

Allometry of Masticatory Loading Parameters in Mammals

MATTHEW J. RAVOSA,^{1*} CALLUM F. ROSS,² SUSAN H. WILLIAMS,³
AND DESTINY B. COSTLEY¹

¹Department of Pathology and Anatomical Sciences, University of Missouri School of
Medicine, Columbia, Missouri

²Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois

³Department of Biomedical Sciences, Ohio University College of Osteopathic Medicine,
Athens, Ohio

ABSTRACT

Considerable research on the scaling of loading patterns in mammalian locomotor systems has not been accompanied by a similarly comprehensive analysis of the interspecific scaling of loading regimes in the mammalian masticatory complex. To address this deficiency, we analyzed mandibular corpus bone strain in 11 mammalian taxa varying in body size by over 2.5 orders of magnitude, including goats, horses, alpacas, pigs, and seven primate taxa. During alert chewing and biting of hard/tough foods, bone-strain data were collected with rosette gauges placed along the lateral aspect of the mandibular corpus below the molars or premolars. Bone-strain data were used to characterize relevant masticatory loading parameters: peak loading magnitudes, chewing cycle duration, chewing frequency, occlusal duty factor, loading rate, and loading time. Interspecific analyses indicate that much as observed in limb elements, corpus peak-strain magnitudes are similar across mammals of disparate body sizes. Chewing frequency is inversely correlated with body size, much as with locomotor stride frequency. Some of this allometric variation in chewing frequency appears to be due to a negative correlation with loading time, which increases with body size. Similar to the locomotor apparatus, occlusal duty factor, or the duration of the chewing cycle during which the corpus is loaded, does not vary with body size. Peak principal-strain magnitudes are most strongly positively correlated with loading rate and only secondarily with loading, with this complex relationship best described by a multiple regression equation with an interaction term between loading rate and loading time. In addition to informing interpretations of craniomandibular growth, form, function, and allometry, these comparisons provide a skeleton-wide perspective on the patterning of osteogenic stimuli across body sizes. *Anat Rec*, 293:557–571, 2010. © 2010 Wiley-Liss, Inc.

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*Correspondence to: Matthew J. Ravosa, Department of Pathology and Anatomical Sciences, University of Missouri School

of Medicine, M303 Medical Sciences Building, One Hospital Drive DC055.07, Columbia, MO 65212. Fax: 573-884-4612. E-mail: ramosam@missouri.edu

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INTRODUCTION

Experimental data regarding the patterning of mechanical stimuli within and across organisms are critical for understanding the functional and evolutionary morphology of the vertebrate skeleton (Wake, 1992). A common assumption of many biomechanical analyses is that the form of a particular structure reflects a specific function, or perhaps that the morphology represents a compromise between several factors (Weibel et al., 1998). In the former case, prior work suggests that load-bearing limb (Biewener, 1982, 1983, 1993; Rubin and Lanyon, 1984; Lanyon and Rubin, 1985) and mandibular (Hylander, 1985; Hylander et al., 1991, 1998; Vinyard and Ravosa, 1998) elements appear broadly designed to exhibit maximum strength with a minimal amount of cortical bone. Further research indicates that this relationship is maintained during the ontogeny of an organism via a feedback mechanism of adaptive modeling and remodeling (Lanyon and Rubin, 1985; Biewener, 1991, 1993; Biewener and Bertram, 1993; Bouvier and Hylander, 1981, 1996). This, in turn, has led to several hypotheses regarding how loading parameters, skeletal safety factors, and load-bearing structures vary predictably with body size (Heglund et al., 1974; Alexander, 1977; Alexander et al., 1977; Biewener, 1982, 1983, 1993; Rubin and Lanyon, 1982, 1984; Hylander, 1985; Lanyon and Rubin, 1985; Biewener and Taylor, 1986; Heglund and Taylor, 1988; Hylander et al., 1998; Vinyard and Ravosa, 1998). Recent intraspecific research suggests links among loading rate, loading time, and peak-strain magnitudes in the mammalian mandible during mastication (Ross et al., 2007a) that have implications for understanding interspecific variation in masticatory form. However, in contrast to the locomotor apparatus, interspecific variation in mammalian masticatory loading parameters is poorly understood. With this in mind, the implications of these prior experimental analyses for the interspecific scaling of mandibular loading patterns are presented below.

