Transports were classified as being either lingual or inertial based on the presence of an aerial phase where the prey lost contact with the jaws and tongue (inertial transport cycle). For each sequence we recorded the mass of the prey. Associations between prey mass and the number of inertial transport cycles used in each feeding sequence were tested by correlation analysis (Pearson correlation coefficient).

Kinematic analysis
Based on the videofluoroscopic recordings we digitized the position of eight of the radio-opaque markers associated with the head, neck and tongue. Landmarks digitized were the two markers on the frontal bone, the anteriormost marker on the lower jaw, the anteriormost marker on the upper jaw, the marker at the base of the quadrate, the posteriormost two markers in the tongue and the marker on the basihyal. In addition, three clearly visible anatomical landmarks were digitized: the dorsal side of the exoccipital bone, the articulation between cervical vertebrae 3 and 4 (C4–C3) and the tip of the premaxillary bone. Finally, two landmarks, defined by the intersection of a line drawn through the basihyal marker and perpendicular to the line describing the long axis of the neck (interconnecting the anatomical landmarks at the exoccipital and the junction of C4–C3), with the neck dorsally and the pharynx ventrally were digitized (Fig. 2A).

Based on the *X*,*Y*-coordinates of these 13 landmarks, we calculated a total of nine kinematic variables associated with the cranial, cervical and hyolingual system from which 35 spatio–temporal variables were extracted for further analysis. On each profile, we extracted the maximal and minimal value, and their respective times of occurrence, and calculated the magnitude of the variation in each variable. In addition, we extracted the value at the onset of mouth opening to describe the positioning of the head, the neck and the hyolingual system at this point in time.

Movements associated with the positioning of the cranio-cervical system were represented by four kinematical profiles: (i) the vertical displacement of the cranium, defined by the *Y*-coordinate of the nose and from which we extracted the timing of its minimal and maximal displacement (ms). (ii) Head slope is defined as the angle between a line interconnecting the markers on the frontal bone and the vertical (Fig. 2B), with a low angle corresponding to the head being more dorsally inclined. We
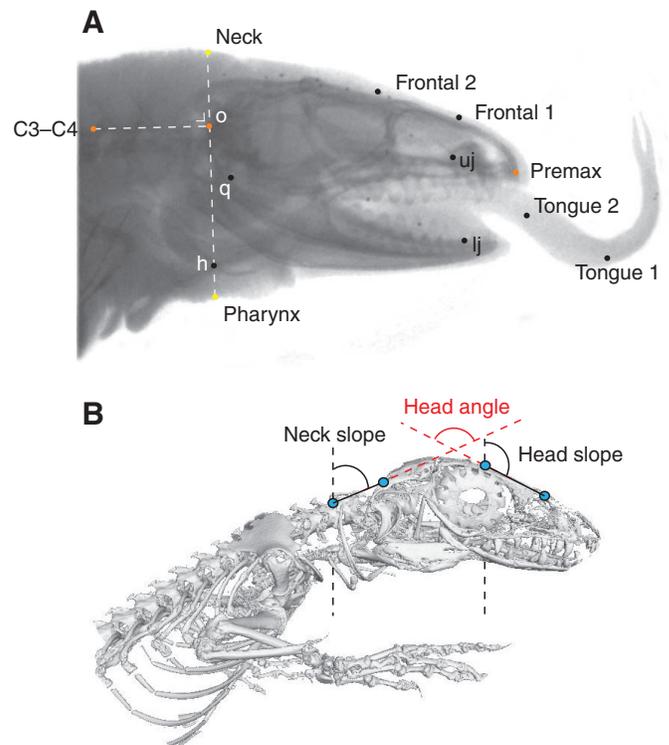

Fig. 2. (A) X-ray image recorded in lateral view after implantation of radio-opaque markers. Markers used for the current analysis were those placed on the upper (uj) and lower jaws (lj), in the tongue (tongue 1, tongue 2), in the basihyal (h), at the base of the quadrate (q) and at the front and back of the frontal bone (frontal 1, frontal 2). Additionally, three anatomical landmarks including the tip of the premaxillary bone (premax), the dorsal side of the exoccipital (o) and the junction of cervical vertebrae 3 and 4 (C4–C3) were digitized (orange circles). Finally, two landmarks defined by the interconnection of a line drawn through the hyoid marker and perpendicular to the long axis of the neck (defined by the landmarks on the exoccipital and C4–C3) with the dorsal (neck) and ventral (pharynx) side of the animal were digitized (yellow circles). (B) Three-dimensional reconstruction of the anatomical elements of *Tupinambis merianae* involved during prey transport: head, neck, vertebral axis and forelimbs; reconstructions were done using Amira software, based on CT-scan (X-Tek MicroCT at the Harvard University CNS facility, Cambridge, MA, USA). The three angular variables used to describe positioning of the neck and the head are indicated: head slope (black), neck slope (black) and head angle (red); see Materials and methods for the data extracted from these variables. The blue points are the radio-opaque markers that were digitized.

