

Scaling of Chew Cycle Duration in Primates

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ABSTRACT The biomechanical determinants of the scaling of chew cycle duration are important components of models of primate feeding systems at all levels, from the neuromechanical to the ecological. Chew cycle durations were estimated in 35 species of primates and analyzed in conjunction with data on morphological variables of the feeding system estimating moment of inertia of the mandible and force production capacity of the chewing muscles. Data on scaling of primate chew cycle duration were compared with the predictions of simple pendulum and forced mass-spring system models of the feeding system. The gravity-driven pendulum model best predicts the observed cycle duration scaling but is rejected as biomechanically unrealistic. The forced mass-spring model predicts larger increases in chew cycle duration with size than observed, but provides reasonable predictions of cycle duration scaling. We

hypothesize that intrinsic properties of the muscles predict spring-like behavior of the jaw elevator muscles during opening and fast close phases of the jaw cycle and that modulation of stiffness by the central nervous system leads to spring-like properties during the slow close/power stroke phase. Strepsirrhines show no predictable relationship between chew cycle duration and jaw length. Anthropoids have longer chew cycle durations than nonprimate mammals with similar mandible lengths, possibly due to their enlarged symphyses, which increase the moment of inertia of the mandible. Deviations from general scaling trends suggest that both scaling of the jaw muscles and the inertial properties of the mandible are important in determining the scaling of chew cycle duration in primates. *Am J Phys Anthropol* 138:30–44, 2009. © 2008 Wiley-Liss, Inc.

The biomechanical factors influencing chewing rate are important determinants of how mammals, including primates, meet metabolic demands. In nonprimate mammalian herbivores food intake rate has been shown to be strongly influenced by the amount of food intake in each ingestion bite, the time required for each ingestion bite, and the rate at which food is processed within the oral cavity (Shipley et al., 1994). The last of these, intra-oral food processing rate, is influenced by chewing frequency (Clutton-Brock and Harvey, 1977), and so the rate at which animals chew can therefore influence the rate at which food is ingested and overall feeding time. What biomechanical factors determine chewing rate in mammals?

Various factors have been hypothesized to influence chewing rate in herbivorous mammals, including body mass, general feeding system size, jaw length, tooth surface area, bite force or stress, jaw muscle cross-sectional area, and food material properties (Amar, 1914; Hendrichs, 1965; Luschei and Goodwin, 1974; Thexton et al., 1980; Fortelius, 1985; Plesh et al., 1986; Inoue et al., 1989; Morimoto et al., 1989; Druzinsky, 1993; Shipley et al., 1994; Liu et al., 1998; Foster et al., 2006). The relative importance of these factors has not been evaluated. Intensive research on primates over the last several decades makes them rich sources of the biomechanical data needed to evaluate the relative importance of these factors. This article uses scaling analyses of chewing rate and feeding system morphology to evaluate hypotheses regarding the determinants of chew cycle durations in primates.

A list of symbols used is presented in Table 1, along with the dimensionality of each. Previous workers, on

scaling of chewing times, have used both frequency and period. In this article, chew cycle duration (chew period) is used, i.e., T_c . Chew frequency data from the literature (F_c in Hz, or chews/second) are converted to chew cycle durations by calculating the inverse $= 1/F_c$. Published scaling coefficients of F_c are converted to scaling coefficients for T_c using the exponent properties $a^{-n} = 1/a^n$ and $(1/a)^{-n} = a^n$. For example, $F_c \propto M_b^{-0.20}$ becomes $T_c \propto M_b^{0.20}$.

What determines chew cycle duration?

Pendulum model. Simple pendulum models are often used to derive predictions regarding scaling of simple oscillatory movements. Pendulum mechanics specify that the natural period (T_p) of an oscillating, gravity-driven, pendulum-like musculoskeletal system is proportional to

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TABLE 1. Symbols

Symbol	Description (Dimensionality)
Temporal variables	
T_p	Natural period (cycle length) of a pendulum (T)
F_p	Natural frequency of pendulum = $1/T_p$ (T^{-1})
T_c	Chew cycle duration (T)
F_c	Chew frequency = $1/T_c$ (T^{-1})
Linear variables	
l or L_p	Pendulum length, i.e., distance from center of rotation to center of mass (L)
L_j	Jaw length (L)
L_m	Muscle length (L)
b_e	Lever arm of jaw elevator muscles (L)
$b_{\text{mass, temp, med.pt.}}$	Lever arm of masseter, temporalis, or medial pterygoid m. (L)
b_d	Lever arm of jaw depressor muscles (L)
Area variables	
A_e	Reduced physiologic cross-sectional area (RPCA) of jaw elevator muscles (L^2)
Mass and volume variables	
M_b	Body mass (M)
M_p	Pendulum mass (M)
M_j	Jaw mass (M)
Force variables	
g	Acceleration due to gravity (MLT^{-2})
k	Spring constant ($ML^{-1}T^{-2}$)
F_b	Bite force (MLT^{-2})
Other variables	
E	Slope of stress strain curve, i.e., Young's modulus for foods and calculation of k for muscles ($ML^{-1}T^{-2}$)
α	Proportional to

L , length; M , mass; T , time.

$2\pi(l/g)^{0.5}$, where l = pendulum length and g = acceleration due to gravity; i.e.,

$$T_p \propto 2\pi\sqrt{\frac{l}{g}} \quad (1)$$

This model can be used to predict the natural period of chewing (T_c) if jaw length (L_j) is assumed to scale proportional to pendulum length: i.e., $L_j \propto l$. As 2π and g are constants, this yields a prediction that $T_c \propto \sqrt{L_j}$, or $T_c \propto L_j^{0.5}$. Data corroborating the simple pendulum model have been presented by Druzinsky (1993) and Shipley et al. (1994). Druzinsky's data, pooled with published data of Fortelius, yield a relationship of $T_c \propto L_j^{0.503}$ [SMA calculated from Druzinsky's Eq. (14)], and Shipley et al. report that $T_c \propto L_j^{0.55}$ (Druzinsky, 1993; Shipley et al., 1994). Although these data support the simple pendulum model, the applicability of a gravity-driven pendulum model to chewing is questionable. Mammal mandibles do not oscillate through an arc centered about the gravity vector. In most mammals they are elevated against gravity so that gravity cannot drive mandible movements during the closing portions of the jaw movement cycle. Moreover, it is not clear that gravity plays a significant role even in jaw opening in mammals. The human mandible, for example, only rotates a few degrees in opening without the aid of depressor muscles, the opening torques being resisted by passive forces in connective tissue and muscular elements in jaw elevator muscles. If these assumptions are valid, then the mammalian chewing ap-

paratus is better modeled as a muscle-driven oscillating pendulum, and predictions regarding the determinants of (and scaling of) primate chew cycle durations must consider the contribution of the mechanics of jaw adductor and depressor muscles.

Spring model. The contribution of muscle mechanics to the natural frequency of rhythmic musculoskeletal movements has often emphasized spring-like behavior of skeletal muscle. Spring-like behavior of muscle-tendon complexes is both an important energy-saving aspect of musculoskeletal design (Alexander, 1984, 1988a,b, 1990, 1991a,b), and an important component of sensorimotor control (Nichols and Houk, 1976; Houk, 1979; Houk et al., 1981). The latter possibility led McMahan (1975, 1984) to use spring constants to model the contribution of muscle mechanics to the natural frequency of rhythmic limb movements during locomotion under the assumptions of different (geometric, elastic, and static stress) scaling models. In his model, the natural period, T is estimated as

$$T \propto \sqrt{\frac{L_m m l^2}{E A b^2}} \text{ or } T \propto \sqrt{\frac{m l^2}{k b^2}} \quad (2)^1$$

where $m l^2$ is the moment of inertia (or resistance to rotation) of a limb of mass m with its center of mass located a distance l from the axis of rotation; b is the lever arm of the muscles; and the spring constant $k = EA/L_m$, where E is the slope of the linear portion of the stress-strain curve (= stiffness) of the muscle, A is the physiological cross-sectional area of the muscle, and L_m is muscle length (McMahan, 1975; McMahan, 1984).² Equation (2) differs from (1) not only in having muscles represented by spring constants driving the oscillations (rather than gravity), but also in specifying the distribution of mass and the lever arms of the input and resistance torques. Incorporating these variables to quantify the geometry of the system enabled McMahan (1975) to estimate the natural periods of limb oscillation during locomotion under different assumptions regarding the scaling of limb length and diameter: under geometric similarity, $T_n \propto M_b^{0.33}$, and under elastic similarity, $T_n \propto M_b^{0.125}$.

A similar approach was taken by Turvey et al. (1988), although in their model gravity reappears as a driving force of the pendulum:

$$T_p = 2\pi\sqrt{\frac{M_p L_p^2}{M_p L_p g + k b^2}} \quad (3)$$

where M_p is pendulum mass, L_p is pendulum length, k is the spring constant for the muscles moving the limb, b is a constant distance from the axis of rotation to the muscle attachments, and the terms $M_p L_p g$ and $k b^2$ in the denominator are input torques (Kugler and Turvey, 1987; Turvey et al., 1988). If the ratio $M_p L_p g / k b^2$ is constant, then the scaling relationships of M_p and L_p determine the scaling of natural period, such that if $M_p \propto L_p^z$, then $T_p \propto L_p^{0.5}$ and $T_p \propto M_p^{0.5/z}$. For example, when $M_p \propto L_p^3$, as

¹This represents an adaptation of McMahan (1975) Eq. (8) in which density is assumed to be constant across body sizes and the letter b is substituted for McMahan's d .