Peak Loads and Strain Similarity

During the lifetime of an organism, its skeleton regularly encounters loading regimes that result in fatigue failure or microdamage to the cortical bone of which it is constructed. Modeling and remodeling of cortical bone counter such fatigue failure and thus maintain the structural integrity of a given skeletal element with respect to predominant loading patterns. This dynamic osteogenic process, termed functional adaptation (Lanyon and Rubin, 1985), is well documented by experimental analyses regarding the functional association between plasticity in mammalian mandibular morphology and response to dietary-related manipulation of jaw-loading patterns. For example, growing monkeys, rats, and rabbits raised on a fracture-resistant diet undergo greater cortical bone modeling and remodeling, and con-

sequently develop greater mandibular corpus depth and cortical bone thickness (Bouvier and Hylander, 1981, 1984; Ravosa et al., 2007, 2008a,b). This pattern likewise characterizes cortical bone osteogenesis in the limbs of birds and mammals subject to modification of locomotor loading patterns (Lanyon and Rubin, 1985; Biewener et al., 1986; Biewener and Bertram, 1993; Rubin et al., 1994). Most convincing in this regard are studies demonstrating that peak-strain magnitudes at a given site become elevated following surgical- or exercise-induced increase in loading levels, and their surface strains return to pre-experimental levels following subsequent increase in cortical bone mass (Lanyon and Rubin, 1985; Biewener and Bertram, 1993; Bouvier and Hylander, 1996). Increase in loading frequency likewise has an osteogenic influence on the formation of cranial and postcranial elements (Goodship et al., 1979; Bouvier and Hylander, 1981; Rubin and Lanyon, 1982; Lanyon and Rubin, 1985; Rubin et al., 1994; Turner, 1998; Mao, 2002).

It is generally assumed that stresses due to elevated peak loads and/or greater cyclical loading stimulate adaptive remodeling and modeling only if the strain produced is of sufficient magnitude to induce osteogenesis in a load-bearing element (Rubin et al., 1994). Empirical evidence from the vertebrate locomotor skeleton suggests that a common physiological range for this adaptive process is 1,500 and 3,500, with corresponding safety factors to yield ranging from 2–4 (Lanyon and Rubin, 1985; Biewener, 1991, 1993). Thus, functional adaptation of cortical bone appears to maintain an adequate safety factor for a homologous skeletal site corresponding to predominant loading regimes experienced *in vivo*. Given the high metabolic costs of cortical bone, such an osteogenic feedback mechanism ensures that a skeletal element is neither too over- or under-built for countering routine loads (Rubin and Lanyon, 1982; Lanyon and Rubin, 1985).

One comparative implication of the presence of a common strain environment for individual locomotor elements is that controlling for behavior, vertebrates of vastly different body sizes exhibit similar peak strains and corresponding safety factors at homologous and non-homologous skeletal sites (Biewener, 1982, 1983, 1991, 1993; Rubin and Lanyon, 1982, 1984; Lanyon and Rubin, 1985; Biewener and Taylor, 1986; Biewener et al., 1986; Keller and Spengler, 1989; Selker and Carter, 1989; Indrekvan et al., 1991; Rubin et al., 1994; van der Meulen and Carter, 1995; Carter et al., 1996; Main and Biewener, 2004). In the feeding apparatus, this size-independent similarity of peak strains characterizes a limited series of 1-kg galagos to 4-kg macaques, where levels along the working-side (WS) mandibular corpus are not significantly different during powerful biting and chewing (Hylander, 1979a; Hylander et al., 1998; Ravosa et al., 2000a,b). What remains unclear is whether this strain similarity is also observed across a wider size range and how these comparable peak-strain