extracted the minimal and maximal head slope (deg.), respectively, representing the most and the least dorsally inclined position of the head, the time to minimal and maximal head slope (ms), the total dorso–ventral rotation of the head (deg.) and the slope of the head at the onset of mouth opening (deg.). (iii) Neck slope, defined as the angle subtended by a line interconnecting the markers on the exoccipital and on the C4–C3 joint, and the vertical (Fig. 2B) such that when the angle increases the neck is more horizontal. From this profile we extracted the minimal and maximal neck slope (deg.), respectively, representing the most inclined and the most horizontal position of the neck, the time to the minimal and maximal neck slope (ms), the total neck rotation (deg.) and neck slope at the onset of mouth opening (deg.). (iv) Head angle, defined as the angle between the line subtended by the cervical markers (exoccipital, C4–C3) and the line subtended by the markers on

Table 1. Summary of the kinematics associated with cranio-cervical movements in *Tupinambis merianae* during intraoral transport and pharyngeal packing of adult and newborn mice

	Intraoral transport		Pharyngeal packing	
	Newborn	Adult	Newborn	Adult
Number of feeding events	8	7	9	6
Number of cycles analyzed	16	13	17	16
Time to minimal vertical displacement of the cranium (ms)	122±37	149±55	157±61	116±48
Time to maximal vertical displacement of the cranium (ms)	478±32	503±91	384±42	404±47
Minimal head slope (deg.)	94.8±1.4	87.4±3.8	95.7±1.6	85.6±3.7
Time to minimal head slope (ms)	363±44	500±73	322±47	343±60
Maximal head slope (deg.)	111.4±1.3	116.3±3.5	108.7±1.3	106.4±1.9
Time to maximal head slope (ms)	244±32	142±54	213±42	174±46
Total rotation of the head (deg.)	16.6±1.2	28.9±2.7	13.0±1.3	20.8±2.6
Head slope at mouth opening (deg.)	103.7±1.5	113.6±3.7	102.1±1.0	98.4±2.2
Minimal neck slope (deg.)	68.0±1.6	65.7±4.4	58.4±2.5	44.7±1.9
Time to maximal neck slope (ms)	417±54	533±87	283±46	400±59
Maximal neck slope (deg.)	80.7±1.4	84.3±4.7	72.0±1.4	57.5±0.5
Time to maximal neck slope (ms)	137±32	90±53	146±41	218±59
Total rotation of the neck (deg.)	12.7±0.8	18.5±2.7	13.7±1.8	12.8±1.6
Neck slope at mouth opening (deg.)	77.1±1.6	79.3±4.0	67.0±2.0	51.5±1.6
Minimal head angle (deg.)	141.4±1.2	134.7±3.0	133.8±2.2	123.3±1.8
Time to minimal head angle (ms)	325±57	330±82	305±38	229±42
Maximal head angle (deg.)	161.5±1.4	165.6±2.4	151.6±1.7	148.3±2.8
Time to maximal head angle (ms)	347±66	819±115	266±52	570±77
Total rotation of the cranium relative to the neck (deg.)	20.1±1.2	30.9±3.0	17.8±1.7	25.1±3.3
Head angle at mouth opening (deg.)	153.4±1.5	144.6±2.2	145.0±1.8	132.9±1.8

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

the frontal bone (Fig. 2B). From this profile, we extracted the minimal and maximal head angle (deg.), the time to minimal and maximal head angle (ms), the total rotation of the cranium relative to the neck (deg.) and the head angle at the onset of mouth opening (deg.) (Table 1).

Gape angle, the angle defined by the tip of upper jaw, the marker at the quadrate–articular articulation and the tip of the lower jaw, was used to quantify movements of the jaws. From this profile we extracted the total duration of the gape cycle (ms), maximal gape (deg.) and the time to maximal gape (ms) (Table 2).

Movements of the hyolingual system were described by four kinematic profiles: (i) tongue position, defined by the distance between the posteriormost tongue marker and the marker in the basihyal. Based on the plots describing the change in tongue position over time, we quantified the time to the maximal anterior and posterior displacement of the tongue (ms), the maximal total tongue

Table 2. Summary of the kinematics associated with jaw and hyolingual movements in *Tupinambis merianae* during intraoral transport and pharyngeal packing of adult and newborn mice

	Intraoral transport		Pharyngeal packing	
	Newborn	Adult	Newborn	Adult
Number of feeding events	8	7	9	6
Number of cycles analyzed	16	13	17	16
Total duration of gape cycle (ms)	598±33	831±110	546±42	609±42
Maximal gape (deg.)	25.7±1.7	42.2±3.0	15.3±0.6	25.5±1.7
Time to maximal gape (ms)	407±31	456±73	341±26	323±26
Number of feeding events	6	4	7	4
Number of cycles analyzed	12	8	13	10
Time to maximal anterior tongue displacement (ms)	327±65	417±111	174±11	201±89
Time to maximal posterior tongue displacement (ms)	525±38	526±96	400±41	475±47
Maximal total tongue displacement (mm)	24.2±1.7	22.2±1.1	26.9±2.7	14.9±1.4
Speed of tongue retraction (cm s^{-1})	1.7±0.2	1.5±0.2	2.4±0.4	0.8±0.1
Time to maximal tongue elongation (ms)	305±50	608±148	154±19	282±85
Time to maximal tongue shortening (ms)	300±62	553±126	391±39	402±63
Time to maximal dorsal displacement of the basihyal (ms)	151±40	380±96	280±55	219±33
Time to maximal ventral displacement of the basihyal (ms)	512±55	588±204	285±59	384±72
Total vertical displacement of the basihyal (mm)	6.3±0.7	5.4±0.5	5.5±0.9	6.8±0.7
Time to maximal compression of the pharynx (ms)	160±44	443±122	269±53	177±44
Time to maximal expansion of the pharynx (ms)	508±54	700±194	235±66	472±65
Total pharynx expansion (mm)	6.5±0.8	4.7±1.1	5.1±0.7	5.5±1.0