²See Appendix for derivation of k .

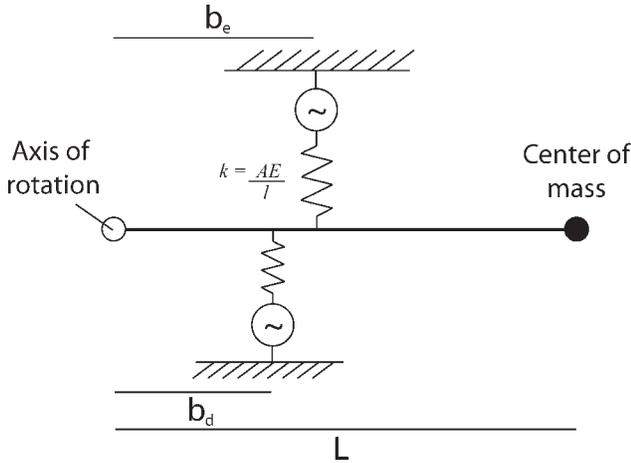


Fig. 1. Diagram of model of jaw muscle and mandible system employed in this study: Each muscle is modeled as a force generator and a spring, in series cf. (Lappin et al., 2006). b_e , lever arm of jaw elevator muscles; b_d , lever arm of jaw depressor muscles; L , distance from center of rotation to center of mass of mandible.

predicted by geometric similarity (Hill, 1950), then $T_p \propto L_p^{0.5}$ and $T_p \propto M_p^{0.17}$. When $M_p \propto L_p^4$, as predicted by elastic similarity scaling (McMahon, 1975), then $T_p \propto L_p^{0.5}$ and $T_p \propto M_p^{0.125}$. Importantly, T_p is always proportional to pendulum length with an exponent of 0.5, as predicted by the simple pendulum model, but its scaling relationship to pendulum mass varies as a function of the proportionality between M_p and L_p .

If the gravity-driven pendulum model of the mammal chewing system is rejected, as we argue, then to predict the natural periods of mammal chewing, Eq. (3) must be modified by replacing the gravity-driven torque in the denominator with the torque generated by the depressor muscles, yielding

$$T_c = 2\pi \sqrt{\frac{M_j L_j^2}{k_d b_d^2 + k_e b_e^2}} \quad (4)$$

with the terms in the denominator representing torques for the jaw depressors ($k_d b_d^2$) and elevators ($k_e b_e^2$) (see Fig. 1). This equation can then be used to predict scaling of primate chew periods using estimates of the scaling of b_e , b_d , and the cross-sectional areas of jaw elevators and depressors. (Note that this model does not assume constancy of b , as does that of Turvey et al. [1988]). Morphometric estimates of jaw elevator lever arm (b_e) scaling are available (Hylander, 1985; Spencer, 1999; Ravosa et al., 2000) as data on the scaling of primate jaw elevator cross-sectional areas (Anapol et al., 2008), but data for jaw depressor muscles are not known. However, if one assumes either that the ratio $k_d b_d^2 / k_e b_e^2$ is constant, or that the scaling of the jaw elevator torques is the limiting factor in determining jaw cycle duration, the denominator of Eq. (4) can be simplified. In support of the latter assumption, it can be argued that elevating the mandible against food resistance certainly requires more force than depressing the mandible. Making this assumption, the *Spring Model* of masticatory natural period reduces to McMahon's model [Eq. (2)]:

$$T_c = 2\pi \sqrt{\frac{M_j L_j^2}{k_e b_e^2}} \quad (5)$$

In this article, the *Spring Model* in Eq. (5) is used to predict scaling of primate chew periods from scaling relationships of jaw length (L_j), jaw mass (M_j), jaw elevator lever arms, and the spring constant (k) representing the jaw elevator muscles, derived from scaling analyses of jaw elevator cross-sectional areas, A_e (Anapol et al., 2008). The scaling of all variables is expressed relative to jaw length, so that Eq. (5) can be reduced to a prediction regarding scaling of chew period relative to jaw length.

Three predictions are made using this *Spring Model*: the first, referred to as the *Spring-Empirical Model*, incorporates empirically based scaling estimates of the morphological variables measured in this study. The second, the *Spring-Spencer Model*, uses the empirically documented scaling estimates presented here except for an estimate of the scaling of b , which is instead based on three-dimensional analysis of skull morphology by M. Spencer, i.e., $b \propto L_j^{1.035}$ (Spencer, 1999). The analysis of Spencer is unique in being based on three-dimensional measurements of all jaw muscle resultants, and because in Eq. (5) the exponent of b increases its influence on the predicted scaling coefficient. The third prediction, the *Spring-Isometry Model*, predicts the scaling of chew period using Eq. (5) but assuming isometric scaling of all the components of the feeding system: i.e., $M_j \propto L_j^3$; $A_e \propto L_j^2$; $L_m \propto L_j^1$; $b \propto L_j^1$. Isometry of jaw elevator muscle reduced physiologic cross-sectional area (RPCA, used here to estimate A_e) is often assumed (e.g., Hylander, 1985), primarily based on data on scaling of muscle mass (Cachel, 1980; Ross, 1995), and some workers have documented isometry of jaw elevator muscle PCSA in strepsirrhines (Perry and Wall, 2005). The scaling of T_c predicted by the *Spring-Isometry Model* is included here for comparison with the empirically documented values.

MATERIALS AND METHODS

Chew period, T_c

Chew period data were collected from video recordings of freely moving primate subjects at the Lincoln Park Zoo, Brookfield Zoo, and Duke Lemur Center, and from bone strain recordings of restrained animals. 7748 chewing cycles from 426 chewing sequences were recorded from 86 individuals in 35 species of primates and data on chewing frequencies in 43 species of non-primate mammals were collated from the literature. The laboratory animals were fed a variety of food types, including apple, grapes, dried apricots, nuts (almonds, Brazil nuts, cashews), with foods cut into pieces of a size that could easily be fed to the animals with a pair of forceps. The zoo animals were filmed eating the range of foods normally fed to them: no attempt was made to control food material properties in this study. T_c , length of time between successive maximum gapes, was estimated from video records of complete chewing sequences (30 frames/sec) or as the time between peak bone strain in the mandibular corpus (collected at a range of frequencies ranging from 1–10 KHz) (Ross, 2001; Ross et al., 2007a,b). Descriptive statistics for T_c recorded from each individual animal and calculated species means are presented in Table A1.

Body mass, M_b

Sex and age of the animals were recorded; body mass was taken from the literature (Nowak, 1991; Smith and Jungers, 1997; Fleagle, 1999). The mean of male and female body masses was used for interspecific scaling analyses with the exception of *Gorilla*. For *Gorilla*, female body mass was used because chew frequency data were available only for females and because of the high degree of sexual size dimorphism in this species.

Jaw dimensions

The following measurements were taken on specimens at the Field Museum of Natural History, Chicago, IL: L_j , jaw length (mm) from condyion to infradentale; M_j , jaw mass (mg); masseter lever arm (mm), with jaw in centric occlusion, from condyion to rostral edge of scar of masseter origin on zygomatic arch; temporalis lever arm (mm), from condyion to superiormost point on coronoid process of mandible; medial pterygoid lever arm (mm), with jaw in centric occlusion, from condyion to rostral edge of scar of medial pterygoid origin on pterygoid plates. When possible, morphological measurements were taken from wild-caught representatives of the same species from which the chewing frequency data were obtained. When this was not possible, data were obtained from mandibles of zoo specimens of the same species or specimens of similarly sized congeners. Descriptive statistics for morphological variables are presented in Table A1.

Statistical analyses

The possible effect on T_c of the relative timing of a chew cycle in a sequence of chews (Fish and Mendel, 1982; De Gueldre and De Vree, 1988) was evaluated by calculating correlation coefficients between chew cycle number and T_c in all chewing sequences. Comparisons of chew cycle duration against chew number corrected for multiple comparisons (Bonferroni) were significant in only 22 out of 426 sequences (5%). In 12 of these sequences, there was a significant positive relationship (i.e., cycle duration increased through the sequence) and in 10 sequences there was a significant negative relationship (i.e., cycle duration decreased through the sequence). These results suggest no consistent relationship between cycle duration and chew number across sequences, making it reasonable to pool all chews in calculation of average chew cycle durations.

Interspecific scaling relationships between pairs of variables (e.g., T_c , M_b , L_j , M_j , A_m) were documented using the slope of the standardized major axis (SMA) (= reduced major axis, or RMA). SMA was preferred over least-squares regression (LSR) or major axis (MA) because: the aim of this study was to test hypotheses regarding the functional relationships between variables using slope estimates; mean values of both Y and X variables were certainly measured with error, primarily equation error,³ but also measurement error; and the units of measurement in Y and X variables were usually different (e.g., time and length or time and mass)

³Measurement error is error in measuring the true value; equation error is error due to the values for the species means not falling on the SMA, major axis or regression line.

(LaBarbera, 1989; Warton et al., 2006). Consequently, there is no reason to preferentially weight deviations from the line in either Y or X directions. SMA achieves equal weighting of these deviations because it is the major axis of the distribution of X and Y variables calculated using standardized data, and then rescaled to the original axes.

