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# Chewing variation in lepidosaurs and primates

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## SUMMARY

**Mammals chew more rhythmically than lepidosaurs. The research presented here evaluated possible reasons for this difference in relation to differences between lepidosaurs and mammals in sensorimotor systems. Variance in the absolute and relative durations of the phases of the gape cycle was calculated from kinematic data from four species of primates and eight species of lepidosaurs. The primates exhibit less variance in the duration of the gape cycle than in the durations of the four phases making up the gape cycle. This suggests that increases in the durations of some gape cycle phases are accompanied by decreases in others. Similar effects are much less pronounced in the lepidosaurs. In addition, the primates show isometric changes in gape cycle phase durations, i.e. the relative durations of the phases of the gape cycle change little with increasing cycle time. In contrast, in the lepidosaurs variance in total gape cycle duration is associated with increases in the proportion of the cycle made up by the slow open phase. We hypothesize that in mammals the central nervous system includes a representation of the optimal chew cycle duration maintained using afferent feedback about the ongoing state of the chew cycle. The differences between lepidosaurs and primates do not lie in the nature of the sensory information collected and its feedback to the feeding system, but rather the processing of that information by the CNS and its use feed-forward for modulating jaw movements and gape cycle phase durations during chewing.**

Key words: mastication, bone strain, videofluoroscopy, kinematics, lizards, mammals.

## INTRODUCTION

Cyclic intra-oral food processing (chewing) is practiced by members of several lineages of extant amniotes and fishes (Claes and De Vree, 1991a; Claes and De Vree, 1991b; Grubich, 2000; Reilly et al., 2001; Sibbing, 1982; Vincent and Sibbing, 1992). Mastication is a specific type of chewing that was characterized primitively by transverse movements of precisely occluding teeth, but which has subsequently diversified into a wide range of jaw kinematic and muscle activity patterns (Crompton, 1995; Crompton and Hylander, 1986; Crompton and Parker, 1978; Hiiemae, 2000; Hiiemae, 1976; Hiiemae, 1978; Weijs, 1994). Mastication evolved in the morphological context of reduced mandibular postdentary bones, reduced tooth replacement to a condition of diphyodonty, a shift from ankylosis of the teeth to the dentary to anchoring the teeth to the mandible *via* a richly innervated periodontal ligament, and the evolution of γ-motoneuron control of muscle spindles (Crompton, 1985; Crompton, 1989; Crompton, 1995; Crompton and Hylander, 1986; Hopson and Barghusen, 1986; Ross et al., 2007b). Comparisons with lepidosaur chewing behavior led us to hypothesize that the periodontal afferents and γ-motoneurons improve chewing performance by facilitating 'feed-forward modulation' of chewing behavior in response to and anticipation of changes in internal (material) and external (bolus) properties within and between chewing sequences. We hypothesized that these behavioral changes improved chewing performance by minimizing variance in chew cycle duration around the chewing system's optimal frequency, minimizing the energetic cost of the work performed on the food, and allowing the system to operate for longer periods without fatigue (Ross et al., 2007a; Ross et al., 2007b).

### Feed-back and feed-forward modulation of mammalian mastication

The concepts of feed-back and feed-forward control are central to our hypothesis. The periodontal afferents considered to be important in the evolution of mammalian mastication transduce information on the orientation, magnitude, rate and position of bite forces on the teeth into neural signals for use in 'feed-back' and 'feed-forward' control of jaw movements (Appenteng et al., 1982; Byers, 1985; Hannam, 1969; Hannam and Farnsworth, 1977; Johnsen and Trulsson, 2003; Johnsen and Trulsson, 2005; Larson et al., 1981; Loescher and Robinson, 1989; Takahashi-Iwanaga et al., 1997; Trulsson, 2006; Trulsson and Johansson, 1996; Türker, 2002; Türker and Jenkins, 2000). Similarly, fusimotor control of muscle spindle sensitivity *via* γ-motoneurons to muscle spindles decouples control of muscle spindle sensitivity from control of their host muscles, enabling spindle response properties to be tuned to expected motor tasks (Prochazka et al., 1988), facilitating feed-forward or anticipatory control of mastication (Appenteng et al., 1980; Gottlieb and Taylor, 1983; Masuda et al., 1997). Muscle spindles modulate the timing and periodontal afferents modulate

the magnitude of feed-forward control (Hidaka et al., 1999; Hidaka et al., 1997; Komuro et al., 2001a; Komuro et al., 2001b; Ottenhoff et al., 1992a; Ottenhoff et al., 1992b). What is feed-forward control and why would it be advantageous during the evolution of mammalian chewing?

Feed-forward control is best understood in contrast to the more commonly experienced feed-back control (Leigh, 2004). Feed-back control of a system, including musculoskeletal systems, uses information on the state of the variable being controlled (such as bite force, jaw position or jaw velocity) to alter the input into the system (such as motor unit recruitment). The controller is error-driven, i.e. the output of the controller is some function of the error between the observed state of the system and the desired state. A simple example from common experience is feed-back control of the cruise control system in a car. The cruise control in a car compares information on the actual speed of the car with the desired speed entered into the controller: the error between the two is used to control the amount of power being sent to the drive wheels. An example from the feeding system is feedback control of bite force during forceful biting on a hard object, such as a nut shell. The task set to the controller (the brain) is to break open the nut by biting on it between the teeth. Bite force applied to the nut is increased and estimated using efference copy and periodontal afferents while the state of the nut is tracked by estimating gape distance (using muscle spindles and joint receptors) and energy emitted as it cracks (using auditory receptors). One problem with feed-back control is the delay between when error from the desired state is detected and when changes in the system can be implemented. For example, even monosynaptic, reflex, feed-back control of muscle force operates with delays because of a series of time-dependent processes: the time it takes for action potentials to propagate along afferent nerves to the central nervous system (CNS), the time for the action potential to cross the synapse between afferent and efferent neuron, the time it takes for action potentials to propagate from the CNS down efferent nerves to the muscles, the time for information to cross the synapse between efferent neuron and muscle cell at the motor end plate, the time for action potentials to propagate down the sarcolemma, and the time associated with excitation–contraction coupling. Even in very fast muscle fibers supplied by large motoneurons these delays can amount to several tens of milliseconds, by which time the state in the periphery may well have changed. In the case of the nut, when the shell breaks suddenly, feed-back control would not occur fast enough to prevent the teeth slamming together. Feed-forward control offers one way to avoid this delay: the control system anticipates needed changes based on sources other than the controlled variable. In the case of the cruise-controlled car, a gyroscope might monitor whether the car starts to go up a hill, and the controller would use this information to predict how much extra power will be needed to maintain a constant speed before the actual speed of the car drops. In the case of forceful biting on the nut, co-contraction of jaw opening muscles (digastric) stiffens them so as to decrease the velocity of jaw movement when the nut breaks, and intrinsic viscoeleastic properties of the jaw elevators prevent them from shortening too quickly.

We hypothesized that feed-forward control of mastication enables motor commands appropriate for the material properties of the food to be fed forward to the jaw muscles before the teeth make contact with the food (Hidaka et al., 1999; Hidaka et al., 1997; Ross et al., 2007b; Weijs and De Jong, 1977) dampening the effects of tooth-food-tooth contact at the start of the slow close phase of the chewing cycle (Abbink et al., 1999; Ottenhoff et al., 1992a; Ottenhoff et al., 1996; Wang and Stohler, 1991). We hypothesized that this feed-forward control facilitated rate-modulation rather than time-modulation of bite force (i.e. mammals modulate bite force during mastication by varying the rate at which the force is generated, rather than by varying the time over which it is generated) (Ross et al., 2007a). We argued that these differences in bite force control explain why mammals have less variable cycle durations than lepidosaurs (Ross et al., 2007b).

The present paper tests these hypotheses using bone strain data from the mandibular corpus of three *Tupinambis merianae* and data on variance in durations of the phases of the gape cycle (Hiiemae, 1978; Bramble and Wake, 1985). In the process, we also evaluate hypotheses regarding how the durations of the gape cycle phases relate to each other and to overall chew cycle duration.