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

displacement (mm) and the speed of tongue retraction ($cm\,s^{-1}$). (ii) The compression of the tongue base is defined as the distance between the two posterior tongue markers (Fig. 2). From this kinematic profile we extracted the time to maximal tongue elongation (ms) and the time to maximal tongue shortening (ms). (iii) The dorso–ventral displacement of the basihyal is defined as the distance between the basihyal marker and the marker on the dorsal neck perpendicular to the hyoid marker. From this profile we extracted the time to the maximal dorsal and ventral displacement of the basihyal (ms) and the total vertical displacement of the basihyal (mm). (iv) The pharyngeal compression is defined as the distance between the two markers perpendicular to the long axis of the neck at the level of the basihyal marker. From this kinematic profile we extracted the time to maximal compression and extension (ms), as well as the total pharyngeal compression (mm) (Table 2).

Data set

The data set is thus composed of three matrices that represent the movements associated with the three systems involved during prey transport in *T. merianae* (Tables 1 and 2): the cranio-cervical system, the jaw system and the hyolingual system. The three matrices were established for intraoral and pharyngeal packing cycles separately.

First, 20 variables quantifying the movements of the cranio-cervical system were extracted (Table 1). Among the 20 variables, two illustrate the vertical displacement of the cranium, six summarize the slope of the head, six describe the changes in the neck slope and the last six variables are used to illustrate the head angle, which quantifies the position of the head relative to the neck. These variables are crucial to assess the contribution of the head–neck system to transport and pharyngeal packing. The movements of the jaw system are summarized by three variables typically used in studies of feeding behavior: the total duration of the transport cycle, the maximal gape angle and the time to maximal gape angle (Table 2). The movements of the hyolingual system are quantified using 12 variables (Table 2). Four variables illustrate the displacement of the tongue, two other variables describe the elongation of the tongue, three variables summarize the vertical displacement of the basihyal and the last three variables quantify the compression of the pharynx.

A total of 62 cycles were analyzed across the three individuals. Of those, 29 were intraoral transport cycles, 16 with newborn mice (four, four and eight cycles for each of the three individuals, respectively) and 13 with adult mice as prey (three, five and five cycles for each of the three individuals, respectively). These cycles were drawn from eight feeding events of newborn mice (two, two and four for each of the three individuals, respectively) and seven feeding events of adult mice (two, three and two for each of the three individuals, respectively). For pharyngeal packing 33 cycles were analyzed, 17 of which were for newborn mice (six, four and seven cycles for each of the three individuals, respectively) and 16 for adult mice (four, six and six cycles for each of the three individuals, respectively). These cycles were drawn from nine feeding events of newborn mice (four, two and three for each of the three individuals, respectively) and six feeding events of adult mice (two, two and two for each of the three individuals, respectively). The cycles were selected randomly among the numerous cycles occurring during the recorded transport sequences. Whereas the data sets for cranio-cervical and jaw movements are represented by all three individuals, tongue movements were quantified for two individuals only as the basalmost tongue marker was often obscured by prey in the third individual. Consequently,

hyolingual kinematics represent two individuals for which 20 intraoral transport cycles – 12 for newborn mice (four and eight cycles, respectively) and eight for adult mice (three and five cycles, respectively) and 23 pharyngeal packing cycles – 13 for newborn mice (six and seven, respectively) and ten for adult mice (four and six, respectively) – were analyzed.

Statistical analysis

All statistical analyses were performed using SPSS 15.0 for Windows (SPSS, Chicago, IL, USA). Data were $\log_{10}$-transformed prior to run analysis to fulfil assumptions of normality and homoscedascity. After transformation all data were normally distributed and consequently used for subsequent parametric analyses. No effect of predator size was detected and thus will no longer be considered in our analysis. The kinematic data set was divided into three matrices: one describing the movements of the cranio-cervical system, a second one describing the movements of the jaws and a third one describing the movements of the hyolingual apparatus. Intraoral and pharyngeal cycles were analyzed separately throughout.