SMA were calculated across all primates, across strepsirrhines and anthropoids separately, and across nonprimate mammals. To compare the scaling of T_c in primates with that in other mammals, SMA slopes were calculated for chew cycle durations obtained from the literature for a range of mammals (Tables A2, A3) and compared with the primate slopes using SMATR Version 2.0 (Falster et al., 2006) employing methods described in Warton et al. (2006). To estimate whether the slope of the best fit SMA calculated using our data is significantly different from those predicted by alternate hypotheses, SMATR was used to test whether, when a line of the predicted slope is run through the data, the residual and axis scores were significantly correlated (F -test) (Warton et al., 2006). To compare SMA estimates between groups, tests for a common slope employed a likelihood ratio test compared with a chi-squared distribution, and tests for differences in elevation (SMA-“ANCOVA”) employed the WALD statistic (Warton et al., 2006).

To compare the ability of the different models to explain the distribution of the data, it was necessary to use a method that applied equally to all models. SMA minimizes the sum of the triangular areas between the line and each data point (Teissier, 1948), a “geometric peculiarity” of the model (Warton et al., 2006) that is nonetheless easily applied to other lines. Thus, we compared the explanatory power of the competing models using the sums of the triangular areas (calculated for each point using Heron’s/Hero’s formula) between each data point and the hypothesized line. These areas are analogous to the standard error of the estimate in least-squares regression.

RESULTS

Scaling of morphological variables

In Table 2, the statistics for the scaling of morphological variables are presented and slope values are compared with those predicted by isometry. The majority of the linear and mass measures are isometric among primates. Jaw length is isometric with body mass across nonprimates, primates, strepsirrhines, and anthropoids. Slope estimates for primates and nonprimates are not significantly different, but elevation comparisons reveal that primates (difference, 0.117; std error, 44.393; df, 1; $P < 0.001$), strepsirrhines (difference, 0.082; std error, 20.413; df, 1; $P < 0.001$) and anthropoids (difference, 0.130; std error, 41.393; df, 1; $P < 0.001$) all have shorter mandibles than nonprimates. Within primates, anthropoids have shorter mandibles for their body mass than strepsirrhines (difference, 0.048; std error, 6.3443; df, 1; P , 0.012). Among primates, jaw mass is isometric with both jaw length and body mass. Anthropoids have greater jaw mass for their mandible length than strepsirrhines, but only marginally (difference, 0.097; std error, 3.908; df, 1; P , 0.048). Together, these data indicate that jaw mass and length scale isometrically against body mass and each other, but primates have shorter

TABLE 2. Statistics, slope, and intercept comparisons for SMA of morphological variables

Group	<i>N</i>	<i>R</i> ²	<i>P</i>	Slope	Lower 95% CI	Upper 95% CI	<i>F</i> -value ^a	<i>P</i>	Intercept	Lower 95% CI	Upper 95% CI
log ₁₀ jaw mass (<i>M_j</i>) versus log ₁₀ jaw length (<i>L_j</i>)											
Primates	36	0.976	<0.001	3.147	2.982	36	3.268	0.079	<i>b</i> = 3.0? -4.612	-4.91	-4.313
Anthropoids	23	0.983	<0.001	3.102	2.924	3.291	1.38	0.253	-4.5	-4.837	-4.163
Strepsirrhines	13	0.948	<0.001	2.924	2.514	3.401	0.139	0.716	-4.306	-5.019	-3.593
log ₁₀ jaw mass (<i>M_j</i>) versus log ₁₀ body mass (<i>M_b</i>)											
Primates	36	0.956	<0.001	1.025	0.953	1.102	0.464	0.5	<i>b</i> = 1.0? 0.474	0.4109	0.5368
Anthropoids	23	0.944	<0.001	1.027	0.922	1.143	0.258	0.617	0.466	0.359	0.574
Strepsirrhines	13	0.939	<0.001	1.048	0.89	1.235	0.402	0.539	0.487	0.3976	0.5772
log ₁₀ masseter lever (<i>b_{mass}</i>) versus log ₁₀ jaw length (<i>L_j</i>)											
Primates	36	0.958	<0.001	0.9377	0.8731	1.0071	3.348	0.076	<i>b</i> = 1.0? -0.171	-0.2889	-0.0531
Anthropoids	23	0.978	<0.001	0.9386	0.877	1.0045	3.769	0.066	-0.1717	-0.2889	-0.0546
Strepsirrhines	13	0.866	<0.001	0.9243	0.7268	1.1755	0.511	0.49	-0.1513	-0.5121	0.2094
log ₁₀ temporalis lever (<i>b_{temp}</i>) versus log ₁₀ jaw length (<i>L_j</i>)											
Primates	36	0.936	<0.001	1.09	0.998	1.19	3.935	0.055	<i>B</i> = 1.0? -0.7127	-0.8812	-0.5441
Anthropoids	23	0.952	<0.001	1.123	1.017	1.24	5.944	0.024	-0.7838	-0.9889	-0.5788
Strepsirrhines	13	0.856	<0.001	1.097	0.855	1.408	0.656	0.435	-0.7075	-1.1524	-0.2626
log ₁₀ medial pterygoid lever (<i>b_{med.pt.}</i>) versus log ₁₀ jaw length (<i>L_j</i>)											
Primates	36	0.944	<0.001	0.9679	0.8915	1.051	0.646	0.427	<i>B</i> = 1.0? -0.3609	-0.5012	-0.2206
Anthropoids	23	0.971	<0.001	0.9251	0.8559	0.9998	4.347	0.049	-0.2626	-0.3948	-0.1304
Strepsirrhines	13	0.886	<0.001	0.8205	0.6569	1.0249	3.82	0.077	-0.1609	-0.4568	0.135

^a *F*-values measure probability that slope values differ from hypothesized slope at top of column.

TABLE 3. Statistics, slope and intercepts for SMA of chew cycle duration (*T_c*) versus jaw length (*L_j*) and body mass (*M_b*)

Group	<i>N</i>	<i>r</i> ²	<i>P</i>	Slope	Lower 95% CI	Upper 95% CI	Intercept	Lower 95% CI	Upper 95% CI
log ₁₀ chew cycle duration (<i>T_c</i>) versus log ₁₀ jaw length (<i>L_j</i>)									
Nonprimates	43	0.782	<0.001	0.514	0.4435	0.5949	-1.452	-1.612	-1.292
Primates	36	0.566	<0.001	0.583	0.4641	0.7318	-1.435	-1.67	-1.199
Anthropoids	23	0.679	<0.000	0.558	0.4328	0.7199	-1.379	-1.643	-1.115
Strepsirrhines	13	0.062	0.41	0.515	0.281	0.9423	-1.345	-1.878	-0.811

F-values measure probability that slope values differ from hypothesized slope at the top of the column.

mandibles than other mammals and anthropoids have shorter mandibles than strepsirrhines. Lemurids and humans deviate notably from these scaling trends: lemurids have low mandibular mass for their mandible length, and humans have high mass for their length.

The jaw muscle lever arms measured here, predominantly in parasagittal planes, are isometric with jaw length in all but two cases: across anthropoids temporalis lever arm scales with positive allometry against jaw length (slope, 1.123) and medial pterygoid lever arm scales with slight negative allometry against jaw length (slope, 0.925). Anthropoids and strepsirrhine lever arms scale with common slopes and there is only one elevation difference: anthropoids have a shorter medial pterygoid lever arm for their jaw length than strepsirrhines. Averaging the scaling relationships across lever arms of all three muscles yields slope values of 0.998, 0.996, and 0.947 for Primates, Anthropoidea, and Strepsirrhini, respectively.

Analysis of published data (Anapol et al., 2008) suggests isometry of muscle belly length to jaw length ($L_m \propto L_j^{1.0}$) and positive allometry of jaw elevator muscle RPCA (A_e) to mandible length (L_j) (where isometry = $A_e \propto L_j^{2.0}$ (lower-upper 95% CI); primates, $A_e \propto L_j^{2.5(2.1-3.1)}$; prosimians, $A_e \propto L_j^{2.9(1.5-5.7)}$; anthropoids $A_e \propto L_j^{2.5(2.0-3.1)}$).

Scaling of chew cycle duration

Table 3 presents the scaling relationships between chew cycle duration (*T_c*) and jaw length (*L_j*) across non-

primate mammals, anthropoid primates, and strepsirrhines. The best fit SMAs for primates, anthropoids, and nonprimate mammals are compared in Figure 2. Chew cycle duration increases with jaw length as $T_c \propto L_j^{0.514}$ across nonprimate mammals, as $T_c \propto L_j^{0.583}$ across primates as a whole and as $T_c \propto L_j^{0.558}$ across anthropoid primates. Across strepsirrhines, $T_c \propto L_j^{0.515}$, similar to the values for anthropoids and nonprimate mammals, but the correlation is not significant. Obvious departures from the general primate scaling trend explain the lack of a correlation between *T_c* and *L_j* among strepsirrhines (see Fig. 2). Most notably, *Loris* and *Nycticebus* fall above the primate SMA lines, with long cycle durations for their body size, whereas the lemurids (*Eulemur*, *Lemur*, and *Propithecus*) have shorter cycle durations than expected for their body size or jaw length.