## Hypotheses

### Slow-close

Variance in the slow close (SC) phase of the gape cycle is central to our hypothesis regarding feed-forward control of bite force because SC is the phase when bite force is applied to the food item. SC duration has been shown to vary with food hardness in both lizards and mammals (Herrel et al., 1996; Hiiemae et al., 1995; Hiiemae et al., 1996; Metzger, 2009; Schaerlaeken et al., 2008; Thexton and Hiiemae, 1997; Yamada and Haraguchi, 1995; Yamada and Yamamura, 1996) but it is not known to what extent this variation in SC duration impacts variation in overall gape cycle duration. Our hypothesis, that the lower cycle duration variance in mammals is attributable to feed-forward, rate-modulation of bite force during SC, predicts that variance in SC duration significantly impacts variance in overall cycle duration in both mammals and lizards and that SC duration is less variable in mammals than in lizards. In addition, if rate-modulation of bite force is an important factor in reducing variance in SC and cycle duration in mammals compared with lepidosaurs, then in lepidosaurs the duration of bite force production will covary with bite force magnitude.

### Slow open

Slow open (SO) is the phase when the tongue is protracted to collect sensory information on the external properties, mass and mobility of the food item and to fit to the food item in preparation for transport. Our hypothesis linking differences in cycle duration variance to SC duration variance makes no predictions regarding the role of SO in driving overall cycle durations. However, our data analysis revealed that lepidosaurs and primates do not differ in SC variance. SO is the most variable phase in mammals (Schwartz et al., 1989; Thexton et al., 1980; Yamada and Yamamura, 1996) and lizards (Delheusy and Bels, 1992; Herrel et al., 1996; Herrel and De Vree, 1999; Herrel et al., 1999; Metzger, 2009) suggesting that SO duration variance might contribute significantly to total cycle duration variance in both groups. We compared variation in SO in lepidosaurs and mammals and estimated the relative importance of SO variance in driving cycle duration variance.

### Fast open and fast close

Fast open (FO) begins as mandible opening velocity increases and the tongue and hyobranchium are pulled down and back, transporting the food towards the pharynx. FO ends as the mandible ceases to open and is followed by fast close (FC), as the jaws are rapidly closed onto the food item and the hyobranchial apparatus nears its extreme posteroventral position. Once again, our hypothesis linking variation in cycle duration to variation in SC duration makes no direct predictions regarding FO and FC, but SC variance proved not to be the source of differences between lizards and mammals.

Within sampled mammals and lizards, variation in FO and FC duration is less than that in other phases (Delheusy and Bels, 1992; Herrel et al., 1996; Herrel and De Vree, 1999; Herrel et al., 1999; Thexton and Hiiemae, 1997; Thexton et al., 1980; Yamada and Yamamura, 1996), predicting that FO and FC would contribute the least to variance in total cycle duration in both lepidosaurs and mammals. To test this hypothesis we compared variation in FO and FC durations in lepidosaurs and mammals and estimated the relative importance of FO and FC variance in driving cycle duration variance.

### Total cycle duration

In addition to testing these hypotheses, we also evaluated whether variation in total cycle duration within lizards and mammals is associated with isometric or allometric changes in relative phase durations within the gape cycle. For example, mammals might maintain low variance in total cycle duration by maintaining the temporal shape of the gape cycle, i.e. changes in cycle duration in mammals might be associated with isometric changes in phase durations. Alternately, mammals might maintain low variance by trading off increases in duration of one phase with decreases in duration of another.

## MATERIALS AND METHODS

### Subjects

Subjects and sample sizes are listed in Table 1. These data were collected during studies of feeding behavior in lepidosaurs and primate mammals that were not specifically designed to test the hypotheses addressed here, however, the sample is appropriate in several important ways. First, the primates and the lepidosaurs that were studied all chew with long sequences of cyclic jaw movements, so that intra-individual variability in cycle durations derives from similar behavioral contexts. Second, because many of the lepidosaurs and all the primates studied are omnivorous, it was possible to use variation in food properties between and within chewing sequences to elicit the intra-individual variation in jaw kinematics that is the focus of this study. We also included data on two herbivorous lizard species (*Uromastix* and *Corucia*) and the insectivorous–carnivorous *Sphenodon* because these species have been documented previously to engage in long chewing sequences (Gorniak et al., 1982).

Table 1. Sample sizes in this study

| Species | Individuals | Feeding sequences | Gape cycles |
|---|---|---|---|
| Lepidosaurs | | | |
| *Agama stellio* | 4 | 8 | 154 |
| *Corucia zebrata* | 2 | 4 | 115 |
| *Pogona vitticeps* | 6 | 114 | 1417 |
| *Tiliqua scincoides* | 3 | 90 | 1162 |
| *Tiliqua rugosa* | 1 | 7 | 65 |
| *Tupinambis merianae* | 3 | 70 | 455 |
| *Sphenodon punctatus* | 3 | 18 | 151 |
| *Uromastix acanthinurus* | 2 | 4 | 42 |
| Totals | 24 | 315 | 3561 |
| Mammals | | | |
| *Eulemur fulvus* | 3 | 43 | 595 |
| *Cebus apella* | 3 | 844 | 9280 |
| *Chlorocebus aethiops* | 2 | 15 | 188 |
| *Macaca mulatta* | 1 | 39 | 718 |
| Totals | 9 | 941 | 10781 |
| Overall totals | 33 | 1256 | 14342 |

Kinematic data were available from three juvenile *Sphenodon punctatus* (Sphenodontidae, carnivorous); six *Pogona vitticeps* (Agamidae, omnivorous); three *Tiliqua scincoides* (Scincidae, omnivorous); two *Tiliqua rugosa* (Scincidae, omnivorous); two *Corucia zebrata* (Scincidae, herbivorous); three *Tupinambis merianae* (Teiidae); two *Uromastix acanthinura* (Leiolepididae, herbivorous); three adult male *Eulemur fulvus* (Lemuridae, folivorous–omnivorous); two adult (one male and one female) *Chlorocebus aethiops* (Cercopithecidae, omnivorous–frugivorous); three adult male *Cebus capucinus* (Cebidae, frugivorous–omnivorous); and one adult female *Macaca mulatta* (Cercopithecidae, omnivorous) (Fleagle, 1999; Metzger and Herrel, 2005). The lizards were purchased through commercial dealers and housed in terraria located at the Laboratory for Functional Morphology in the Department of Biology, University of Antwerp, Belgium, as described elsewhere (Herrel et al., 1996; Herrel and De Vree, 1999). The three *Sphenodon* were studied at the Kiwi House in Otorohanga, New Zealand (Schaerlaeken et al., 2008). The three *Eulemur fulvus* were borrowed from the Duke Lemur Center and studied at Stony Brook University. The two *Chlorocebus aethiops* individuals were borrowed from Dr Susan Larson at Stony Brook University. The *Cebus apella* and *Macaca mulatta* were studied at University of Chicago. All procedures were approved by the relevant Institutional Animal Care and Use Committees (Duke University, Stony Brook University, University of Chicago, University of Antwerp), as well as, when necessary, by the Scientific Committee at the Duke Lemur Center, and by the Department of Conservation, *Te Papa Atawhai*, New Zealand (permit number WK-18692-RES).

### Methods

#### Bone strain recordings

Mandibular bone strain amplitudes have been shown to provide reasonable estimates of changes in relative bite force through time (Hylander, 1986; Weijs and De Jong, 1977). Therefore, we predicted that if lizards time-modulate bite force then they should exhibit significant positive correlations between peak mandibular bone strain magnitudes and the time of mandibular loading, and higher correlation coefficients between peak strain magnitude and load time than between peak strain magnitude and loading rate. Mandibular bone strain data were recorded from three *Tupinambis merianae* using delta rosette strain gages. The gages were placed on the buccal aspect of the mandibular corpus while the animals were sedated with ketamine (150 mg kg$^{-1}$ body mass). The periosteum was scraped away from the gage sites, the bone degreased, and the gages bonded to the bone using cyanoacrylate adhesive (Elmer's Products, Inc., Columbus, OH, USA). The lead wires were tunneled under the skin to the back of the animal and sutured to the skin. The gage elements were connected to strain amplifiers, i.e. as one arm of a Wheatstone bridge, and the elements calibrated using shunt calibrations. After the animals recovered from anesthesia, strain data were recorded the same day and daily for 5 days after, as the animals ate a range of foods. Data were recorded to computer at 1000 Hz, converted to microstrain, then used to calculate magnitudes and orientations of maximum ($\varepsilon_1$) and minimum ($\varepsilon_2$) principal strains. The principal strain values were imported into IGOR Pro 4.0 (WaveMetrics, Lake Oswego, OR, USA) where the following variables were extracted from each chewing cycle (see Ross et al., 2007a). (1) Peak strain magnitude: the magnitude of the largest values of $\varepsilon_1$ during the closing stroke; (2) peak strain timing: the time at which peak strain

magnitudes ($\varepsilon_1$) were reached; (3) 5% timing: the time at which 5% of peak strain magnitude was reached in loading; (4) load time: the amount of time between 5% of peak strain in loading and peak strain; (5) load rate: for each chew cycle, the average loading rate between 5% of peak and peak, i.e. $\delta y/\delta x$, where $\delta y$=peak magnitude and $\delta x$=load time.