For each of the three kinematic data sets associated with intraoral transport, we performed a discriminant function analysis (DFA) to identify which kinematic variables best discriminated between prey sizes. We used a stepwise model and used the probability (at α=0.05) of the *F*-ratio as the criterion for entry/removal. We only considered variables that displayed standardized canonical coefficients greater than 0.70. For classification, prior probabilities for groups were computed based on group size based on the within-groups covariance matrix. Next, predicted group membership was established, and probabilities of group membership were calculated. Based on the results of the DFAs on the three data sets (cranio-cervical, jaw and tongue) of intraoral transport, we retained all discriminating variables and compiled them into a new matrix, which was subjected to a new discriminant analysis. This allowed us to contrast cranio-cervical, jaw and hyolingual movements in discriminating between transport cycles associated with prey of different size (i.e. small *versus* large mice), and to address whether transport of larger prey is indeed associated with the recruitment of the cranio-cervical system as expected for inertial transport cycles. The same procedure was then applied to the three kinematic data sets associated with pharyngeal transport.

RESULTS
Kinematics of prey transport

The following paragraphs will give a brief, qualitative overview of prey transport kinematics in *T. merianae* feeding on a single prey type that differs in its absolute size. The kinematics of prey transport in *T. merianae* differ dramatically depending on whether animals feeds on newborn or adult mice. The kinematic profiles are different in shape, magnitude and levels of variability (Figs 3–6), suggesting that prey size strongly affects the movements and actions of the cranio-cervical, jaw and hyolingual systems. Moreover, distinct kinematic differences were observed between feeding stages (intraoral transport *versus* pharyngeal packing; Tables 1 and 2). For jaw movements, prey transport cycles are composed of four phases as described previously for lizards [slow-opening (SO), fast-opening (FO) ending at maximal gape, fast-closing (FC) and a slow closing power-stroke phase (SC-PS) (see Bramble and Wake 1985; McBrayer and Reilly, 2002b)]. Both intraoral and pharyngeal cycles of large prey involve a longer cycle duration and a larger gape (Table 2; Fig. 3A; Fig. 4A; Fig. 5A; Fig. 6A). For intraoral cycles one noticeable difference between adult and newborn mice is the presence of a distinct SO II stage during transport of mice (Table 2; Fig. 3A; Fig. 5A). Regardless of the size of the prey, jaw movements
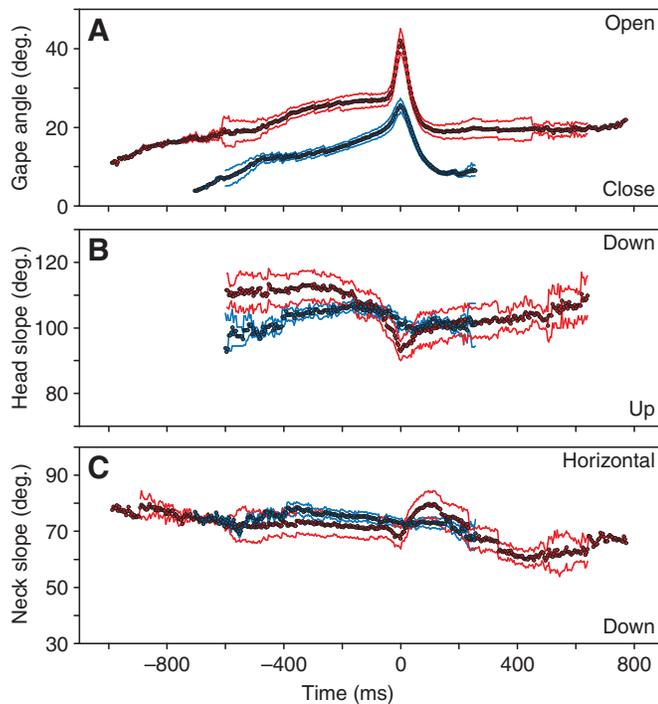
Fig. 3. Mean kinematical profiles (±s.e.m.) illustrating the movements of the jaw and cranio-cervical systems during intraoral transport. From top to bottom the changes in (A) gape angle, (B) head slope and (C) neck slope over time are illustrated. See Materials and methods for details. Cycles for all individuals were aligned at the onset of maximal gape, then mean profiles were calculated and plotted. Different prey types are indicated by colors: the red symbols and lines represent large prey (mouse); blue lines small prey (pinkie). Note how the transport of large prey is associated with greater gape angles and cranio-cervical movements. Moreover, a significant increase in cycle duration is observed during the transport of large prey.

Fig. 4. Mean kinematical profiles (±s.e.m.) illustrating the movements of the jaw and cranio-cervical systems during pharyngeal packing. From top to the bottom the changes in (A) gape angle, (B) head slope and (C) neck slope over time are illustrated. See Materials and methods for details. Cycles for all individuals were aligned at the onset of maximal gape, then mean profiles were calculated and plotted. Different prey sizes are represented by different colors (mouse=red; pinkie=blue). Note the reduced involvement of the cranio-cervical system during pharyngeal packing compared with intraoral transport (Fig. 3). Note also the larger gape angle, cycle duration and change in head slope associated with packing of large prey.

during pharyngeal cycles are reduced in duration and magnitude (Table 2; Fig. 4A; Fig. 6A).