These slope estimates for primates and nonprimates are not significantly different but primates have longer cycle durations than nonprimates of similar mandible lengths (WALD statistic, 25.646; df, 1; *P* < 0.001) (difference, 0.143; std error; 25.646; df, 1; *P* < 0.001) a relationship that persists among primate suborders: slope estimates for nonprimates and anthropoids are not significantly different (WALD statistic, 32.655; df, 2; *P* < 0.001). The nonprimate elevation is also significantly different from that of anthropoids (difference, 0.156; std error; 32.530; df, 1; *P* < 0.001). Chew period and jaw length are not correlated among strepsirrhines, so the primate slope is driven primarily by anthropoids.

Evaluating the models

Table 4 summarizes the scaling exponents (expressed in terms of L_j) used to make predictions regarding the scaling of $T_c \propto L_j$ under three iterations of the *Spring Model*. (The scaling of $T_c \propto L_j$ predicted by the pendulum model is not included in Table 3, but is $T_c \propto L_j^{0.5}$.) In Figure 3, the SMAs for anthropoids and primates as a whole are presented, along with the lines corresponding to the various models. Figure 4 presents the sums of the triangle areas between the various lines and each of the data points, a number analogous to the standard error of the estimate for least squares regression.

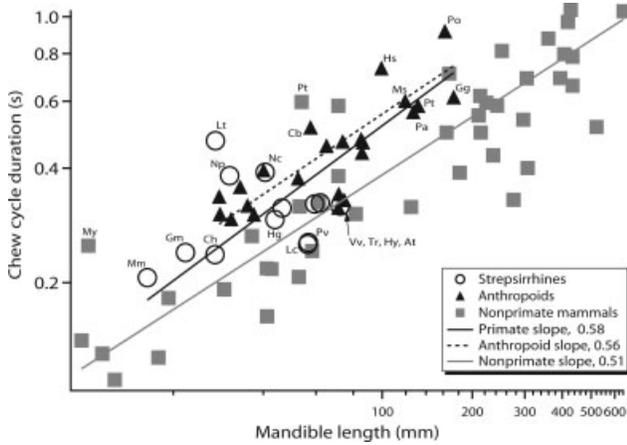


Fig. 2. Bivariate plot of chew cycle duration (T_c) against jaw length (L_j). Standardized major axes (SMAs) for nonprimate mammals, primates, and anthropoids are included. Key: At, *Ateles paniscus*; Cb, *Cebus apella*; Ch, *Cheirogaleus major*; Gg, *Gorilla gorilla*; Gm, *Galago moholi*; Hg, *Hapalemur griseus*; Hs, *Homo sapiens*; Hy, *Hylobates concolor*; Lc, *Lemur catta*; Lt, *Loris tardigradus*; Mm, *Microcebus murinus*; Ms, *Mandrillus sphinx*; My, *Myotis*; Nc, *Nycticebus coucang*; Np, *Nycticebus pygmaeus*; Pa, *Papio papio*; Po, *Pongo pygmaeus*; Pt, *Pteropus*; Pt, *Pan troglodytes*; Pv, *Propithecus verreauxi*; Tr, *Trachypithecus francoisi*; Vv, *Varecia variegata*.

The proportionality predicted by the Pendulum Model, $T_c \propto L_j^{0.5}$, is closest to the observed best fit SMA line for primates as a whole, for anthropoids, and for strepsirrhines (see Fig. 3). None of these SMA lines differs significantly from the predicted slope of 0.5 (nonprimates, $F, 0.137, P, 0.714$; primates, $F, 1.85, P, 0.183$; anthropoids, $F, 0.796, P, 0.382$; strepsirrhines, $F, 0.01, P, 0.923$).

The proportionality of T_c and L_j predicted by the *Spring-Empirical Model* was estimated using the scaling exponents in Table 2 and the scaling exponents for $A_e \propto L_j$ calculated from the data set of Anapol et al. (2008). These values were entered into Eq. (5) to calculate the scaling of chew cycle duration relative to jaw length predicted by assuming (i) that the contribution of the jaw muscles to the natural frequency of the feeding system is captured by modeling the muscles as springs and (ii) that the morphological variables scale as documented above. Under this *Spring-Empirical Model*, the predicted proportionality across all primates is $T_c \propto L_j^{0.824}$, outside the 95% confidence limits of the best fit SMA, but near its upper limit (see Fig. 2). The *Spring-Spencer Model* incorporates the scaling exponents documented here except for the scaling of $b \propto L_j$ in the denominator, which was assigned the exponent 1.035 presented by Spencer (1999), rather than the 0.999 documented here (Table 2). The *Spring-Spencer Model* predicts a proportionality of $T_c \propto L_j^{0.788}$ for all primates, marginally different from the *Spring-Empirical Model*, and also outside the 95% confidence limits of the best fit SMA (see Fig. 3). The chewing period scaling predicted by the *Spring-Isometry Model*, i.e., assuming overall geometric similarity in all feeding system components ($M_j \propto L_j^3$; $A_e \propto L_j^2$; $L_m \propto L_j^1$; $b \propto L_j^1$), is also presented in Table 3. This yields a predicted proportionality of $T_c \propto L_j^{1.0}$, well outside the 95% confidence limits of the best fit SMA (see Fig. 3).

DISCUSSION

What determines chew cycle duration?

The data presented here demonstrate marked deviation of strepsirrhine primates from the scaling trends characterizing anthropoid primates and nonprimate mammals. Indeed, strepsirrhines do not show significant correlations between chew period and either jaw length

TABLE 4. Exponents used in iterations of Spring model

	v	w	x	y	z	ϕ	Best fit SMA	Lower 95%	Upper 95%
Source of exponent	$M_j \propto L_j^v$	L_j^w	$A_e \propto L_j^x$	$L_m \propto L_j^y$	$b \propto L_j^z$	$T_c \propto L_j^\phi$			
<i>Spring-Empirical</i>									
Primates	3.147	2	2.5	1	0.999	0.824	0.583	0.4641	0.7318
Anthropoids	3.102	2	2.5	1	0.996	0.805	0.558	0.4328	0.7199
Strepsirrhines	2.924	2	2.9	1	0.947	0.565	0.515	0.281	0.9423
<i>Spring-Spencer</i>									
Primates	3.147	2	2.5	1	1.035	0.788	0.583	0.4641	0.7318
Anthropoids	3.102	2	2.5	1	1.035	0.766	0.558	0.4328	0.7199
Strepsirrhines	2.924	2	2.9	1	1.035	0.477	0.515	0.281	0.9423
<i>Spring-Isometry</i>									
Primates	3	2	2	1	1	1	0.583	0.4641	0.7318
Anthropoids	3	2	2	1	1	1	0.558	0.4328	0.7199
Strepsirrhines	3	2	2	1	1	1	0.515	0.281	0.9423

The scaling exponents of the morphological variables versus L_j listed in the cells above are keyed to the formula below via the letters at the top of each column. The best fit SMA and its 95% confidence limits are presented for comparison with ϕ .

$$T_c = 2\pi \sqrt{\frac{L_j^v L_j^w}{L_j^z \left(\frac{L_j^x}{L_j^y}\right)^2}} = T_c \alpha L_j^\phi$$