### Videofluoroscopy marker placement

Jaw kinematics in the *Eulemur*, *Macaca* and *Chlorocebus* were measured using digital videofluoroscopy. Prior to the first data recording session radio-opaque markers were placed on the dentition or in the bone of the mandibular corpus with the animals under isofluorane anesthesia. In the *Eulemur* and *Chlorocebus* one marker was placed on the buccal surface of each of three upper teeth (the canine and $M^1$ on one side and premolar $P^4$ on the other) and lingual face of two lower teeth (the canine and either $P_4$ or $M_1$ on one side). These dental markers consisted of small round stainless steel balls or disks 1 mm in diameter bonded to the tooth with bisphenol glycidal methacrylate resin (Bis-GMA, Scotchbone Multipurpose™ and Z-250™, 3M, St Paul MN, USA). Marker placement involved etching the tooth surface with 35% phosphoric acid for 15–30 s followed by rinsing with water and drying with air. The Bis GMA was placed on the surface and cured using a photoinitiator. The distances between markers were measured to the nearest 0.1 mm with digital calipers. In *Chlorocebus*, *Eulemur* and *Macaca*, Vitallium™ bone screws (OFSQ13, 3I Implant Company, West Palm Beach, FL, USA) were placed in the inferior borders of each hemi-mandible below the lower canine (described below).

### Reflective marker methods

Three-dimensional measures of jaw movements in *Cebus*, *Macaca* and some of the lizards were made using six-camera Vicon 460 motion capture systems at University of Chicago and University of Antwerp. In the lizard studies markers were glued to the skin overlying the bone. Markers were manufactured by hand by taking polyethylene spheres (McMaster-Carr, Atlanta, GA, USA), melting a small area on one part of the sphere to create a flat region, and then conforming retro-reflective tape (Scotchlite High Gain Sheeting 7610, 3M Corporation, St Paul, MN, USA) to the surface of the sphere. The flat side of the marker was affixed to the animal using either cyanoacrylate gel adhesive (for *Pogona*) or 5 $mm^2$ pieces of double-sided transparent tape (for *Tiliqua* and *Tupinambis*). Optical markers were anchored to the mandible of the *Cebus* using a bone screw system consisting of 2.7 mm×10 mm titanium cortical bone screws (Veterinary Orthopedic Implants, South Burlington, VT, USA; TI-ST 270.10) chronically implanted in the bones of the face. These screws protrude percutaneously, and have a threaded hole tapped down the shaft for attachment of a second, smaller screw with a reflective, optical marker on it. The mandible and cranium each had at least three markers attached to it, so as to document independent translations and rotations of the mandibles. Data were collected at a spatial resolution of ±0.05 mm and a temporal resolution of 250–1000 Hz, depending on the speed of movement of the species being studied.

### Recording procedure

The primates were restrained in a commercially available primate restraint chair (XPL-517-CM, PlasLabs, Lansing, MI, USA) in a sitting position with their arms and legs restrained but their head and neck moving freely. After recovery from anesthesia (30–60 min) the primates were presented with foods cut into pieces roughly 5–10 mm in maximum diameter: apple, raisin, grape, prune and almond. The lepidosaurs were fed unrestrained. Invertebrate prey fed to the lepidosaurs included field crickets (‘field cricket’, *Gryllus campestris*), house crickets (‘cricket’, *Acheta domestica*), king mealworms (‘superworm’, *Zophobas morio*), migratory locusts (‘locust’, *Locusta migratoria*), waxworms (‘waxworm’, *Galleria mellonella*), adult yellow mealworm beetles (‘beetle’, *Tenebrio molitor*), and yellow mealworm larvae (‘mealworm’, *Tenebrio molitor*). The herbivorous lizard species (*Corucia*, *Uromastix*) also ate tomato, kiwi, endive and/or apple. Feeding behavior in the *Sphenodon* was recorded at 25 Hz using a digital camcorder (Sony) (Schaerlaeken et al., 2008).

Videofluoroscopic data were collected at Stony Brook University with a Philips Maximus M150 (*Eulemur* and *Chlorocebus*), at University of Chicago using an OEC 9600 C-arm (*Macaca*), and at University of Antwerp using a Philips Optimus M200 videofluoroscopy unit (Philips Electronics, Netherlands) (*Pogona*, *Tiliqua*, *Tupinambis*). In all three cases the image intensifiers were retrofitted with Redlake high-speed digital video cameras (Stony Brook, Redlake Motion Pro; University of Chicago, Redlake Motion Pro 500; University of Antwerp, Redlake Motion Pro 2000) (Redlake MASD LLC, San Diego, CA, USA). Only fluoroscopic recordings where the animal remained in lateral view were used to avoid measurement distortion due to parallax.

### Extraction of kinematic variables

#### Videofluoroscopic data

Jaw kinematic data for the primates *Eulemur*, *Chlorocebus* and *Macaca* were extracted from the videofluoroscopy images using MiDAS motion analysis software (Xcitex, Boston MA, USA). The two-dimensional Cartesian coordinates of the jaw markers were digitized. Out of plane rotation about a vertical axis perpendicular to the palatal plane was estimated as the arc-cosine of the apparent distance between the two palatal points divided by the actual distance (Miller and Petak, 1973) and feeding cycles in which the head rotated out of plane by greater than 15 degrees at any time were discarded. Various data smoothing algorithms in IGOR-Pro were examined to find the one that eliminated noise while retaining the relative timing of maximum gape, minimum gape, and the time of the FC-SC and SO-FO transitions. We selected a second order Savitzky–Golay smoothing algorithm with a box width of 15 points. Fourier analysis revealed that this smoothing preserved frequency components below 10 Hz while eliminating noise. Kinematic data for the lepidosaurs, were calculated as reported elsewhere (Herrel et al., 1996; Herrel and De Vree, 1999; Herrel et al., 1999; Schaerlaeken et al., 2008).

#### VICON data

Three-dimensional reconstruction of marker positions was performed by the Vicon Workstation software. The relative movements of the mandible and cranium were calculated from these data as Euler angles. These data were output and filtered with a band-pass filter with filter cutoff frequencies determined by residual analysis (Winter, 1990).

For both videofluoroscopic and Vicon data the start of FC was identified as the time of maximum gape; the start of SC as the time between maximum and minimum gape of the negative peak in the second derivative of gape with respect to time; the start of SO at minimum gape and the end at the time between minimum and maximum gape of the negative peak in the second derivative of gape with respect to time (Fig. 1). Only gape cycles in which all the phases [slow open (SO), fast open (FO), fast close (FC), slow close (SC)] were present were used for statistical analysis.

### Statistical analysis

Relationships between bone strain magnitudes, strain loading rate and strain loading time were used to evaluate the manner in which bite force magnitudes are modulated during chewing (Ross et al., 2007a). Correlation coefficients were calculated between bone strain magnitudes and both strain load rate and load time. Multiple regression models were calculated in SPSS 16.0 with strain magnitude as the dependent variable and both load rate and load time entered simultaneously as independent variables.

To determine whether lizards and mammals differ in levels of variance in the durations of the gape cycle phases and overall gape cycle durations, average coefficients of variation (CVs) for the two classes were compared using *t*-tests (Ross et al., 2007b). Single factor (five levels: SO, FO, FC, SC and TC) ANOVAs of CVs within lizards and mammals were used to determine whether the phases of the gape cycle showed different levels of variance, and *post-hoc* tests (Games and Howell) were used to test for differences between lizards and mammals in how these effects are manifest.