The positioning of the head and neck has been implicated in prey transport and is predicted to play a major role in inertial feeding cycles. As reported previously (Smith, 1982; Smith, 1986; Cleuren and De Vree, 1992; Metzger, 2005), a posterior and dorsal movement of the cranio-cervical system rotates the head dorsally during mouth opening with the dorsalmost position being achieved near the end of the FO phase and coinciding with rapid tongue retraction (Fig. 3). During intraoral transport cycles associated with large prey, the head is depressed more at the onset of the cycle, and the head slope exceeds the horizontal at maximal gape (Table 1; see Movie 1 in Supplementary material). Although head rotation is present during intraoral cycles associated with small prey, movements are greatly reduced (Table 1; Fig. 3B). Pharyngeal packing cycles associated with large prey are also accompanied by an initial dorsal rotation of the head followed by a return of the head to its resting position. The timing is, however, different with the dorsal rotation of the head occurring after maximal gape (Fig. 4B). The neck is also an important component of prey transport and the scale of its involvement is dependent on prey size. During the intraoral transport cycles of small prey the neck remains largely stationary. By contrast, intraoral transport cycles of large prey involve an initial downward rotation of the cervical column during the SO phase followed by a rapid increase during the FC phase, indicating that
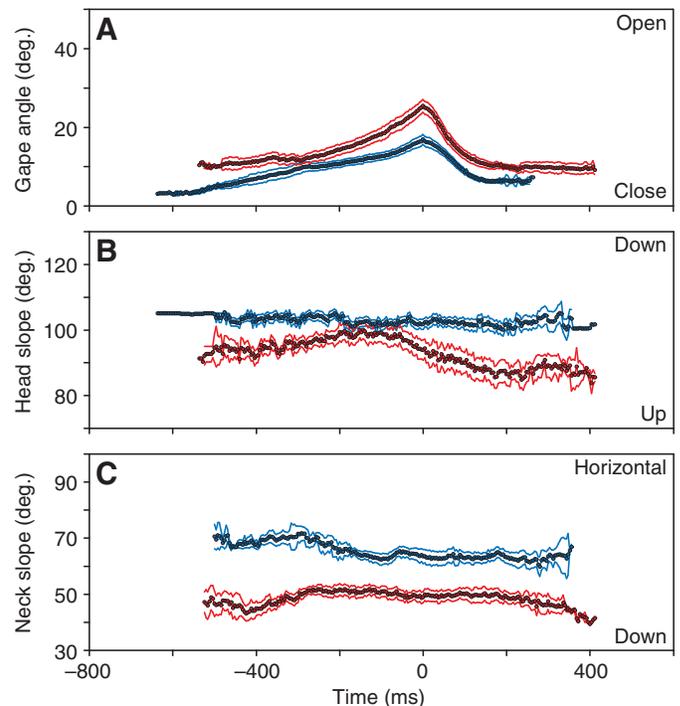
the neck is rotated to a more horizontal position (Fig. 3C). During pharyngeal packing cycles, the neck is more inclined compared with intraoral transport cycles (Table 2; Fig. 3C; Fig. 4C). The neck remains stationary during pharyngeal packing cycles and does not appear to contribute to prey movements (Fig. 4C).

Each cycle is associated with a single protraction–retraction cycle of the hyolingual apparatus. During the SO phase, the basihyal moves anteriad, pushing the tongue forward during intraoral transport (Fig. 5B). The tongue elongates and moves anteriorly during the SO phase with the tip always protruding outside of the mouth beyond the jaw margins. At the beginning of the FO phase the tongue shortens and is quickly retracted into the pharyngeal space. For intraoral cycles, tongue protrusion is greater when processing large prey (Fig. 5B). However, the tongue appears to be more active during pharyngeal packing cycles associated with small prey (Table 2; Fig. 6B). Dorso–ventral hyoid movements are negligible during intraoral transport cycles of large prey but, when processing small prey, there is as distinct dorsal displacement during the initial SO phase, followed by a return to the resting position after the FC phase (Fig. 5C). Dorso–ventral movement of the basihyal is, however, greatly reduced during pharyngeal packing cycles (Fig. 6C).