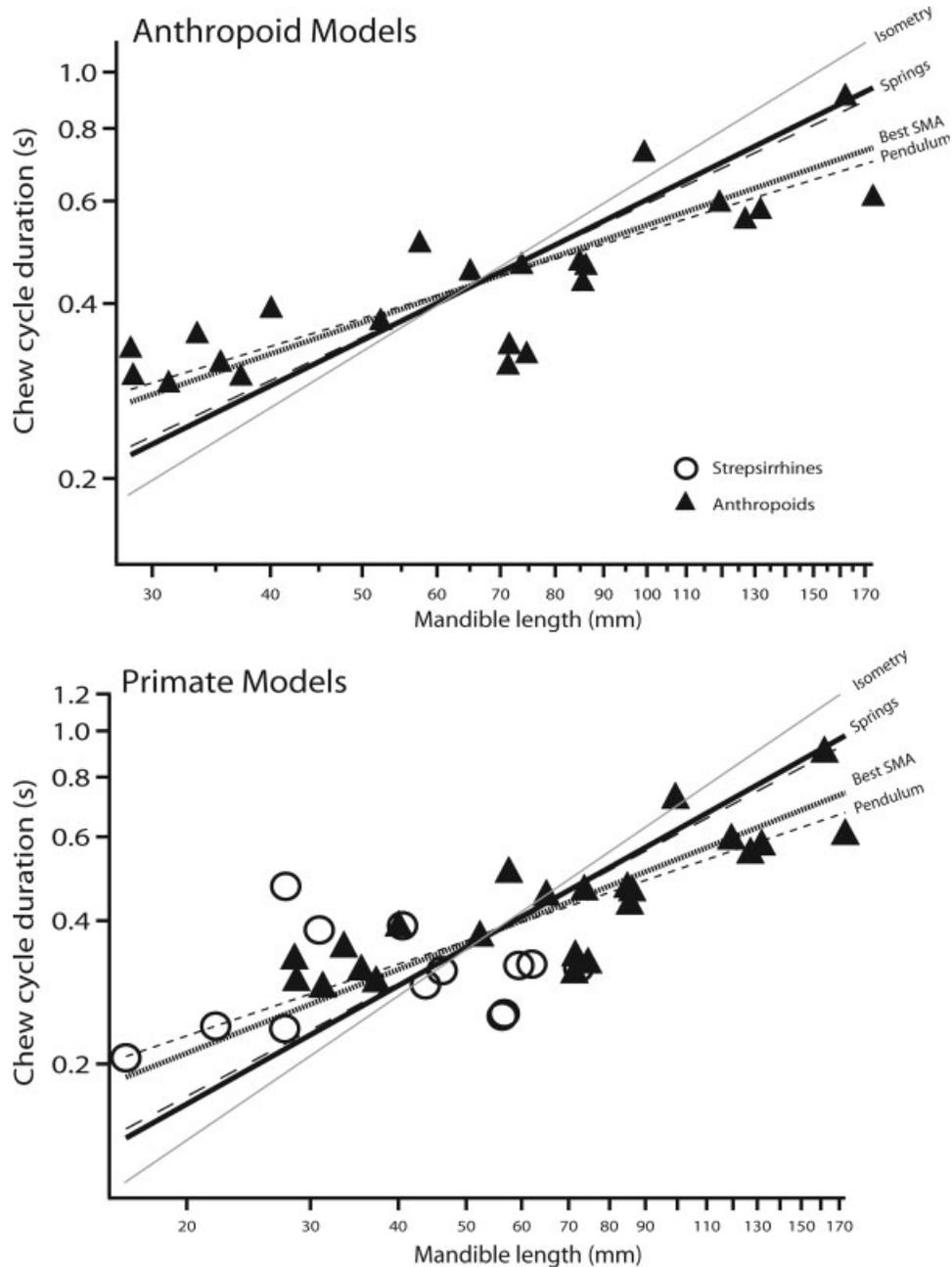


Fig. 3. Bivariate plots of chew cycle duration (T_c) versus mandible length (L_j) in anthropoids only (top) and primates (bottom). The lines representing the different models evaluated in this paper are added to the plots. Solid “Springs” line is the *Spring–Empirical Model*; dashed “Springs” line is the *Spring–Spencer Model*. Slopes correspond to exponent e in Table 4.

or body mass. Consequently, strepsirrhines are excluded from discussions of the determinants of primate chew cycle duration: possible reasons for their divergence from the general trends are presented below.

The scaling of $T_c \propto L_j$ predicted by the pendulum model falls within the 95% confidence limits of the proportionality suggested by our data, but the scaling predicted by the spring model falls outside (Figs. 3 and 4; Table 4). Although the gravity-driven pendulum is not a realistic model of the mammal chewing system, the relationship predicted by the pendulum model is closest

to the observed relationships. As Druzinsky (1993, p 433) noted: “one can make a reasonable estimate of the ‘natural frequency’ of the masticatory system using only the length of the jaw . . .” Why does the pendulum model perform the best out of all the models evaluated if it is biomechanically unrealistic? In the simple pendulum model, pendular oscillation is driven by the constant, g , in the denominator, and is resisted by the moment of inertia of the pendulum, which, with constant shape, is determined by the pendular length in the numerator raised to the power of 0.5. Any incorporation into the numerator

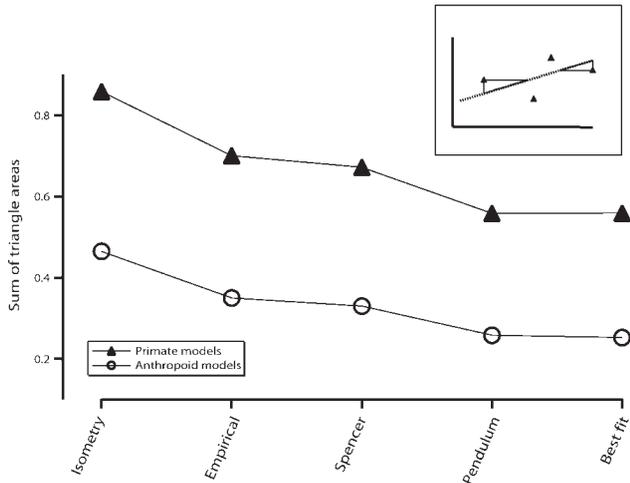


Fig. 4. Plot of triangle areas (y-axis) between data points and lines representing functions listed on x-axis. Triangle areas, diagrammed in inset, were calculated using Heron's formula, and represent an SMA analog of the standard error of the estimate in a least-squares regression.

of factors impacting the moment of inertia of the system will not affect the predicted scaling of $T_p \propto L_p$ if these factors also impact the torques in the denominator appropriately. Specifically, the success of the pendular model in predicting scaling of chew period suggests that if the moment of inertia of the chewing system scales $\propto L_j^n$, the torques driving mandibular oscillation during chewing scale $\propto L_j^{n-1}$. The spring model predicts exponents significantly higher than the observed exponent of ~ 0.5 ; i.e., $T_c \propto L_j^{\sim 0.8}$ using empirical scaling relationships. Which of the components of the model is most likely to be in error?

Moments of inertia in the numerator

The spring models estimate the moment of inertia of the system as $M_j L_j^2$ and some of the variance in T_c with L_j appears to be due to the fact that this numerator does not fully quantify variation in rotational inertia of the system. Jaw mass scales isometrically to jaw length across primates as a whole, as captured by the scaling exponents in Table 2, but there is variation about the best fit line. Animals that have heavy or short mandibles for their length also exhibit longer or shorter cycle durations (respectively) than predicted. Specifically, lemurs have lighter mandibles for their jaw length than predicted and chew with shorter cycle lengths than predicted, whereas *Homo* and *Cebus* have heavier mandibles for their length than expected and chew with longer cycle lengths than expected (see Fig. 5).

The impact of rotational inertia on scaling of T_c may also be revealed by differences between anthropoids and strepsirrhines in T_c scaling. The SMA line describing the relationship between T_c versus L_j in anthropoids is transposed above that of nonprimate mammals and the majority of strepsirrhines, indicating that anthropoids have comparatively longer cycle lengths for their mandible lengths (see Fig. 3). A plot of mandible mass against mandible length reveals that anthropoids and strepsir-

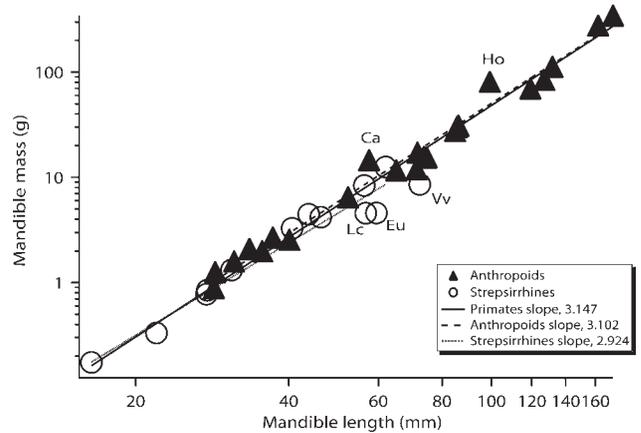


Fig. 5. Bivariate plot of mandible mass (M_j) (g) versus mandible length (L_j) (mm). Key: Ca, *Cebus apella*; Eu, *Eulemur fulvus*; Ho, *Homo sapiens*; Lc, *Lemur catta*; Vv, *Varecia variegata*. Note that *Homo* and *Cebus* have heavier mandibles than predicted for their mandible lengths, whereas lemurs have lighter mandibles.

rhines cluster very tightly together about a line of isometry. SMA-“ANCOVA” reveals anthropoids as a whole to have heavier mandibles for their length than strepsirrhines, but the elevational difference is minor (0.097) and barely significant ($P = 0.048$). Clearly the lemurs with light mandibles are driving this result, and removing them from the strepsirrhine sample renders the anthropoid/strepsirrhine elevations not significantly different.

A better explanation for the differences between anthropoids and strepsirrhines in chew cycle duration scaling may be differences in distribution of mass relative to the axis of rotation related to symphyseal morphology. The estimate of rotational inertia used here (i.e., $M_j L_j^2$) assumes that the mass of the mandible is concentrated at the center of mass and that the distance from the center of mass to the rotational axis scales proportional to $L_j^{1.0}$. Intertaxon differences in the distribution of mass relative to the rotational axis, or in the position of the rotational axis, could produce taxonomic differences in intercept or elevation of SMA lines. Anthropoids have relatively anteroposteriorly and dorsoventrally thicker symphyseal regions than strepsirrhine primates (Ravosa, 1991), suggesting that at equivalent jaw lengths, the centers of mass of anthropoid mandibles may lie further from the axis of rotation than in strepsirrhines. This would increase the moment of inertia of the mandible in anthropoids and may account for their longer chewing cycle durations.

In a similar vein, negative allometry of rotational inertia relative to $M_j L_j^2$ within anthropoids might explain why the *Spring-Empirical Model* overestimates T_c at large body sizes. This would occur if the distance from the center of rotation of mandible to the center of mass scaled with negative allometry relative to L_j . These considerations suggest that better data are needed on the rotational inertia and locations of the instantaneous centers of rotation and centers of mass of primate chewing systems (Zhang et al., 2001).