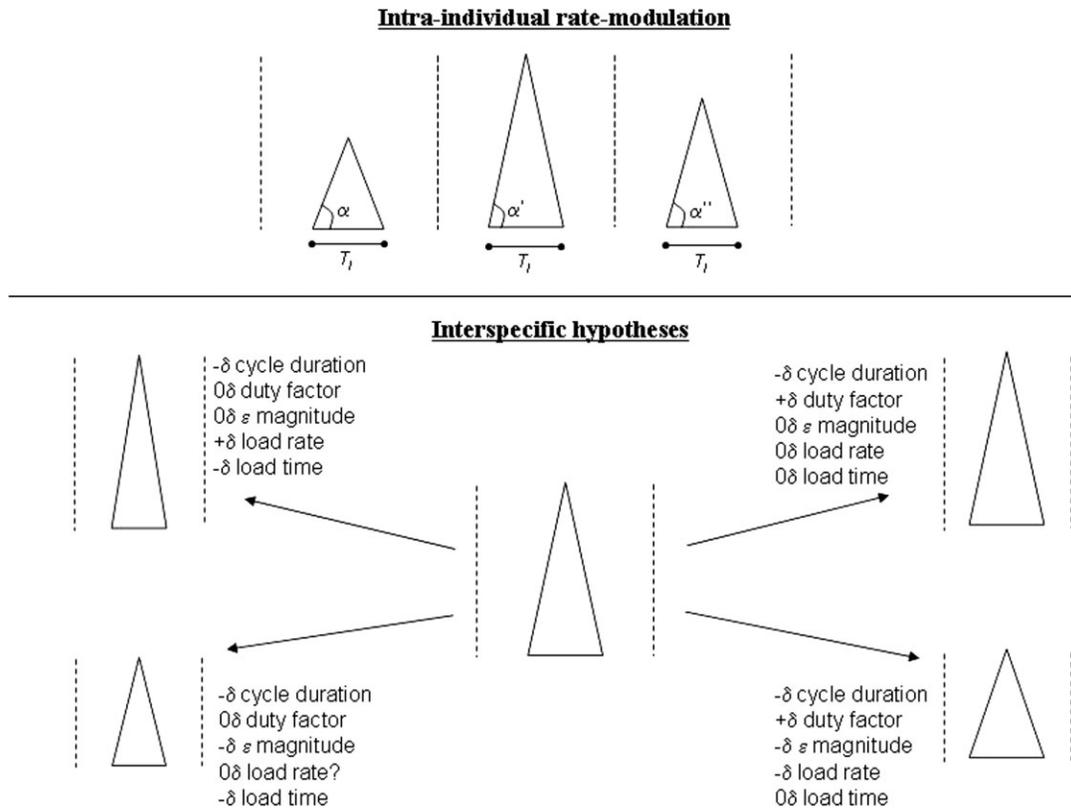


Fig. 1. Top: Diagram illustrating relationships between mandibular corpus strain magnitude, loading time (T_l), loading rate (α), and duty factor documented in intraindividual analyses by Ross et al., (2007a) assuming relatively invariant cycle duration within mammalian species, as documented by Ross et al., (2007b). Bottom: Diagram illustrating hypotheses regarding relationships between mandibular corpus strain magnitude, loading time, loading rate, and duty factor in association with size related decrease ($-\delta$) in chew cycle duration in interspecific comparisons. The central figure illustrates the relationships between these variables in a large animal. The arrows point away from this central figure towards four possible resulting shapes in mandibular loading profiles in the context of $-\delta$ in chew cycle duration. The top left

figure illustrates the hypothesis predicted by comparison with the locomotor system: peak strain magnitude and duty factor are both relatively constant associated with decrease in loading time and increase in loading rate. Bottom left: an alternate possibility is that peak strain magnitude decrease in smaller animals and duty factor remains constant, resulting in decrease in loading time and (possibly) constant loading rates. The two figures to the right illustrate increase in duty factor because load time remains constant. The top right figure hypothesizes that if peak strain magnitude remains constant, then load rate could remain constant. In contrast, the bottom right figure suggests that if peak strain magnitude decrease, then load rate would also decrease.

magnitudes are achieved in the context of interspecific size-related changes in chewing frequency?

Chewing Frequency, Occlusal Duty Factor, Load Rate, and Load Time in the Mandible

Dynamic variation in loading frequency and loading duration plays an important role in adaptive cortical bone modeling and remodeling in load-bearing skeletal elements. Specifically, there is a functional association between loading frequency and cortical bone microdamage or fatigue failure within normal physiological ranges (McElhaney, 1966; Carter et al., 1977; Carter and Spengler, 1978; Hylander, 1979b; Bouvier and Hylander, 1981, 1982, 1984, 1996; Schaffler et al., 1989; Rubin et al., 1994), and the rate at which bones are loaded is an important determinant of the osteogenic response (Goodship et al., 1979; Biewener, 1982, 1983; Rubin and Lanyon, 1982; Rubin et al., 1994; Turner, 1998). In this context, the observation that smaller mammals exhibit higher chewing frequencies than larger animals (Hir-

aiwa, 1978; Fortelius, 1985; Druzinsky, 1993; Gerstner and Gerstein, 2008; Ross et al., 2009a; contra Hiiemae, 1978) suggests that smaller animals might not only experience a higher number of loading cycles per unit time but also they may load their mandible faster than larger animals, with possible detrimental effects on bone strength. Recent experimental work in mammals has demonstrated that adult intraspecific variation in the modulation of peak-strain magnitudes, a proxy for bite force, is primarily correlated with variation in loading rate and less so with loading time within a power stroke (Ross et al., 2007a; also Fig. 1). This is posited to facilitate more rhythmic mastication at a constant frequency, thus simplifying mechanisms of motor control (Ross et al., 2007a).