In order to quantify the relative contributions of variance in the different phases of the gape cycle to overall gape cycle variance, multiple regression analyses were performed on data collected within individuals. The analyses were performed within individuals because low variance in cycle durations in mammals is an intra-individual phenomenon (Ross et al., 2007b). $\text{Log}_{10}$ transformation did not fully eliminate skewness and kurtosis from all of the variables in this study and some mammals exhibited heteroscedascity, with higher variance in phase durations at lower total cycle duration. Nevertheless, for every individual for which data were available multiple regression models were calculated with $\log_{10}$ total cycle duration as the dependent variable and the durations of $\log_{10}$FC, $\log_{10}$SC, $\log_{10}$SO, and $\log_{10}$FO phases as the independent variables. The relative importance of the predictor variables in each model was assessed using Johnson's 'relative weight' (Chao et al., 2008; Johnson, 2000), "the proportionate contribution each predictor makes to the squared multiple correlation coefficient when that coefficient is expressed as the sum of contributions from the separate predictors" (Johnson, 2000). To calculate this relative weight, the independent variables (in his case the gape cycle phase durations) were replaced with a set of variables that are highly correlated with the original independents but which are not correlated with each other. Regression of $y$ ($\log_{10}$TC) on these orthogonal factors results in relative weights that sum to the $R^2$ of the multiple regression model. The multiple regression models were run in SPSS 16.0 using the Multiple Regression procedure, which was also used to obtain diagnostics of multicollinearity (see Ross et al., 2007a). The multiple regressions were run including data from chewing cycles on all foods and using only chewing cycles when the animals were eating fruits and vegetables.

In order to determine whether changes in cycle duration are associated with changes in the proportions of the cycle made up by each phase, percent phase duration [e.g. (SO×100)/TC] was regressed against total cycle length. Significant regressions represent changes in temporal shape of the chew cycle with changes in cycle duration.

## RESULTS

### Do lepidosaurs time-modulate bite force?

Mandibular bone strain data were used to determine whether lizards time-modulate bite force during the SC phase of the gape cycle, as predicted by our hypothesis (Ross et al., 2007b). Table 2 presents correlation coefficients between peak bone strain magnitudes, mandibular strain load rate and mandibular strain load time. Fig. 2 presents bivariate plots of strain magnitude against load rate for all three individuals and for strain magnitude against load time in *Tupinambis* 3. In all individuals strain magnitude is significantly, positively and strongly correlated with load rate. In one individual, *Tupinambis* 3, strain magnitude is also significantly correlated with load time, but in *Tupinambis* 2 and 5 strain magnitude is not correlated with loading time. *Tupinambis* 3 ate several kinds of foods so correlation coefficients were also calculated for each food separately. When eating frogs and adult mice, *Tupinambis* 3 showed

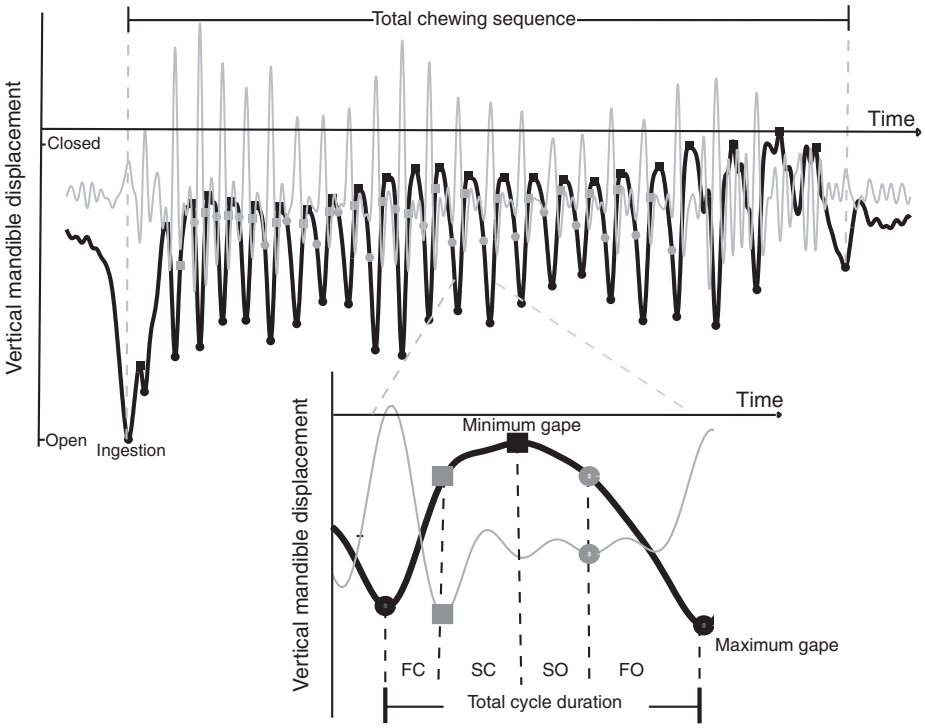


Fig. 1. Plots defining the kinematic variables discussed in the text. Data from primate *Cebus*. The upper graph plots the open–close displacements of the lower jaw during a complete chewing sequence (from ingestion to final swallow) (black line). The grey line represents the second derivative of the black line. The enlarged portion of the chewing sequence graph (below) represents a single gape cycle, divided into the four gape cycle phases. The black square represents minimum gape. The black circles represent maximum gape. Total cycle duration ($T_c$) is the time between maximum gapes. The grey squares represent the fast-close slow-close transition: the position of the largest negative peak between maximum gape and minimum gape on the second derivative (grey line). The grey circle on the black line represents slow-open fast-open transition: the position of the largest negative peak on the second derivative between minimum gape and maximum gape in the following chew. These four variables define the boundaries of the four gape cycle phases fast-close (FC), slow-close (SC), slow-open (SO) and fast-open (FO).

Table 2. Correlation coefficients between mandibular bone strain, $\varepsilon_1$ magnitudes, loading rates and loading times in three *Tupinambis*

| | | Magnitude *vs* load rate | Magnitude *vs* load time | Strain load rate *vs* strain load time |
|---|---|---|---|---|
| *Tupinambis* 2 | *r* | 0.831** | 0.104 | –0.246* |
| | *P* | <0.001 | n.s. | n.s. |
| | *N* | 71 | 65 | 65 |
| *Tupinambis* 3 | *r* | 0.628** | 0.754** | 0.162 |
| | *P* | <0.001 | <0.001 | n.s. |
| | *N* | 34 | 34 | 34 |
| *Tupinambis* 5 | *r* | 0.921** | –0.258 | –0.566* |
| | *P* | <0.001 | n.s. | 0.04 |
| | *N* | 15 | 14 | 14 |

n.s., not significant, i.e. $P>0.05$; *$P<0.05$; **$P<0.01$.

no significant correlations between strain magnitude and either rate or load time. When eating grasshoppers, *Tupinambis* 3 resembled the other two individuals in showing a significant correlation between strain magnitude and load rate but not load time ($r$=0.834, $P$=0.005) and when eating new-born 'pinkie' mice, strain magnitude was correlated with both strain rate ($r$=0.782, $P$=0.002) and load time ($r$=0.939, $P$<0.001). Multiple regression of strain magnitude against both rate and time revealed that in both *Tupinambis* 2 and 5 strain magnitude is primarily dependent on strain rate and only secondarily on load time, whereas the reverse is true in *Tupinambis* 3 (Table 3). Thus, the predictions of our hypothesis are rejected: the relatively higher variance in chew cycle duration in these lepidosaurs is not associated with time-modulation of bite force during SC. Rather, *Tupinambis* resembles mammals in rate-modulating bite force during chewing (Ross et al., 2007a).