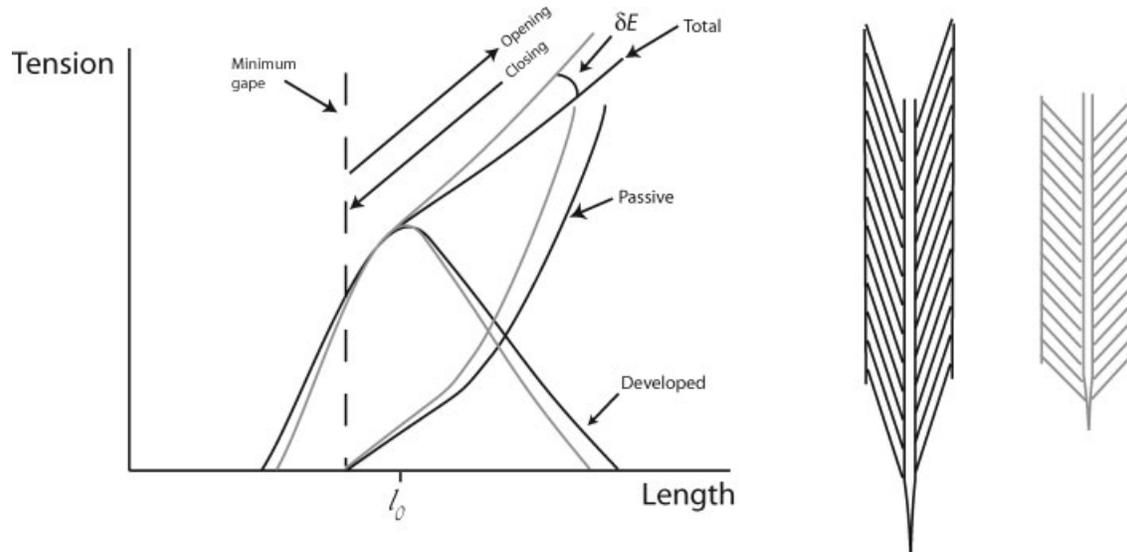


Fig. 6. Diagram illustrating impact of decreasing relative fiber length on length-tension curves in a pinnate muscle. Figure illustrates functions describing normalized tension against normalized muscle length. Increasing pinnation (represented by gray traces) associated with decreased relative fiber length produces increased overall muscle stiffness (δE). The total muscle tension is hypothesized to be approximately linear across the range of opening and closing.

Torques in the denominator

Predictions of the *Spring-Empirical Model* might also deviate from the observed because of errors in the scaling coefficients for the variables used to estimate $k = EA_e/L_m$. Our data suggest that $L_m \propto L_j^{1.0}$ with high correlation coefficients, making it unlikely that errors in muscle length scaling are responsible. We used the scaling of RPCA of primate jaw elevator muscles documented by Anapol et al. (2008) to estimate A_e : if the scaling exponents for $A_e \propto L_j$ were even more strongly positively allometric than the 2.5 observed for primates and anthropoids (i.e., in the range of 2.9–3.0) the *Spring-Empirical Model* would accurately predict chewing frequency. Such strong allometry of jaw elevator muscle RPCA in primates seems unlikely to us, but this hypothesis can only be evaluated once better data are available. McMahon (1975, 1984) assumed constant E across different animal sizes; however, both passive and active muscle stiffness are influenced by muscle architecture (Gans and Bock, 1965). For example, differences in pinnation between gastrocnemius and semimembranosus have been shown to be associated with differences in muscle stiffness, both in the passive component associated with connective tissues and in the active component of the muscle, due to decreasing relative fiber lengths (Walmsley and Proske, 1981; Woittiez et al., 1983; Woittiez, 1984; Cui et al., 2007). Thus, decreases in relative fiber length with size in primate feeding systems would result in increased muscle stiffness and higher values of E (see Fig. 6). To evaluate this possibility, we examined the relationship of muscle fiber length relative to muscle belly length in our muscle architecture data set (Anapol et al., 2008) and found these measures to be isometric. At present, size-related changes in jaw muscle architecture cannot be said to explain the deviations of the *Spring-Empirical Model*. One possibility, which we are

unable to evaluate for lack of data, is that there are size-related differences in fiber types in primate chewing muscles, with an increasing proportion of fast-twitch fibers producing faster muscles. Better data on size-related changes in fiber types of primate jaw muscles are needed.

Spring-like properties of jaw muscles

Although the pendulum model better explains size-related changes in chew cycle durations than the *Spring-Empirical Model*, its lack of biomechanical realism leads us to reject the gravity-driven pendulum model. Moreover, examination of Figure 3 suggests that the *Spring-Empirical Model* provides a reasonable estimate of the scaling of chew cycle periods across anthropoids and primates as a whole. Here we marshal arguments in support of using spring constants to model the contribution of jaw muscles to the natural frequency of the masticatory system. Springs are mechanical elements that, when they are stretched, store elastic potential energy that is subsequently returned to generate movement and force in a magnitude proportional to their length. For the jaw elevator muscles to behave as springs, it is necessary that during opening they at least store potential energy associated with jaw opening as elastic strain energy in titin, cross-bridges, ligaments, tendons, and other connective tissue elements (Cavagna et al., 1980; Alexander, 1984, 1988a,b, 1990; Lindstedt et al., 2002). Intuitively, there seems little doubt that some strain energy is stored in the jaw elevator muscles during jaw depression then recovered during jaw elevation. This can be appreciated by feeling the force exerted at the teeth by opening one's own jaw wide enough to insert two fingers between upper and lower incisors,

then relaxing the jaw depressors. Direct evidence in support of this hypothesis comes from calculations of the passive components of length tension curves in the masseter of pigs and opossums, which indicate that passive tension increases rapidly during jaw opening (Thexton and Hiiemae, 1975; Anapol and Herring, 1989).

However, observations on the masseters of several mammal species suggest that this muscle reaches its optimal length not in occlusion, but at larger gapes. This is true in rat (Nordstrom and Yemm, 1974), opossum (Thexton and Hiiemae, 1975), cat (MacKenna and Turker, 1978), pig (Anapol and Herring, 1989), rabbit (Weijs et al., 1989), and humans (van Eijden et al., 1995). Thus, the energy stored in the jaw elevator muscles is not sufficient to drive the lower teeth into occlusion even in the absence of food, let alone in the presence of a bolus. Rather, during the slow-close/power stroke phase of the chewing cycle muscle activity must increase to continue tooth movement through the food bolus. We hypothesize that spring-like behavior of jaw muscles during slow-close/power stroke phase might be expected because it confers advantages for motor control. This advantage derives from another property of simple springs: a constant relationship between the force generated by it and its change in length; i.e., its stiffness. J.C. Houk has long argued that an important function for skeletomotor reflexes is maintenance of relatively constant stiffness of the muscles, simplifying motor control tasks and providing “a spring-like interface between the body and its environment” (Houk, 1979, p 112). The ability to maintain relatively constant muscle stiffness enables muscles to operate within restricted portions of their length–tension curves, enhancing stability and predictability of muscle movements (McMahon 1984).

During the slow-close/power stroke phase of the chewing cycle, high forces are applied between the teeth over relatively small displacements and, arguably, very precise control of both force and displacement is required for efficient mastication while minimizing the risk of tooth breakage and wear. Although the jaw unloading and jaw opening reflexes can protect the teeth with little delay (Orchardson and Cadden, 1998; Türker, 2002), intrinsic muscle stiffness acts as an important low-pass filter to jaw movements (Wang and Stohler, 1991), just as it does in muscles in other systems (Nichols and Houk, 1976; Huyghues-Despointes et al., 2003; Nishikawa et al., 2007). Mammalian jaw muscles are expected a priori to have a comparatively constant slope in the length–tension curve because of their highly pinnate architecture (McMahon, 1984). Moreover, the ability to control stiffness (Proeschel and Morneburg, 2002; Shiller et al., 2002, 2005), perhaps to avoid damage to the teeth when eating food with different properties (Burdet et al., 2001), suggests that Houk’s hypothesis can reasonably be applied to the feeding system. Certainly the role of proprioceptors in controlling muscle activity during the power stroke of mastication is well documented (Hidaka et al., 1997; Masuda et al., 1997; Hidaka et al., 1999; Komuro et al., 2001; Tsuboi et al., 2003).

Of course, if it is realistic to model jaw muscles using spring constants, it might also be the case that cyclic storage and recovery of strain energy provides significant energy savings during mastication. The benefits of cyclic energy storage in connective tissue elements of skeletal muscles powering locomotion are well documented (Alexander, 1984, 1988a,b, 1990, 1991a,b; Ahlborn et al.,

2006), but the significance of this for mastication has received little consideration. This deserves further attention.

Why are strepsirrhines different?

Strepsirrhines do not exhibit significant correlations between chew cycle length and mandible length. As noted above, this is because lemurs tend to chew faster than expected for their mandible lengths and lorids tend to chew slower. The biomechanical explanation for the faster chewing in lemurs may lie in a reduced rotational inertia associated with lighter mandibles [and possibly longer muscle fiber lengths (Perry and Hartstone-Rose, 2008)], but the complimentary explanation does not apply to lorids. *Loris*, *Nycticebus pygmaeus*, and *N. coucang* are characterized by relatively slow arboreal quadrupedalism (Nekaris and Stevens, 2007) and low metabolic rates, and it is tempting to suggest that their long chew cycle durations are related to a systemic slow-down in activity. It is also important to note that scaling of chew cycle duration in strepsirrhines can only be estimated over a limited size range compared with that of anthropoids. These unavoidable taxonomic constraints might also account for the lack of a correlation between jaw length and chew cycle duration in strepsirrhines.