The bottom diagram in Fig. 1 presents alternate ways that size-related increase in chewing frequency might be accommodated so as to maintain constant peak-strain magnitudes, constant occlusal duty factors (i.e., duration of chewing cycle during which the corpus is loaded), or constant mandibular loading rates. As illustrated in the

top right of the bottom diagram (Fig. 1), increase in chewing frequency (i.e., decrease in chew cycle duration) in smaller species might be associated with constant loading times and constant peak strain magnitudes, along with increase in occlusal duty factor (mandible loading duration expressed as % of chew cycle duration, i.e., negative scaling of occlusal duty factor). However, this would run counter to observations in the locomotor system in which data from a diverse mouse-to-horse size series shows that duty factor does not vary with body mass (Biewener, 1983). Another possibility (Fig. 1, bottom) is that smaller organisms might exploit a less fracture-resistant diet, requiring less jaw-muscle force during biting and chewing, thus lowering masticatory stresses (Scapino, 1981; Ravosa and Hylander, 1994; Ravosa and Hogue, 2004) and reducing food processing time (Gorniak and Gans, 1980; Thexton et al., 1980; Hylander et al., 1987, 1992, 2000; Weijs et al., 1989; Thexton and Hiiemae, 1997). In the context of decrease in loading time (Fig. 1, bottom left), lower mandibular peak-strain magnitudes in smaller animals could result in constant loading rates if occlusal duty factor remained constant. However, this would contradict strain similarity in the mandible predicted by analogy with the locomotor system and observations from the primate corpus (Hylander et al., 1998; Ravosa et al., 2000a,b). Data from the locomotor system suggest that (Fig. 1, top left) occlusal duty factors and corpus peak-strain magnitudes should remain constant across body sizes, in association with decreases in loading time and increases in loading rate with decreases in body size. The fourth possibility presented in Fig. 1 (bottom right) is that smaller organisms decrease peak-strain magnitudes with decrease in chew cycle duration, requiring decrease in loading rate, but allowing constant loading times and increasing occlusal duty factor with decrease in body size.

Here, we evaluate these hypotheses by determining whether mandibular peak-strain levels are constant or change with body size, and whether allometric changes in chewing rate/frequency are accompanied by constant or size-related changes in occlusal duty factor. Specifically, experimental bone-strain data from the mammalian mandibular corpus during postcanine chewing are used to test five hypotheses regarding interspecific variation in masticatory loading parameters: (1) chewing frequency should decrease with body size; (2) occlusal duty factor should not vary with body size; (3) peak-strain magnitudes should be similar across body size; (4) chewing frequency should be related to variation in loading time and/or loading rate; (5) peak-strain magnitude should be related to variation in loading time and/or loading rate. This analysis provides novel evidence on dynamic loading patterns (Hylander, 1979a,b; Lanyon and Rubin, 1985) that closely track how an organism uses a given morphology during its lifetime (Bock and von Walther, 1965). A second objective of this research is to integrate information on *in vivo* loading patterns for masticatory and locomotor elements (cf., Heglund et al., 1974; Biewener, 1982, 1983, 1991, 1993; Rubin and Lanyon, 1982, 1984; Lanyon and Rubin, 1985; Heglund and Taylor, 1988), which is critical for comparing and contrasting loading environments that influence musculoskeletal adaptations and morphological variation across a range of body size. A final goal was to identify outstanding issues regarding the scaling of masticatory

loading parameters that could benefit from future investigation.