### Do lepidosaurs and primates differ in magnitudes of variation in the gape cycle phases?

Levels of variance in the durations of the four phases of the gape cycle were compared within and between primates and lepidosaurs using ANOVA and Game and Howell *post-hoc* tests (Fig. 3). Our hypothesis predicted that the lower levels of variance in gape cycle duration in mammals would be associated with lower levels of variance in SC duration as well (Ross et al., 2007b). The average CV for total gape cycle duration is significantly lower in the primates than in the lizards (21% *vs* 32%) ($CV_{TC}$: $t$=3.222, $P$=0.003), but

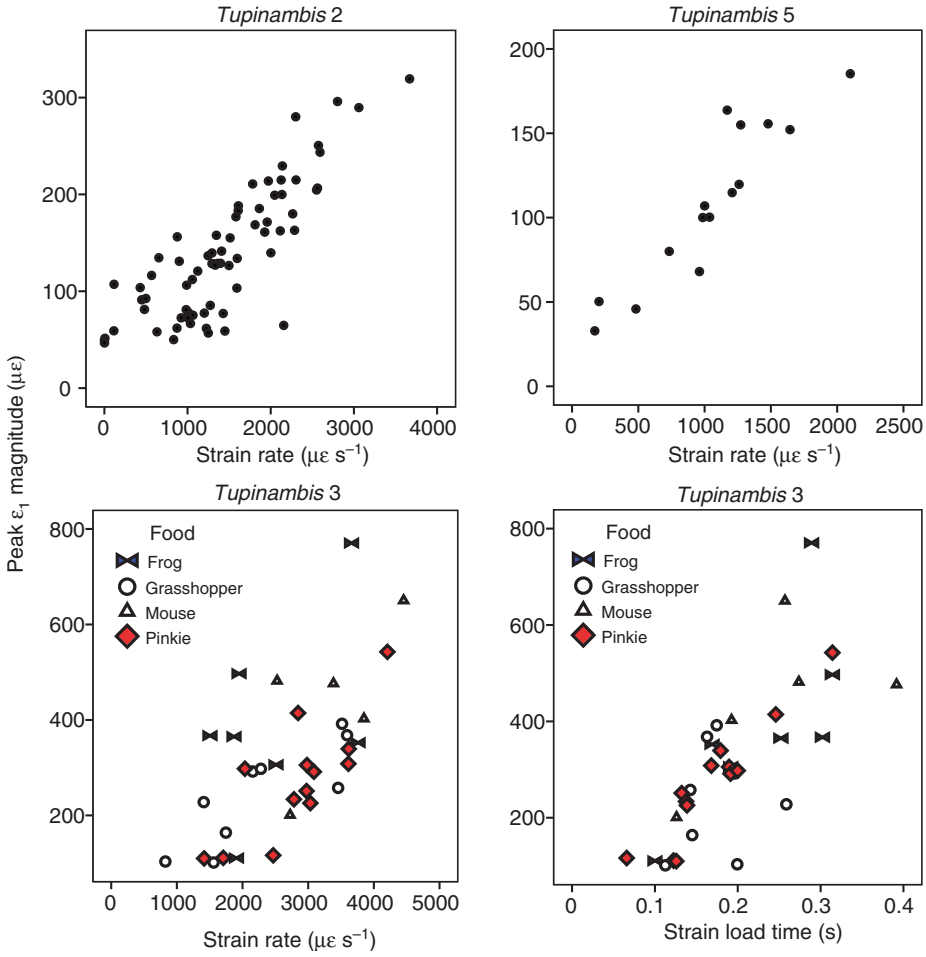


Fig. 2. Bivariate plots of $\varepsilon_1$ peak magnitude in microstrain ($\mu\varepsilon$) against strain rate ($\mu\varepsilon\,s^{-1}$) for *Tupinambis* 2 and 5, and against both strain rate and load time in *Tupinambis* 3. *Tupinambis* 2 and 5 only ate grasshoppers. $\varepsilon_1$ was not significantly correlated with load time in *Tupinambis* 2 and 5.

Table 3. Results of multiple regression analyses of $\varepsilon_1$ magnitudes against loading rates and loading times in *Tupinambis* 2, 3 and 5

| Individual | adjusted $r^2$ | Variable | Beta coefficients† | Partial correlations‡ | Tolerance§ |
|---|---|---|---|---|---|
| 2 | 0.775*** | load rate | 0.906*** | 0.883 | 0.939 |
| | | load time | 0.327*** | 0.562 | 0.939 |
| 3 | 0.820*** | load rate | 0.519*** | 0.780 | 0.974 |
| | | load time | 0.670*** | 0.849 | 0.974 |
| 5 | 0.885*** | load rate | 1.109*** | 0.946 | 0.680 |
| | | load time | 0.369** | 0.698 | 0.680 |

†Beta coefficients for strain magnitude against each individual variable are given with their significance levels.
‡Partial correlation coefficients for the multiple regression model.
§The tolerance for a variable is the proportion of the variance in that variable not accounted for by other independent variables in the model. A low value indicates that the variable contributes little to the model independent of the other variables, and is an indicator of multicollinearity.
$P$>0.05, not significant; *$P$<0.05, **$P$<0.01, ***$P$<0.001.

contrary to our hypothesis, the variance in SC duration in lepidosaurs is not significantly different from that in primates, and nor is variance in SO (Fig. 3). However, variance in FO and FC in primates is significantly different and *larger* than that in lizards ($CV_{FC}$: primates 38%; lizards, 29%, $t$=–2.102, $P$=0.04; $CV_{FO}$: primates 73%; lizards, 39%, $t$=–3.639, $P$=0.001; Fig. 3). These results are also evident in the bar graphs shown in Fig. 4, which illustrate the mean CVs of the four phases of the gape cycle for each species. The high CVs for FO duration are evident in the four primate species on the left end of the graph: the CVs for FC are less obviously different in the graph, but on average they are significantly different and higher in primates.

Separate single factor ANOVAs of CVs reveal that the phases differ significantly in their levels of variance within lizards and primates (Fig. 3). Among lizards, the highest variance is seen in SO and SC. The CVs for these two phases differ significantly from the mean CVs for FC and total cycle duration (at $P$<0.001). Among primates, the highest variance is seen in FO and SC. These CVs differ significantly from the mean CV for FC and total cycle duration. The CV for SO is only significantly different from that for total cycle duration. Notably, among lepidosaurs variance in total cycle duration is only significantly lower than variance for SO and SC durations, but among primates the variance in total cycle duration is significantly different and lower than that of all its constituent phases ($P$<0.01).

### How are phase durations related to total cycle duration?

The only way that total cycle duration can be less variable than its constituent phases is if increases in durations of some phases of the gape cycle are accompanied by decreases in durations of other phases. To test this hypothesis, correlation coefficients were calculated between the durations of the phases of the gape cycle, as well as between each of the phase durations and overall cycle duration. These calculations were performed within each individual animal. All nine primate individuals exhibited significant negative correlations between both FC and SC durations, and SO and FO durations. Seven individuals also showed significant negative correlations between SO and SC durations and one exhibited a negative relationship between SO and FC. In contrast, only five out of 23 lepidosaur individuals exhibited *any* negative correlations between durations of gape cycle phases: two had negative correlations between SC and FC durations; two had negative correlations between SO and FO durations; and one exhibited significant negative correlations between FC and both SO and total cycle duration. These results corroborate the hypothesis that mammals exhibit less variance in overall gape cycle durations than in the four phases of the cycle because increases in durations of some phases are accompanied by decreases in durations in other phases.

### The relative contributions of gape cycle phases to variance in total cycle durations

The relative contributions of variance in the four phases of the gape cycle to variance in total cycle duration are summarized in the bar plots of Johnson's relative weights in Fig. 5. These stacked bar plots present the data for each individual animal, as species averages and as primate and lepidosaur averages. The primates are to the left of each plot; the lizards are to the right. Johnson's relative weights suggest that primates and lizards differ in the following regards: in