Torque model

Reviewers of this article have questioned whether it is realistic to model the chewing muscles using spring constants. We have reviewed the evidence in support of the above hypothesis. An alternate model might be a simple *Torque Model* that does not include spring constants in the denominator, as in Eq. (5), but simple torques based on A_e and b :

$$T_c = 2\pi \sqrt{\frac{M_j L_j^2}{A_e b_e}} \quad (6)$$

It is important to note that when E is assumed to remain constant across body sizes, the *Spring* and the *Torque Models* predict identical scaling relationships between T_c and L_j . This is because, although the term b has an exponent of 2.0 in the *Spring Models* and 1.0 in the *Torque Model*, both L_m and b are proportional to $L_j^{1.0}$, and L_m appears in the denominator of $k = EA_e/L_m$ in the *Spring Models* [Eq. (5)]. We cannot provide any evidence at present to choose between these models, but the evidence for spring-like behavior of primate jaw muscles leads us to prefer that model.

The importance of the tongue

A final note is necessary on the importance of considering the role of the tongue in determining the natural frequency of primate jaw movements. The mass of the tongue probably acts on the mandible through various attachments, such as through m. genioglossus, or through the mylohyoid “sling,” and must therefore influence the moment of inertia of the chewing system. Moreover, during the jaw cycle the tongue cycles forward and back to retrieve and position the food bolus between the

teeth and the timing of jaw movements appears to be dependent on the timing, as well as the pattern (Hiemae et al., 1995; Hiemae and Palmer, 1999), of tongue movements. Incorporation of the tongue into models of the natural period of the chewing system may account for discrepancies between observed and estimated scaling of chew cycle duration in primates.

CONCLUSIONS

Our data suggest that chew cycle duration increases with body size in primates in a manner predicted by a simple pendulum model of the feeding system. However, a gravity-driven pendulum model is biomechanically unrealistic. A model of jaw oscillation that uses spring constants to model the contribution of jaw elevator muscles to the natural frequency of the system generates the next best estimate of the scaling of chew cycle duration relative to jaw length documented here. Moreover, it is defensible on biomechanical grounds. Potential energy associated with jaw opening stored as elastic strain energy in ligaments, tendons, and other connective tissue elements is certainly recovered upon jaw elevation, but the rate of jaw elevation is modulated by the central nervous system to bring the teeth into contact with the food and each other in a manner that will not damage them (Lund and Kolta, 2006). Thus, the intrinsic properties of the muscles predict spring-like behavior of the jaw elevator muscles during opening and fast close phases of the jaw cycle, but modulation of stiffness by the central nervous system maintains spring-like properties of jaw muscles during the slow-close/power stroke phase. The importance of jaw muscle function in determining chew cycle scaling emphasizes that the positive allometry of these jaw elevator muscle physiologic cross-sectional areas is important in minimizing the increases in cycle duration accompanying increases in feeding system size.

Our data also suggest that the scaling of the inertial properties of the mandible are important in determining the scaling of chew cycle duration in primates. Lemurids have light mandibles for their length and chew more quickly than expected; *Homo* and *Cebus* have heavy mandibles for their length and chew more slowly than expected; anthropoids have longer chew cycle durations than nonprimate mammals with similar mandible lengths, possibly due to their enlarged symphyses, which increase the moment of inertia of the mandible. Further work on the inertial properties of jaws and jaw muscles in primates are clearly needed.

Finally, it is noteworthy that the chewing system may resemble the locomotor system in several important respects, reflecting common motor control and biome-

chanical strategies. In both systems afferent information is used to modulate the resonant frequency of the musculoskeletal system through interactions between reflexes and the intrinsic, passive properties of muscle tissue that minimize variance in muscle stiffness (Nishikawa et al., 2007; Ross et al., 2007a,b).

ACKNOWLEDGMENTS

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APPENDIX

Derivation of spring constant, k , for muscle

This derivation is an expansion of the equation in Figure 3A of McMahon (1975). Note that the x -axis in McMahon's Figure 3A should be labeled $\Delta x/l$.

$$k = \frac{\Delta F}{\Delta x} \quad (\text{A1})$$

If

$$E = \frac{\Delta F/A}{\Delta x/l} \quad (\text{A2})$$

then

$$\Delta F = \frac{EA\Delta x}{l} \quad (\text{A3})$$

Substituting (A3) into (A1) yields

$$k = \frac{EA\Delta x}{l\Delta x}$$

which simplifies to

$$k = \frac{EA}{l} \quad (\text{A4})$$

TABLE A1. Means of morphometric variables and descriptive statistics for chew period used in inter-specific scaling analyses

Species	Cycle length (s)					Body mass (kg)	Mandible length (mm)	Mandible mass (g)	Masseter lever (mm)	Temporalis lever (mm)	Medial pterygoid lever (mm)
	N	Mean	Std. Dev.	Minimum	Maximum	Mean	Mean	Mean	Mean	Mean	Mean
<i>Allenopithecus nigroviridis</i>	275	0.472	0.1458	0.231	1.122	4.825					
<i>Alouatta caraya</i>	69	0.468	0.1753	0.297	1.023	5.375	86.18	31.16	47.76	25.88	30.70
<i>Aotus sp.</i>	692	0.395	0.1447	0.179	1.305	0.794 ^a	40.08	2.56	20.57	7.99	16.46
<i>Ateles sp.</i>	696	0.315				8.775 ^b	71.31	12.00	36.60	17.07	28.98
<i>Callicebus donacophilus</i>	44	0.302	0.0674	0.165	0.462	0.991	37.22	2.69	19.56	8.86	13.10
<i>Callimico goeldi</i>	572	0.294	0.0484	0.198	0.627	0.484	31.22	1.59	17.92	6.91	13.55
<i>Callithrix geoffroyi</i>	84	0.337	0.0653	0.198	0.561	0.359	28.47	0.89	16.00	8.56	13.12
<i>Cebus apella</i>	115	0.512	0.1321	0.231	0.957	3.650	57.53	14.58	34.18	18.05	24.86
<i>Cercopithecus neglectus</i>	166	0.470	0.1607	0.231	1.089	5.450	73.71	15.80	34.66	19.28	27.76
<i>Cheirogaleus medius</i>	264	0.237	0.0516	0.165	0.495	0.283	27.56	0.78	14.46	8.64	9.67
<i>Chlorocebus aethiops</i>	151	0.458	0.1138	0.285	0.941	4.240	65.05	11.65	33.31	19.63	24.06
<i>Colobus guereza</i>	159	0.439	0.1297	0.099	0.858	13.500	85.56	30.11	45.77	27.16	31.03
<i>Daubentonia madagascariensis</i>	112	0.324	0.0752	0.165	0.594	2.555	62.02	12.56	44.55	25.62	25.63
<i>Eulemur fulvus</i>	413	0.322	0.0994	0.231	0.944	2.038	59.42	4.59	25.26	15.00	16.96
<i>Eulemur fulvus albifrons</i>	78	0.243	0.0412	0.165	0.363	2.038					
<i>Eulemur mongoz</i>	69	0.227	0.0406	0.165	0.396	1.620					
<i>Eulemur fulvus collaris</i>	12	0.259	0.0418	0.198	0.330	2.050					
<i>Eulemur coronatus</i>	136	0.197	0.0327	0.132	0.297	1.655					
<i>Eulemur fulvus sanfordi</i>	44	0.205	0.0281	0.165	0.297	1.830					
<i>Galago moholi</i>	43	0.240	0.0526	0.165	0.396	0.187	21.98	0.33	11.86	4.98	9.32
<i>Gorilla gorilla</i>	160	0.615	0.1229	0.165	1.122	71.500 ^c	173.37	346.26	88.93	49.38	69.29
<i>Hapalemur griseus</i>	41	0.293	0.0548	0.198	0.528	0.987	43.74	4.47	23.93	12.13	13.35
<i>Homo sapiens</i>		0.733				60.207	99.31	80.90	60.94	36.19	46.81
<i>Hylobates concolor</i>	134	0.330	0.0627	0.264	0.594	7.705	74.60	15.51	37.35	23.20	27.42
<i>Lemur catta</i>	113	0.255	0.0713	0.165	0.627	2.210	56.64	4.56	24.15	12.90	17.56
<i>Leontopithecus rosalia</i>	68	0.319	0.0569	0.198	0.429	0.609	35.44	1.99	19.77	9.40	15.28
<i>Loris tardigradus</i>	27	0.472	0.0813	0.363	0.693	0.264	27.66	0.85	15.17	7.73	9.95
<i>Macaca mulatta</i>	158	0.476				8.800	84.87	27.70	41.07	23.34	29.15
<i>Mandrillus leucophaeus</i>	238	0.601	0.1736	0.198	1.287	15.000	119.35	70.40	53.85	27.85	41.65
<i>Microcebus murinus</i>	46	0.206	0.0313	0.165	0.297	0.061 ^d	16.37	0.17	9.54	4.02	6.75
<i>Nycticebus coucang</i>	27	0.390	0.0600	0.297	0.528	0.679	40.60	3.27	21.77	12.85	17.31
<i>Nycticebus pygmaeus</i>	89	0.382	0.0576	0.264	0.594	0.376	30.86	1.31	16.52	9.51	10.93
<i>Otolemur crassicaudatus</i>	66	0.314	0.0470			1.110	46.20	4.19	28.60	13.00	17.96
<i>Pan troglodytes</i>	82	0.584	0.1766	0.297	1.188	52.750	131.79	112.84	64.93	40.77	50.89
<i>Papio papio</i>	62	0.562	0.0727	0.429	0.759	12.100	127.02	84.40	53.51	33.65	44.22
<i>Pithecia pithecia</i>	273	0.376	0.0793	0.198	0.891	1.760	52.32	6.48	27.55	12.32	22.72
<i>Pongo pygmaeus</i>	251	0.916	0.3008	0.330	3.663	57.150	162.04	278.94	77.84	54.40	66.53
<i>Propithecus tattersalli</i>	54	0.270	0.0378	0.231	0.429	3.390					
<i>Propithecus verreauxi</i>	127	0.252	0.0451	0.165	0.462	3.250 ^e	56.27	8.36	29.64	13.97	18.37
<i>Saguinas oedipus</i>	637	0.303	0.0631	0.165	0.858	0.411	28.64	1.26	14.84	7.59	13.08
<i>Saimiri sciureus</i>	67	0.357	0.0630			0.721	33.46	2.09	17.78	10.43	15.24
<i>Trachypithecus francoisi</i>	762	0.342	0.0886	0.132	0.990	7.525	71.53	17.18	40.76	18.78	28.89
<i>Varecia variegata rubra</i>	266	0.318	0.0634	0.165	0.528	3.490	72.32	8.54	28.97	17.66	19.48