MATERIALS AND METHODS

Interspecific Sample

The mandibular bone-strain data analyzed for this study were recorded in three different laboratories in connection with other studies (Hylander et al., 1991, 1998, 2000; Ross and Hylander, 1996; Herring and Teng, 2000; Liu and Herring, 2000a,b; Ravosa et al., 2000a,b; Herring et al., 2001; Liu et al., 2004; Ross et al., 2007a; Williams et al., 2009, 2010). Feeding data were available for 3,070 chewing cycles from 40 experiments on 37 subjects in 11 mammalian species varying in body size by over 2.5 orders of magnitude (i.e., 800–500,000 g), including seven primate taxa (four anthropoids and three strepsirrhines) as well as goats, horses, alpacas, and miniature pigs (Table 1). During the 40 experimental sessions or “experiments,” data on alert feeding behaviors were recorded while a subject was presented food items of differing material properties. Our analyses focused only on bone-strain data from the mandibular corpus during the mastication of fracture-resistant foods, which minimized potentially confounding sources of error. Indeed, such foods fall in the upper range of the elastic modulus and toughness values of items processed by wild primates (Williams et al., 2005). As some species were represented by more than one subject, species means were generated by calculating the mean for an experiment for each individual, then figuring the mean of all of the experiments for an individual, with the species mean in turn based on the average values of one or more individuals. Therefore, all interspecific analyses are based on a total N of 11.

Bone-Strain Analyses

In vivo bone-strain data during postcanine biting and chewing were collected with delta or rectangular rosette strain gauges. Such gauges allow one to detail strain levels and directions along a planar surface. In these analyses, peak-strain magnitudes are used as a proxy for bite force, however, it is important to note that this is indicated only for primates during isometric transducer biting and may be affected by gauge location. Indeed, gauge position varied among experiments, although all the data discussed here were collected from the lateral aspect of the mandibular corpus below the molars or premolars. Some gauges were placed closer to the lower (ventral) border of the mandibular corpus and others at mid-corpus height (Table 1). Details of the methods for strain-gauge implantation, recording, and the calculation of principal strain values from the raw strain data are provided in the primary studies for each taxon (Table 1 and citations above). While this may result in unwanted interspecific noise in bone-strain levels, arguably such variation is comparable to the variability in strain magnitudes due to routine differences in the application of bite forces along the postcanine tooth row (or strains collected during racetrack versus treadmill locomotion—Lanyon and Rubin, 1985). Studies of locomotor strain data have similar disparities in terms of identifying functionally similar sites across taxa (e.g., fish hypurals versus turkey tibiae—Lanyon and Rubin, 1985), which highlights a potential difficulty in performing interspecific bone-strain

TABLE 1. Sample and Experimental Information

Species	Animal/ Exp. (N)	Chew cycles	Gage sites	Sample rates (Hz)	Food items	Body mass (kg) ^d
<i>Eulemur fulvus</i> ^a (brown lemur)	3/3	411	Midcorpus below P ₄ , M ₁ or M ₂	1,000	Prune, raisin, grape, apple	2.2
<i>Varecia variegata</i> ^a (ruffed lemur)	2/3	155	Midcorpus below M ₁ , below M ₁ or M ₂ at lower border	1,000	Prune, raisin, apple, pineapple, strawberry	3.6
<i>Otolemur crassicaudatus</i> ^{a,b} (greater galago)	4/4	151	Midcorpus below M ₁ , below M ₁ at lower border	500/600/2,700	Prune, raisin, gummy bear	1.2
<i>Macaca fascicularis</i> ^b (crab-eating macaque)	4/5	315	Below M ₁ or M ₂ at lower border	500	Monkey chow, apple	4.5
<i>Macaca mulatta</i> ^a (rhesus macaque)	3/3	324	Below P ₄ or M ₁ at or near lower border	2,700	Almond, prune, apricot, taffy, jawbreaker, apple, grape	6.5
<i>Chlorocebus aethiops</i> ^a (vervet monkey)	1/2	150	Midcorpus below P ₄ , below M ₁ at lower border	1,000/10,000	Prune, apple, grape, corn, pineapple	3.6
<i>Aotus trivirgatus</i> ^{a,b} (owl monkey)	3/3	698	Below M ₁ at or near lower border, below M ₂ at lower border	2,700/10,000	Prune, apricot, carrot, apple, gummy bear, plantains	0.8
<i>Capra capra</i> ^{b,c} (goat)	5/5	167	Midcorpus, below M ₁ near lower border	250/10,000	Hay, pig chow, sweet grain	60.0
<i>Lama pacos</i> ^b (alpaca)	4/4	146	Midcorpus, below M ₂ near lower border	10,000	Hay	60.0
<i>Sus scrofa</i> ^c (pig)	6/6	455	Below 1st molari- form tooth	500	Pig chow	50.0
<i>Equus caballus</i> ^c (horse)	2/2	98	Below M ₂ near lower border	10,000	Hay	500.0

Experiment Institution:

^aStony Brook University (Ross et al., 2007a).