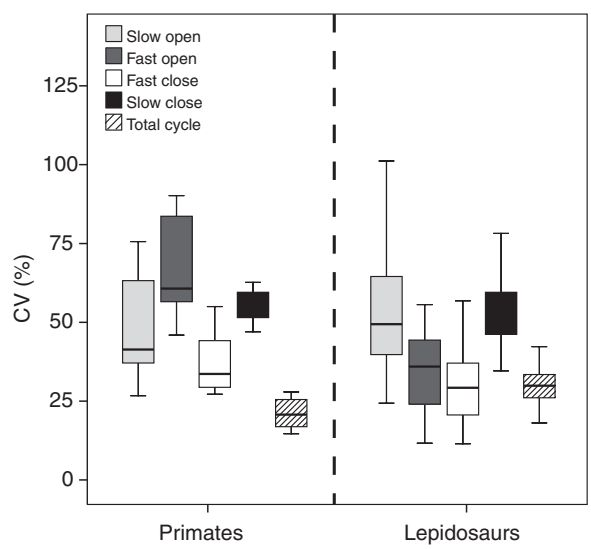


Fig. 3. Box plot of average coefficients of variation (CVs) of total gape cycle duration (cycle CV) and the CVs of the phases of the gape cycle (SO, FO, FC, SC) in lepidosaurs and primates. Outliers were deleted. Single factor ANOVAs of CVs reveal significant effects of phase (five levels: SO, FO, FC, SC and TC) on CVs within both lepidosaurs and primates. Among lepidosaurs, CVs of slow open ($CV_{SO}$) and slow close ($CV_{SC}$) are not significantly different from each other but differ from CVs of fast close and total cycle ($CV_{FC}$ and $CV_{TC}$; $P$<0.001); the CV for fast open ($CV_{FO}$) does not differ from any of the other CVs. Among primates, $CV_{FO}$ and $CV_{SC}$ are not significantly different from each other but differ significantly from $CV_{FC}$ and $CV_{TC}$; $CV_{SO}$ is only significantly different from $CV_{TC}$. Among primates $CV_{TC}$ is different and lower than the CVs of all its constituent phases ($P$<0.01). $CV_{SO}$ and $CV_{SC}$ in primates are not significantly different from those in lizards; $CV_{FC}$ and $CV_{FO}$ in primates are significantly different and larger than those in lizards ($CV_{FC}$: $t$=–2.102, $P$=0.04; $CV_{FO}$: $t$=–3.639, $P$=0.001).

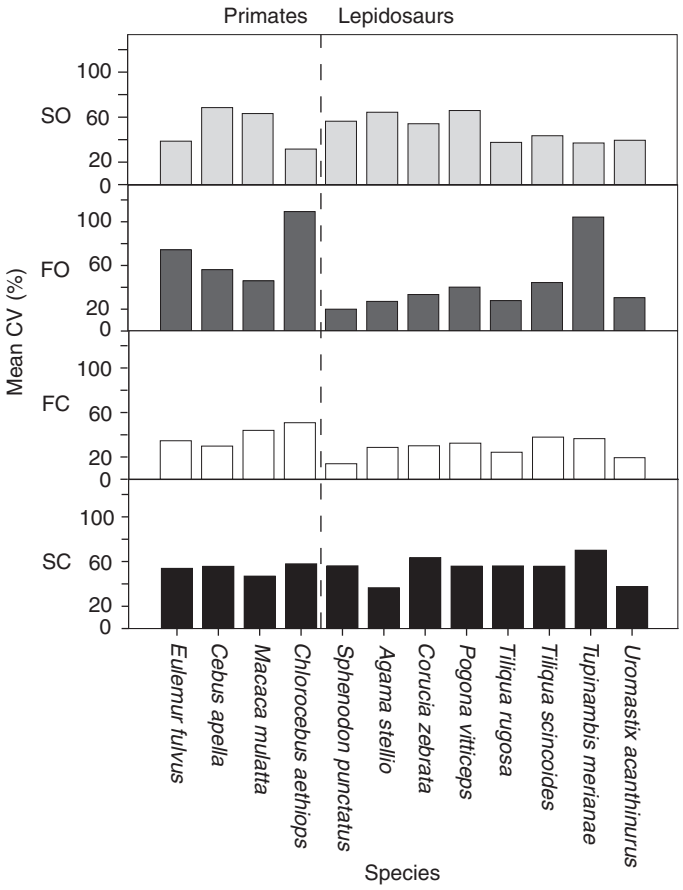


Fig. 4. Bar plots of the coefficients of variation (CVs) of the four phases of the gape cycle for the species studied here. Note the higher CVs for FO duration in the four primate species to the left. On average, the CVs for FC are significantly different and higher in primates than in lepidosaurs. Note also that contrary to the predictions of Ross et al. (Ross et al., 2007a), SC duration is not less variable in primates than it is in lepidosaurs. See Fig. 3 for primate and lepidosaur means.

lepidosaurs, variance in total cycle duration is more strongly influenced by variance in SO than is the case in primates; in primates, variance in total cycle duration is more strongly influenced by variance in FO than is the case in lepidosaurs; and in primates variance in total cycle duration is more evenly influenced by variance in all four gape cycle phases than is the case in most lepidosaurs. When Johnson's relative weights are calculated only from chewing cycles in which the primates or lepidosaurs ate fruit or vegetables (specifically, apple, tomato, kiwi and endive) the same results were obtained.

### Variance in the temporal shape of gape cycle phases

To investigate the relationship between changes in total cycle duration and the relative durations of the gape cycle phases, the durations of the gape cycle phases were expressed as phase proportions (i.e. percentages of total cycle duration) and regressed against total cycle duration. The slopes of these relationships are plotted in Fig. 6 by individual, species and averaged across primates and lepidosaurs. In the plot of individuals, circles indicate non-significant regression relationships. Significant relationships between a phase proportion and total cycle duration indicate changes in the proportion of total cycle duration made up by that phase as total cycle duration changes. Positive slopes (above the zero line) indicate that increases in total cycle duration are accompanied by increases in the proportion of total cycle duration made up by that phase. Negative slopes (below the zero line) indicate that increases in total cycle duration are accompanied by decreases in the proportion of total cycle duration made up by that phase. Fig. 6 reveals that lepidosaurs differ from primates in showing decreases in relative FO and FC duration and increases in relative SO duration with increases in total cycle duration, i.e. increases in total cycle durations in lepidosaurs are accompanied by increases in SO at the expense of FO and FC. Primates, however, maintain more consistent relationships between relative phase durations. The anthropoid primates show negative relationships between relative FC and total cycle duration, and one lemur exhibited increases in the relative durations of the slow phases, but generally speaking the slope values for the primates were smaller (closer to zero) than those in lepidosaurs. It is also notable that in the majority of animals studied here the relative duration of SC changes little with increases in total cycle duration. One lemur and two of the *Sphenodon* show increases in relative SC with total cycle duration, and three *Agama* show decreases in relative SC duration; otherwise relative SC duration remains fairly consistent across lepidosaurs and primates.

## DISCUSSION

We have shown previously that mammals not only chew with less variable gape cycle durations than lepidosaurs, but that mammals also modulate bite force during the slow close phase of the gape cycle primarily by varying the *rate* at which force is generated (Ross et al., 2007a; Ross et al., 2007b). We hypothesized that these two results might be causally linked: i.e. the lower variance in gape cycle durations seen in mammals might be attributable at least in part to rate modulation of bite force during SC. Noting that mammals possess sensorimotor system components used in feed-forward control that are not found in lepidosaurs (i.e. γ-motoneurons and periodontal afferents), we further hypothesized that these novel sensorimotor components facilitated this rate modulation of bite force during SC, and that this might enable mammals to chew more rhythmically than lepidosaurs. This hypothesis predicts that SC duration should be an important determinant of total cycle duration in lizards and mammals, that SC duration should be less variable in mammals than in lizards, and that lizards should time-modulate rather than rate-modulate bite force during chewing.

The data presented here violate some of these predictions, requiring a re-evaluation of our hypothesis. Although SC durations are significantly correlated with total cycle durations in nearly all (both primate and lepidosaur) individuals studied, SC durations in primates are not less variable than those in lepidosaurs (Figs 3 and 4). Moreover, like mammals, the three *Tupinambis* individuals that we studied all showed significant positive correlations between peak strain magnitude in the mandible (a surrogate of relative bite force magnitude) and loading rate (Table 3, Fig. 1). Although these strain data are only derived from three individuals, they do suggest that at least some lepidosaurs resemble mammals in rate-modulating bite force during chewing. Thus, although mammals utilize feed-forward control of bite force (Hidaka et al., 1997; Komuro et al., 2001a; Komuro et al., 2001b), and lepidosaurs apparently rely on feed-back control, these differences in motor control strategies are not related to differences in the manner of bite force modulation during SC.