Bold values from literature and our data on *Ateles paniscus* pooled with mean data from *Ateles* sp. from Hiimeae and Kay (Hiimeae and Kay, 1973) and our data on *Macaca mulatta* pooled with data from Luschei and Goodwin (Luschei and Goodwin, 1974).

^a *A. nancymae*.

^b *A. paniscus*.

^c *G. gorilla gorilla*.

^d *M. myoxinus*.

^e *P. verreauxi verreauxi*.

TABLE A2. Mean chew cycle durations, body masses and mandible lengths for non-primate mammals

Genus	species	Body mass (kg)	Cycle duration (s)	Mandible length (mm)	Cycle duration sources
<i>Alces</i>	<i>alces</i>	309	0.513	521.40	(Gross et al., 1993)
<i>Ammotragus</i>	<i>lervia</i>	66	0.584	242.40	(Fortelius, 1985)
<i>Aplodontia</i>	<i>rufa</i>	0.58	0.207	52.60	(Druzinsky, 1993)
<i>Axis</i>	<i>axis</i>	53	0.496	213.56	(Gross et al., 1993)
<i>Bison</i>	<i>bonasus</i>	300	0.969	418.33	(Fortelius, 1985)
<i>Blarina</i>	<i>brevicauda</i>	0.0215	0.111	12.74	(Dötsch, 1986)
<i>Bos</i>	<i>grunniens</i>	250	0.876	394.40	(Fortelius, 1985)
<i>Bos</i>	<i>taurus</i>	512.135	0.793	359.73	(Druzinsky, 1993; Gross et al., 1993)
<i>Camelus</i>	<i>bactrianus</i>	500	1.042	427.39	(Fortelius, 1985)
<i>Canis</i>	<i>familiaris</i>	36.29	0.316	124.90	(Druzinsky, 1993)
<i>Capra</i>	<i>ibex</i>	40	0.709	167.60	(Fortelius, 1985)
<i>Capra</i>	<i>falconieri</i>	64	0.619	212.65	(Fortelius, 1985)
<i>Capra</i>	<i>hircus</i>	17.5	0.389	181.73	(de Vree and Gans, 1976)
<i>Cavia</i>	<i>porcellus</i>	0.9	0.163	41.20	(Byrd, 1981)
<i>Cervus</i>	<i>eleaphus</i>	266	0.536	296.27	(Gross et al., 1993)
<i>Crocidura</i>	<i>russula</i>	0.012	0.169		(Dötsch, 1986)
<i>Cynomys</i>	<i>ludovicianus</i>	0.75	0.217	42.58	(Gross et al., 1993)
<i>Dicrostonyx</i>	<i>groenlandicus</i>	0.05	0.127	17.83	(Gross et al., 1993)
Didelphis	virginiana	2.5	0.303	81.60	Mean ^a
<i>Equus</i>	<i>caballus</i>	650.91	0.785	433.20	(Druzinsky, 1993)
<i>Equus</i>	<i>hemionus</i>	210	0.797	406.76	(Fortelius, 1985)
<i>Equus</i>	<i>caballus</i>	432	0.659	433.20	(Gross et al., 1993)
Felis	sp.	3	0.325	61.40	Mean ^a
<i>Hemitragus</i>	<i>jemlahicus</i>	50	0.55	210.10	(Fortelius, 1985)
<i>Loxodonta</i>	<i>africana</i>	2812.27	1.034	642.00	(Druzinsky, 1993)
<i>Marmota</i>	<i>monax</i>	3.79	0.583	71.30	(Druzinsky, 1993)
<i>Mustela</i>	<i>putorius</i>	1.35	0.218	41.10	(Druzinsky, 1993)
<i>Myotis</i>	<i>lucifugus</i>	0.007	0.25	10.40	(Kallen and Gans, 1972)
<i>Neomys</i>	<i>fodiens</i>	0.0159	0.130	11.58	(Dötsch, 1986)
<i>Odocoileus</i>	<i>virginiana</i>	45	0.594	222.92	(Gross et al., 1993)
<i>Oreamnos</i>	<i>americanus</i>	60	0.813	251.15	(Fortelius, 1985)
Oryctolagus	cuniculus	2.46	0.242	58.30	Mean ^a
<i>Pedetes</i>	<i>capensis</i>	2.3	0.317	52.95	(Offermans and de Vree, 1990)
<i>Pteropus</i>	<i>giganteus</i>	0.48	0.597	53.70	(De Gueldre and De Vree, 1984)
<i>Rangifer</i>	<i>tarandus</i>	104	0.4	306.45	(Gross et al., 1993)
<i>Rattus</i>	<i>norvegicus</i>	0.2	0.192	29.60	(Weijs and Dantuma, 1975)
<i>Sorex</i>	<i>araneus</i>	0.0079	0.141	9.86	(Dötsch, 1986)
<i>Suncus</i>	<i>murinus</i>	0.0412	0.182	19.30	(Dötsch, 1986)
<i>Sus</i>	<i>scrofa</i>	22.3	0.33	275.00	(Herring and Scapino, 1974)
<i>Tapirus</i>	<i>terrestris</i>	272.16	0.689	304.40	(Druzinsky, 1993)
<i>Tayassu</i>	<i>tajacu</i>	27.2	0.496	164.09	(Gross et al., 1993)
<i>Tenrec</i>	<i>ecaudatus</i>	0.7	0.381	71.30	(Oron and Crompton, 1985)
<i>Tupaia</i>	<i>glis</i>	0.15	0.265	36.60	Mean ^a
<i>Ursus</i>	<i>arctos</i>	161	0.432	235.25	(Gross et al., 1993)

^a Mean values taken from Table A3.

TABLE A3. Source data for calculations of species means for nonprimate mammals

Genus	Species	Mass (kg)	Cycle duration (s)	Reference
<i>Oryctolagus</i>	<i>cuniculus</i>	2.500	0.277	(Weijs and Dantuma, 1981)
<i>Oryctolagus</i>	<i>cuniculus</i>	2.900	0.213	(Gross et al., 1993)
<i>Oryctolagus</i>	<i>cuniculus</i>	1.800	0.267	(Fortelius, 1985)
<i>Oryctolagus</i>	<i>cuniculus</i>	2.500	0.158	(Ardran et al., 1957)
<i>Oryctolagus</i>	<i>cuniculus</i>	2.500	0.267	(Yamada et al., 1993)
<i>Oryctolagus</i>	<i>cuniculus</i>	2.500	0.252	(Yamada and Yamamura, 1996)
<i>Oryctolagus</i>	<i>cuniculus</i>	2.500	0.261	(Kakizaki et al., 2002)
Oryctolagus	cuniculus	2.457	0.242	Mean
<i>Tupaia</i>	<i>glis</i>	0.150	0.238	(Hiemae and Kay, 1973)
<i>Tupaia</i>	<i>glis</i>	0.150	0.291	(Fish and Mendel, 1982; Hiemae and Crompton, 1971)
Tupaia	glis	0.150	0.265	Mean
<i>Didelphis</i>	<i>virginiana</i>	2.500	0.215	(Hiemae and Crompton, 1971)
<i>Didelphis</i>	<i>virginiana</i>	2.500	0.392	(Hiemae, 1978)
Didelphis	virginiana	2.500	0.303	Mean
<i>Felis</i>	<i>domesticus</i>	2.500	0.308	(Hiemae, 1978)
<i>Felis</i>	<i>catus</i>	3.500	0.342	(Thexton et al., 1980) ^a
Felis		3.000	0.325	Mean

^a Data estimated by digitizing data in Figure 3 of this reference.

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