^bDuke University (Hylander et al., 1991, 1998; Ross and Hylander, 1996; Ravosa et al., 2000a,b; Williams et al., 2009, 2010).

^cUniversity of Washington (Herring and Teng, 2000; Liu and Herring, 2000a,b; Herring et al., 2001; Liu et al., 2004).

^dBody mass data are the average for the species.

analyses of cranial and postcranial elements. Moreover, locomotor strain data used in similar interspecific scaling analyses are typically from the trot-gallop transition (e.g., Biewener, 1982, 1983, 1993). As there is no homologous behavior in the feeding apparatus, our analyses are based more broadly on strain data from powerful postcanine biting and chewing. Arguably, if such problems were considerable they would undermine all analyses involving the use of corpus strain magnitudes, which is not the case for this study (see Results).

After the animals recovered from anesthesia, strain data were recorded the same day. The animals were presented with a range of food types, depending on the species, however, the analyses for this study are based on hard and/or tough items (Williams et al., 2005). The rosette data were used to calculate magnitudes and orientations of principal strains. Strain (ϵ) is a dimensionless unit equaling the change in length of an object (ΔL) divided by its original length (L). It is measured in micro-strain ($\mu\epsilon$), i.e., 1×10^{-6} strain. By convention, tensile strain is a positive value and compressive strain is a negative value. Maximum principal strain (ϵ_1) is the largest tensile strain, while minimum principal strain is the largest compressive strain (ϵ_2). Peak shear strain ($\gamma_{\max} = \epsilon_1 - \epsilon_2$) is an overall measure of masticatory

stress for each chewing cycle. All loading and unloading parameters are based on this information (Table 2).

Principal-strain values were imported into IGOR Pro 4.0 (WaveMetrics, Lake Oswego, OR) where a series of loading parameters were extracted from each chewing cycle (Ross et al., 2007a; see also Fig. 2 and Table 2). The duration of loading, unloading, loading rate, and unloading rate are measured from the first occurrence of 5% of peak strain (rather than zero strain) in each power stroke because the strain profile often does not drop to zero between the strain associated with the opening phase and that associated with the closing phase. These strains are particularly prevalent in taxa that chew rapidly and experience significant corpus strains during jaw opening.

Ingestion cycles (cycles in which food is brought into the mouth) were excluded and data were only included from chewing cycles in which the animals chewed ipsilateral to the corpus strain gauges, that is, only chewing- or WS bone-strain data are examined here. WS was determined using EMG patterns and/or jaw kinematic data. Chewing sequences were only selected for study if there were five or more cycles of rhythmic chewing. As cycle time is calculated using the relative timing of three successive strain peaks, data on strain magnitude, rate

TABLE 2. Masticatory Loading Parameters

Variable	Description
Peak-strain magnitude	Largest values of ε_1 , ε_2 , and γ_{\max} during the power stroke
Peak-strain timing	Time at which peak principal-strain magnitudes (ε_1 and ε_2) is attained
5% timing	Time at which 5% of peak principal-strain magnitude is reached in loading and unloading
Load time	Amount of time between 5% peak strain in loading and peak strain
Unload time	Amount of time between peak strain and 5% peak strain in unloading
Load rate	For each chew cycle, average loading rate between 5% peak strain in loading and peak, i.e., $\delta y/\delta x$, where δy = peak magnitude and δx = load time
Unload rate	For each chew cycle, average unloading rate between peak and 5% peak strain in unloading, i.e., $\delta y/\delta x$, where δy = peak magnitude and δx = load time
Chewing cycle	Duration of chewing cycle, estimated as average of times from preceding peak to current peak, and from current peak to following peak
Occlusal duty factor	Total load time as a percentage of chewing cycle, i.e., percentage of chewing cycle during which mandibular corpus is loaded
Chewing frequency	Inverse of chewing cycle duration