These results suggest that feed-forward control of bite force in mammals must have functions other than contributing to rhythmicity of chewing movements. The most likely alternate function for this

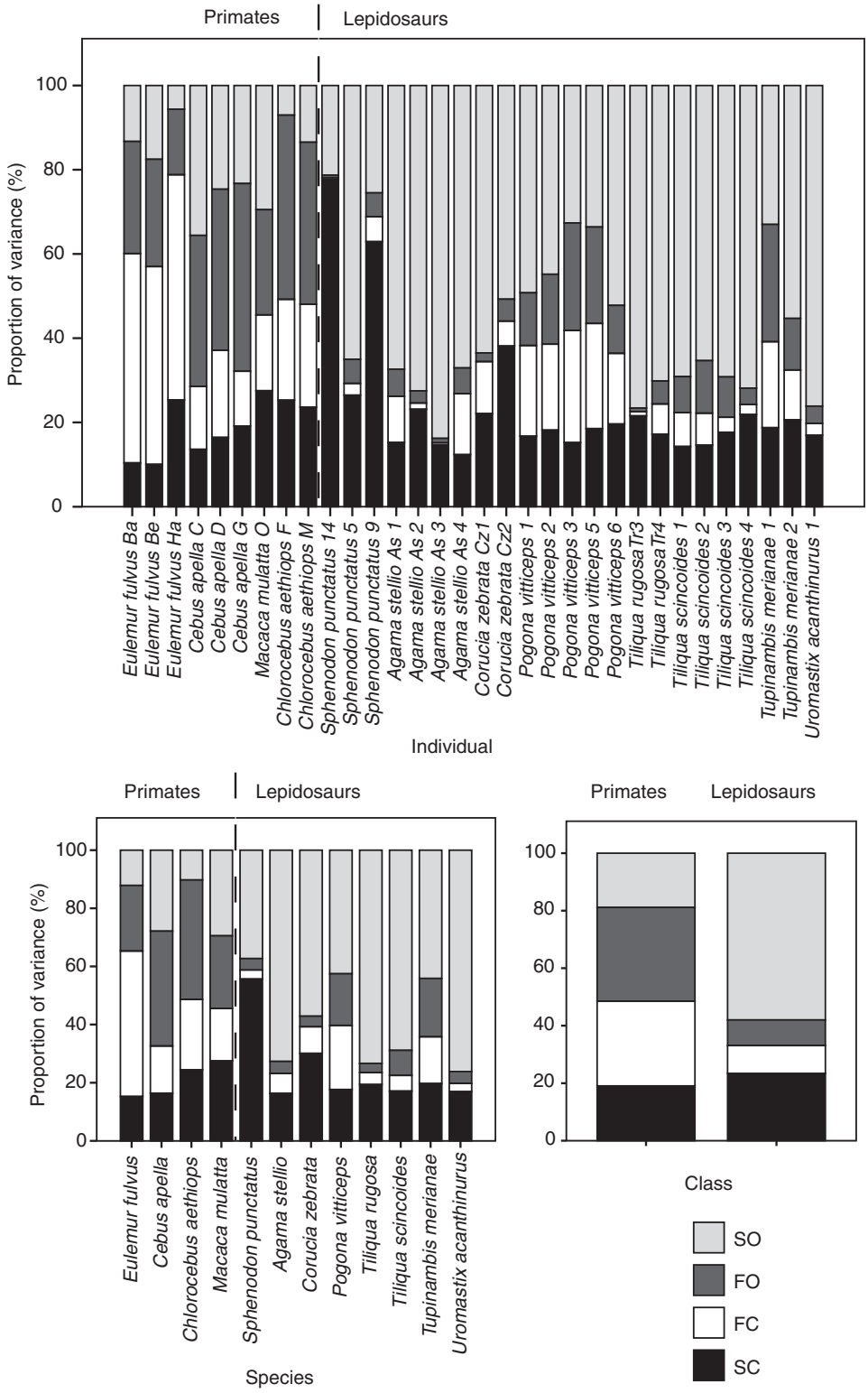


Fig. 5. Top. Stacked bar plots of Johnson's relative weights, which quantify the proportionate contributions of variance in each phase to variance in total cycle duration. The primates are to the left of the plots; the lepidosaurs are to the right. The data for each individual are shown in the top plot (numbers identify individuals), species averages are presented in the bottom left, and the overall averages for primates and lepidosaurs are compared bottom right. In lepidosaurs variance in total cycle duration is more strongly influenced by variance in SO than is the case in primates; in primates variance in total cycle duration is more strongly influenced by variance in FO and FC than is the case in lepidosaurs; and in primates variance in total cycle duration is more evenly influenced by variance in all four gape cycle phases than is the case in most lepidosaurs. These results persist when Johnson's relative weights are calculated only from chewing cycles in which the primates or lepidosaurs ate fruit or vegetables: specifically, apple, tomato and endive.

feed-forward control is reduction in risk of tooth breakage and of tooth wear during mastication (Hidaka et al., 1997; Inoue et al., 1989; Komuro et al., 2001a; Komuro et al., 2001b; Lavigne et al., 1987; Morimoto et al., 1989; Trulsson, 2006). These functions are likely to be important in mammals because they exert relatively high bite forces between hard but brittle surfaces of teeth that are only replaced once during life (Hopson, 1971; Hopson, 1973; Hopson and Crompton, 1969).

### How do mammals have less variable cycle durations than lepidosaurs?

If lepidosaurs and primates do not differ in levels of variance in SC duration, then their different levels of variance in gape cycle durations must be due to differences in other phases of the gape cycle. Other workers have shown that FO and FC duration are less variable than durations of other phases in mammals and lizards (Herrel et al., 1996; Metzger, 2009; Thexton and Hiiemae, 1997; Thexton et al.,