Discrimination of prey types
To better understand exactly which variables discriminate between feeding cycles associated with prey of different size, and to test
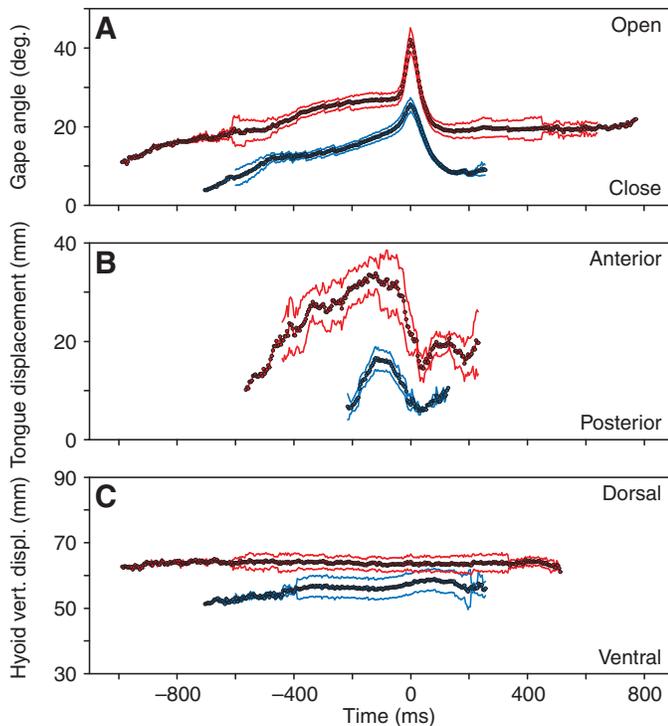
Fig. 5. Mean kinematical profiles (±s.e.m.) illustrating the movements of the jaw and hyolingual systems during intraoral transport. From top to bottom the changes in (A) gape angle, (B) the tongue displacement and (C) the vertical hyoid displacement (hyoid vert. displ.) are illustrated. See Materials and methods for details. Cycles for all individuals were aligned at the onset of maximal gape, then mean profiles were calculated and plotted. Different prey sizes are represented by different colors (mouse=red; pinkie=blue). Note the more rapid tongue movements associated with the intraoral transport of small prey, and the rapid posteriad retraction of the hyobranchium during intraoral transport of large prey. Vertical hyoid displacement is largely absent during the transport of large prey.

Fig. 6. Mean kinematical profiles (±s.e.m.) illustrating the movements of the jaw and hyolingual systems during pharyngeal packing. From top to bottom the changes in (A) gape angle, (B) the tongue displacement and (C) the vertical hyoid displacement (hyoid vert. displ.) are illustrated. See Materials and methods for details. Cycles for all individuals were aligned at the onset of maximal gape, then mean profiles were calculated and plotted. Different prey sizes are represented by different colors (mouse=red; pinkie=blue). Note the more extensive tongue movements associated with the packing of small prey and the general absence of vertical hyoid displacement during pharyngeal packing.

whether feeding on large prey specifically involves modulation of the cranio-cervical system associated with inertial transport cycles, we performed a DFA on the different data sets (head–neck, jaw and tongue kinematics) for intraoral transport and pharyngeal packing cycles separately (Table 3).

For intraoral transport cycles, the DFA performed on the cranio-cervical data set indicated three discriminating variables: the total rotation of the head, the time to maximal neck slope and the head angle at the onset of mouth opening (Table 3). Whereas time to maximal neck slope and head angle at the onset of mouth opening are positively correlated, the total rotation of the head is negatively correlated with the first and only discriminant function retained. This indicates that intraoral transport cycles of large prey differ from those of small prey in that they involve a greater movement of the head and a more depressed head position at the onset of mouth opening. For pharyngeal cycles only maximal neck slope was extracted, indicating that the neck is more inclined when processing large prey (Table 3). Based on jaw kinematics, both intraoral and pharyngeal cycles associated with prey of different size are differentiated by the same variable: the maximal gape angle (Table 3). A greater jaw opening is associated with the transport of large prey. A DFA conducted on the hyolingual kinematics associated with intraoral cycles retained only one variable: the time to maximal contraction of the pharynx (Table 3). Consequently, the pharynx is the most contracted later during intraoral transport cycles
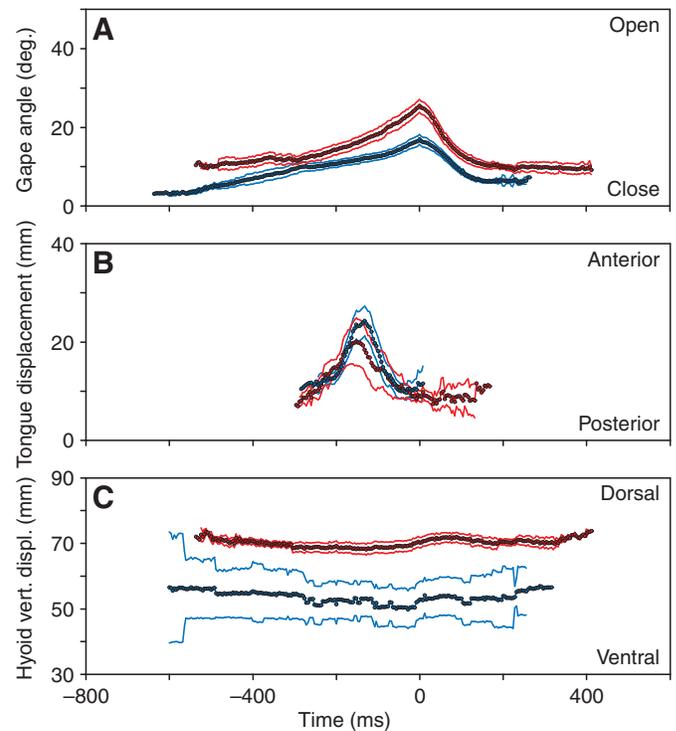
associated with large prey. During pharyngeal packing, the only discriminating variables were the speed of tongue retraction and the time to maximal expansion of the pharynx (Table 3). This indicates that the speed of movement of the tongue is reduced when processing large prey. Moreover, the pharynx is expanded earlier in the cycle for large prey. Classification of the cycles according to prey sizes by the discriminant analysis is generally good, although the kinematics of the hyolingual system were markedly poorer in discriminating between cycles associated with different prey types (Table 3).