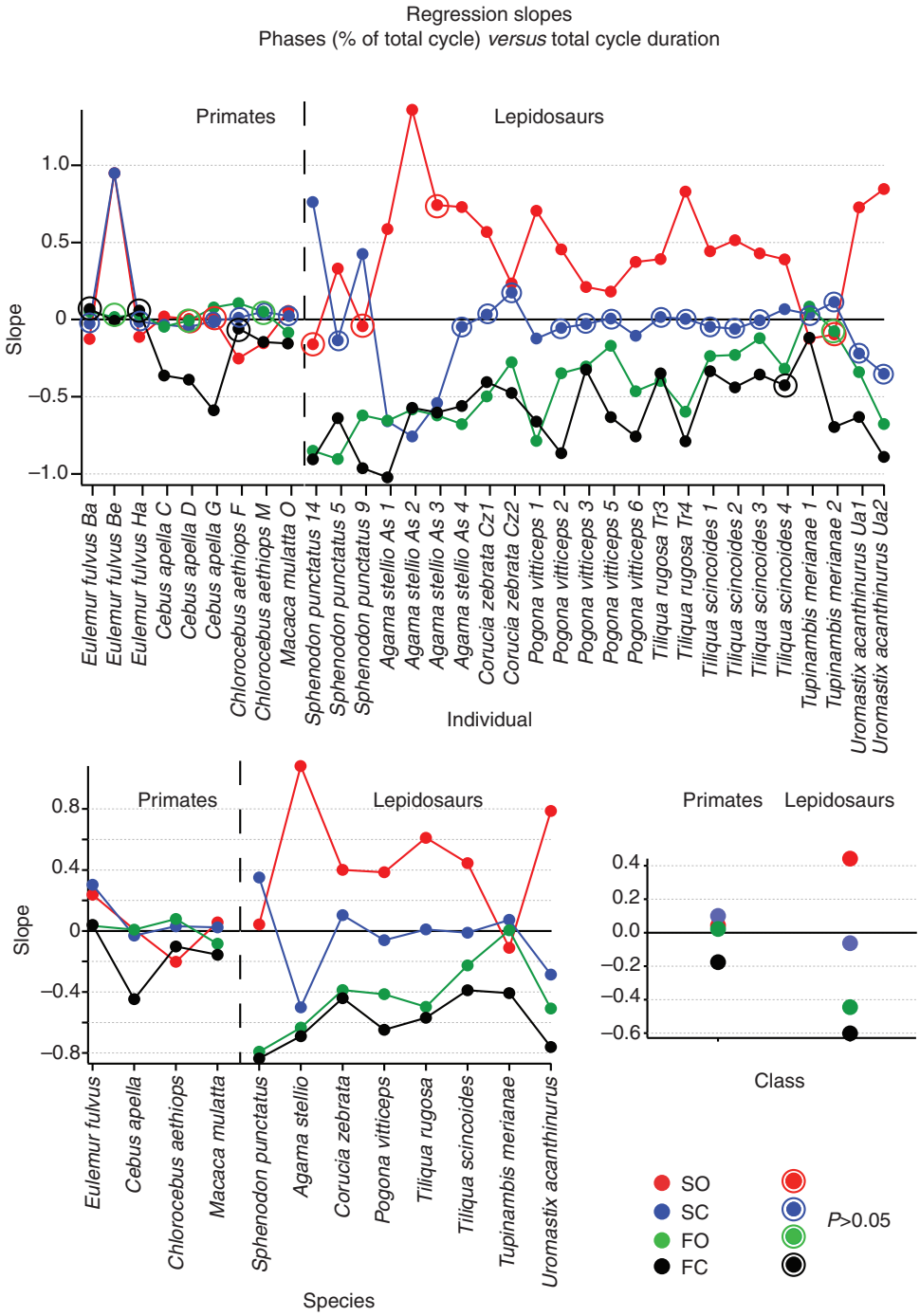


Fig. 6. Slopes of relationships between proportion of gape cycle made up by each phase and total cycle duration. In the top panel, circles surround those points representing non-significant regression relationships. Significant relationships between a phase proportion and TC indicate changes in the proportion of TC made up by that phase as TC duration changes. Positive slopes (above the zero line) indicate that increases in TC duration are accompanied by increases in the proportion of TC made up by that phase. Negative slopes (below the zero line) indicate that increases in TC duration are accompanied by decreases in the proportion of TC made up by that phase. Species averages for these regression slopes are presented in the bottom left panel and primate and lepidosaur averages are presented in the bottom right panel. Numbers after species names in top panel identify individual animals.

1980; Yamada and Yamamura, 1996). Our results confirm these findings for FC: FC is less variable than SO and SC in lepidosaurs and less variable than FO and SC in primates. In contrast, FO is one of the most variable phases in primates but not in lepidosaurs, FO variance is higher in primates than in lepidosaurs, and multiple regression confirms that FO is a more important determinant of cycle duration variance in primates than in lizards (Fig. 5).

Clearly relatively higher levels of variance in FO durations in primates cannot explain the relatively lower variance in primate gape cycle durations. Similar problems confront attempts to link less variable cycle durations in primates to variance in SO durations. Our results do confirm that SO duration is an important determinant of total cycle duration in both lizards and mammals (Herrel et al., 1996; Herrel and De Vree, 1999; Schwartz et al., 1989; Thexton et al., 1980; Yamada and Yamamura, 1996), but SO duration is not less variable in primates than it is in lepidosaurs (Fig. 3). Moreover, among the primates studied, SO is only significantly correlated with TC duration in six out of nine animals.

Why then do primates have less variable gape cycle durations than lizards? The answer to this question emerges from consideration of the relative contributions of variance in the gape cycle phases to variance in overall gape cycle duration. Primates appear to minimize variance in overall gape cycle durations by trading off variance in the phases of the gape cycle, i.e. increases in one phase are accompanied by decreases in other phases. All primate individuals exhibit negative correlations both between SC and FC durations

and between SO and FO durations, and most of them also show significant negative correlations between SO and SC durations. This 'trading off' of phase durations has been observed in non-primate mammals. In rabbits total cycle duration is not affected by food type, but SC durations are longer and opening durations are shorter when eating hard, uncooked rice whereas SC durations are shorter and opening durations are longer when eating soft bread (Yamada and Yamamura, 1996). Similarly, during mastication by macaque monkeys overall cycle durations seem unaffected by food type (banana, 514 ms; chow, 505 ms), but chow chewing cycles are characterized by long SC and short SO durations, whereas banana cycles have short SC and long SO durations (Thexton and Hiiemae, 1997). In contrast to primates, only five of the lepidosaurs exhibited any negative relationships among the phases of the gape cycle, suggesting that lepidosaurs less commonly trade off phase durations than do primates, so that variance in phase durations is more often associated with variance in overall cycle duration.

Despite these trade-offs between phase durations, variance in total cycle duration in primates is more evenly influenced by variance in all four gape cycle phases than is the case in lepidosaurs (Fig. 5). As a result, variance in gape cycle duration in primates is associated with relatively little change in the relative proportions of the gape cycle made up by the different phases (Fig. 6). In contrast, increases in gape cycle durations in lepidosaurs are associated with increases in the proportion of the cycle made up by SO and decreases in the proportions of FO and FC. Hence, multiple regression analyses confirm that, although lepidosaurs do not have more variable SO durations than primates (Fig. 3), SO variance contributes more to variance in total cycle duration in lepidosaurs than in primates (Fig. 6). SO is the phase when the tongue collects sensory information on external physical attributes of the food, such as the size, stickiness, wetness and distribution of the bolus in the oral cavity (Lucas, 2004). Presumably the sensory information collected during SO is used to modulate subsequent repositioning of the food during FO and FC in preparation for food breakdown during SC. In primates this information might play a role in the observed trade-off in variance in the opening phases (a longer SO is associated with a shorter FO, and *vice versa*) or the closing phases (a longer FC is associated with a shorter SC). These trade-offs are less common in lepidosaurs, so that variance in SO phase durations is associated with variance in total cycle duration. This suggests to us that the differences between lepidosaurs and primates do not lie in the nature of the sensory information collected and its feedback to the feeding system during SO, but rather in the processing of that information by the CNS and feed-forward use for modulating other gape cycle phases.

One reviewer suggested that these data do not provide strong evidence for trade-offs in phase durations in mammals if total cycle duration is not constrained, a point with which we agree. However, our hypothesis is that primates gape cycle durations are constrained because gape cycle variance is being actively modulated (and minimized). Mammals (including primates) not only chew with less variable gape cycle durations than lepidosaurs, but in mammals gape cycle duration changes with the size of the animal, something not seen in lepidosaurs (Gerstner and Gerstein, 2008; Ross et al., 2007b; Ross et al., 2009a; Ross et al., 2009b). Thus, we hypothesize that mammals chew close to the natural frequencies of their feeding systems, and that these frequencies vary with animal size because this minimizes energy consumption in the chewing muscles. We hypothesize that this is necessary because the much higher metabolic rates in mammals than lepidosaurs (Nagy, 1987) necessitate not only higher rates of energy acquisition (Karasov and Diamond, 1985; Karasov et al., 1986) and more efficient food processing within each chewing cycle (Crompton, 1971; Crompton, 1989; Crompton, 1995), but also longer periods of time feeding (and chewing) each day. In contrast, lepidosaur gape cycle durations are more variable because they are not constrained, they show less evidence of trade-offs between gape cycle phase durations, and they probably spend less time chewing during the day. Careful comparisons of feeding time in similarly sized lepidosaurs and mammals living on similar diets in similar environments are needed to test this hypothesis. We further hypothesize that mammals possess a central nervous system representation or model of the optimal chew cycle duration that can be achieved in different ways, depending on the ongoing state of the chew cycle estimated from afferent feedback. One selective advantage of this is the maintenance of a relatively constant cycle duration that is close to the optimal chewing frequency for the animal based on the size and shape of its feeding system (Ross et al., 2009a).

## Conclusions

Lepidosaurs chew with more variable gape cycle durations than mammals. The higher rhythmicity of mammals has been argued to be selectively advantageous for animals that chew a lot because it is energetically more efficient (Ross et al., 2007b). It was suggested that one reason for this increased rhythmicity is to be found in feed-forward control of bite force during the SC phase of the chewing cycle. This study found no difference between lepidosaurs and primate mammals in the nature of bite force modulation during mastication, i.e. both lepidosaurs and primates rate-modulate bite force and exhibit no differences in the magnitude of variability in SC. However, primates do differ from lizards in that variation in total gape cycle duration is more evenly affected by variance in all the phases in primates, and total gape cycle variance is lower than its constituent phases. These data suggest that primates trade off variance in some phases for variance in others, so that total cycle duration is less variable than in lepidosaurs. We conclude that primates possess a central nervous system representation or model of the optimal chew cycle duration that is maintained using afferent feedback on the ongoing state of the chew cycle. We also conclude that the differences between lepidosaurs and primates may lie not in the nature of the sensory information collected and its feedback to the feeding system during slow open and slow close, but rather in the processing of that information by the CNS and its use for modulating other gape cycle phases. Periodontal afferents and γ-motoneurons do facilitate feed-forward control of chewing in mammals and not lepidosaurs, but this is not associated with less variable slow open and slow close durations in primates. Rather, this feed-forward control more likely functions to minimize tooth wear and risk of tooth breakage during slow close and to modulate trade-offs in phase durations.

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