Finally, we ran a DFA on a combined data set, including only those variables that were retained in the previous analyses for the three matrices separately. For the analysis on intraoral transport cycles, only one discriminant function was extracted that was positively associated with the total rotation of the head and the time to maximal neck slope (Table 3). Thus, the kinematics of cranio-cervical movements are the best discriminators between cycles associated with prey of different size, with greater head movements being involved during intraoral cycles associated with large prey. For the analysis based on pharyngeal packing cycles, the discriminant function was correlated with three variables (Table 3). One of them is a cranio-cervical variable, maximal neck slope, indicating that the neck is more inclined during pharyngeal cycles of large prey. The other two variables are kinematic features of the hyolingual system: speed of tongue retraction and time to maximal

Table 3. Results of the discriminant function analyses (DFA) performed on the kinematics of movements in *Tupinambis merianae* for intraoral transport and pharyngeal packing of large and small prey

		Intraoral transport		Pharyngeal packing	
Cervical	Eigenvalues		1.58	Eigenvalues	2.86
	Total rotation of the head		−0.56	Maximal neck slope	1
	Time to maximal neck slope		0.68		
	Head angle at the onset of mouth opening		0.58		
	Pinkies (89.8%)		1.09	Pinkies (91.5%)	1.59
	Mice (77.6%)		−1.35	Mice (97.1%)	−1.69
Jaws	Eigenvalues		0.62	Eigenvalues	1.45
	Maximal gape		1	Maximal gape	1
	Pinkies (72.7%)		−0.69	Pinkies (85.5%)	−1.13
	Mice (71.6%)		0.85	Mice (77.9%)	1.20
Tongue	Eigenvalues		0.37	Eigenvalues	2.00
	Time to maximal contraction of the pharynx		1	Speed of retraction	0.91
				Time to maximal inflation of the pharynx	−0.53
	Pinkies (68.4%)		−0.47	Pinkies (87.73%)	1.19
	Mice (56.7%)		0.71	Mice (88.68%)	−1.54
Integrative	Eigenvalues		2.20	Eigenvalues	6.56
	Total rotation of the head		−0.90	Maximal neck slope	0.93
	Time to maximal neck slope		0.93	Speed of retraction	0.50
				Time to maximal inflation of the pharynx	−0.70
	Pinkies (94.2%)		1.15	Pinkies (99.9%)	2.15
	Mice (80.0%)		−1.72	Mice (99.9%)	−2.79

Analyses were performed on kinematic data sets for the cranio-cervical, jaw and hyolingual movements separately, as well as for a combined data set including all discriminating variables. The proportion of cycles correctly classified is indicated between parentheses.

expansion of the pharynx; with reduced tongue movements and earlier expansion of the pharynx when processing large prey. Thus, for pharyngeal packing, both hyolingual and cranio-cervical systems are important in discriminating between cycles associated with prey of different size.

Prey mass and inertial feeding

Our analysis of the correlation between the number of inertial transport cycles used and prey mass show that as prey get larger, *T. merianae* uses significantly more inertial cycles to move the prey from the buccal cavity toward the pharynx and esophagus (R^2=0.35; P=0.001) (Fig. 7).

DISCUSSION

Our data indicate that inertial transport, involving a significant contribution of the cranio-cervical system, is the main mechanism used by *T. merianae* to transport large prey. At the start of a transport cycle, the head is moved downward and the neck extended thus reducing the angle between the head and neck. Next, the head rotates rapidly dorsally around the atlanto–occipital joint and, in doing so, transfers momentum to the prey. Although the use of inertial transport has previously been documented for tegu lizards (McBrayer and Reilly, 2002a; Metzger, 2005), varanids (Smith, 1982; Smith, 1986; Metzger, 2005) and *Caiman* (Cleuren and De Vree, 1992), our data set is the first to explicitly test the contribution of inertial components to prey transport for prey of different mass. Our data show that when processing large prey the rotation of the head is greater as the head starts its movement from a lower position and ends its movement at a higher position, exceeding the horizontal. Moreover, our data show that the head is higher at mouth opening during the pharyngeal packing of large prey, suggesting a close functional relationship between the jaw and cranio-cervical systems.

Although this functional integration probably goes hand-in-hand with extensive feedback between the two systems to assure proper coordination, little is known about the control of the cranio-cervical system and its interaction with the jaw and hyolingual systems.

In accordance with previous studies (Elias et al., 2000; Metzger, 2005), our data show that the manipulation of small prey is largely dependent on movements of the hyolingual system, suggesting that the specialized, long and bifurcated tongue of *T. merianae* is still able to assume its ancestral function if prey mass is small enough. During these cycles, the bifurcated anterior part of the tongue specialized for chemoreceptive purposes moves under the prey whereas the more fleshy posterior part (McDowell, 1972) contacts and actually transports the prey backwards in the oral cavity. However, as the size of the prey relative to the tongue increases, the magnitude of tongue displacement is reduced, the speed of protrusion and retraction decreases, and contributions of the hyoid to prey transport are different. Rather than assisting the tongue in pulling back the food, the hyoid appears to be retracted rapidly to make space for the posteriad displacement of the prey initiated by the cranio-cervical system. The observed qualitative changes in kinematics associated with the transport of different size prey items are supported by our DFA. When constructing a matrix of variables from the different functional systems (jaw, hyolingual and cranio-cervical) that are good discriminators between transport cycles associated with prey of different size, the DFA retains only variables associated with the recruitment of the cervical system as principal discriminators, at least for intraoral transport cycles. Thus, an increase in the size of the prey leads to the greater recruitment of the cervical system characteristic of inertial transport.

This pattern is also confirmed by our data on the number of inertial cycles that animals use to transport mice; as the prey mass gets bigger, animals use significantly more inertial cycles (Fig. 7).
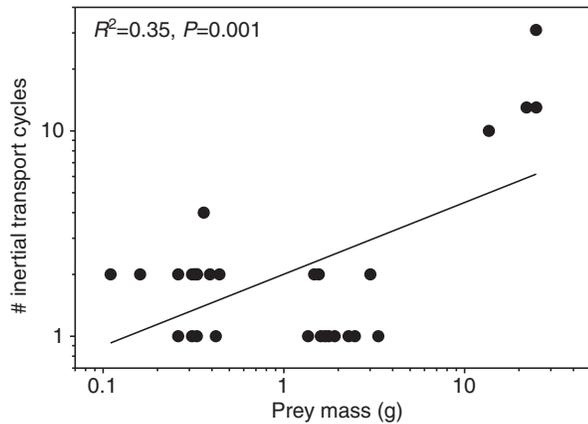
Fig. 7. Scatter plot illustrating how the number of inertial cycles used by *Tupinambis merianae* increases significantly with prey size. Note the exponential increase in number of intertial transport cycles used for prey with a mass above 10 g. Axes are log-scales.

Although this is in contrast to previous data for *Varanus* where no effect of prey mass on the number of transport cycles could be demonstrated (Condon, 1987), our present data suggest that rather than being a continuous and gradual increase, it appears as if a threshold for lingual transport is reached at a mass of about 10 g, after which the number of inertial cycles used goes up exponentially (i.e. from one or two cycles to 10 or 20 cycles) (see Fig. 7). Clearly, providing a wide range of prey masses is crucial to detect the sudden increase in number of inertial transport cycles used. Our data thus provide support for a mechanical link between tongue size and the use of inertial transport and consequently, the elongation of the tongue and decrease in tongue surface area observed in lizards relying predominantly on vomerolfaction, may have triggered the evolution of inertial transport in those taxa eating occasional large prey such as vertebrates.

Despite the importance of the cranio-cervical system during transport of large prey, previous data based on external high-speed video recordings indicated an extensive use of the tongue during inertial transport in tegu lizards (Elias et al., 2000). Although our data confirm the fact that the tongue retains its anterior–posterior movements during inertial transport, our results also show that the degree of tongue movement, and in particular the speed of tongue movement, is reduced when transporting large prey. More strikingly, and in contrast to our initial prediction, the hyoid no longer moves anterior–posteriorly during inertial transport but rather shows a rapid posterior displacement during the FO phase. This suggests a radically divergent function of the hyolingual system during intraoral transport. Our data thus illustrate the importance of using X-ray data when making inferences about movements of the hyolingual system during prey transport. Unexpectedly, our data for *Tupinambis* are in strong contrast to data on *Varanus*, another lizard with a highly specialized tongue, which relies on inertial movements to transport prey (Smith, 1982; Smith, 1986; Metzger, 2005). Whereas in *Varanus* the hyobranchium has taken over the role of the tongue during transport and pharyngeal packing (Smith, 1986), our data show that in *Tupinambis* the tongue is the principal agent involved in intraoral transport of small prey and solely responsible for pharyngeal packing. However, similar to *Varanus* (Smith, 1986), our data show a strong decoupling between tongue and hyoid movements in *Tupinambis*. Whereas both the tongue and hyoid are involved in the transport of small prey, the hyoid no longer contributes to the transport of large

prey and pharyngeal packing in general. The striking differences in the dependence on the movements of hyoid in *Varanus* compared with *Tupinambis* are likely to be associated with the higher degree of morphological and functional specialization of the tongue towards chemoreceptive purposes in *Varanus* (McDowell, 1972; Smith, 1986; Schwenk, 1988; Schwenk, 2000).

In summary, our data show that the dependence on the cervical system increases with prey size, resulting in changes in kinematics and the recruitment of inertial transport cycles as prey get heavier relative to the size of the tongue. These data provide a direct mechanical link between the size of the tongue and the use of inertial transport; thus, supporting the assertion that the evolution of long tongues with a relatively low surface area may have gone hand-in-hand with the evolution of inertial transport in lizards that eat large prey. In contrast to our expectations, however, the tongue in *Tupinambis* is still the principal agent in the transport of small prey and is solely responsible for pharyngeal packing, in contrast to previous results for *Varanus*, a species with an even more highly derived and specialized tongue structure.

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