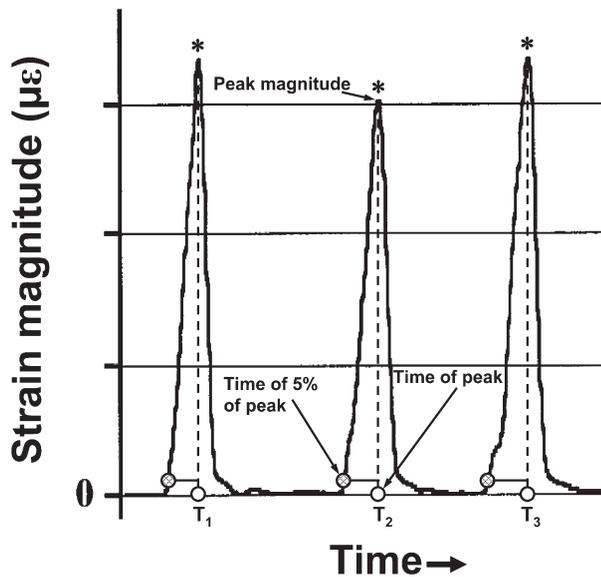


Fig. 2. Depiction of masticatory parameters derived from mandibular corpus strain data (after Ross et al., 2007a). Plot of WS strain magnitude from lateral aspect of the corpus in a greater galago (data from MJR collected at Duke University). Three chews ipsilateral to the strain gauge are shown. The following data were extracted from each power stroke: time (open circles) and magnitude (asterisks) of peak strain, and time at which 5% of peak strain was attained in loading (cross-hatched circles). The duration of loading was calculated as the time from 5% of peak strain to peak strain. The loading rate was figured as peak-strain magnitude divided by loading duration. Cycle time was estimated as the duration of time from the preceding peak to the following peak, divided by two. In the second cycle illustrated earlier, cycle time = $(T_3 - T_1)/2$.

and duration from the first and last noningestion cycles were used to calculate cycle durations and frequencies for neighboring cycles (Fig. 2). Most of the original data sets did not allow the distinction between puncture-crush and tooth-tooth contact cycles, so both types of data were included.

Statistical Analyses

To evaluate predictions and explore the association between a given masticatory loading parameter and

body mass, interspecific bivariate correlation analyses were used ($P < 0.05$); an $\alpha = 0.10$ is used to identify potential biological trends especially given the small sample size. Body mass is used as the independent variable to facilitate direct comparisons with prior analyses of masticatory and locomotor loading parameters (e.g., scaling of chewing and stride frequency—Heglund et al., 1974; Heglund and Taylor, 1988; Druzinsky, 1993; Gerstner and Gerstein, 2008; Ross et al., 2009a), to characterize and identify general patterns of size-related change in masticatory loading parameters, and because we had no *a priori* reason to assume that interspecific variation in mandibular form would independently influence corpus strain patterns. In comparisons focused on the scaling of chewing frequency, bivariate least-squares regressions were calculated using natural logarithms.

Interspecific multiple regression analyses ($P < 0.05$) were used to develop a model that best explains the relationship between variation in loading parameters (rate, time) and principal-strain magnitudes (ε_1 and ε_2), as well as loading rate and time (and body mass) versus chewing frequency. Thus, two sets of multiple regression models were run with either principal-strain magnitude or chewing frequency as the dependent variable and loading rate and strain rate as the independent variables to determine which of these variables has the greatest influence. This was evaluated using beta coefficients, which are standardized regression slope coefficients obtained when variables are converted to z-scores. Beta coefficients express the relative standardized strengths of the effects of the independent variables on strain magnitude. Multicollinearity between independent variables in a multiple regression equation (i.e., loading rate and loading time) significantly influences estimates of their partial slope coefficients. The correlation between the estimators of the partial slope coefficients is the inverse of the correlation between the independent variables, such that a high degree of multicollinearity undermines conclusions regarding the relative impacts of the two independent variables on the dependent variable. To assess the degree of multicollinearity, correlation, and partial correlation coefficients between strain rate and loading rate are also calculated as well as the “tolerance” statistic. The partial correlation is the strength of the correlation between the dependent variable and an independent variable holding the other independent variable constant. The tolerance is that proportion of the

TABLE 3. Interspecific Analyses of Masticatory Loading Parameters

Variable	Body mass (r) ^a
Corpus peak shear strain (γ_{\max})	-0.141
Corpus peak tensile strain (ϵ_1)	0.123
Corpus peak compressive strain (ϵ_2)	0.310
Occlusal duty factor	-0.045
ϵ_1 loading time	0.474*
ϵ_1 unloading time	0.395
ϵ_2 loading time	0.556*
ϵ_2 unloading time	0.093
ϵ_1 loading rate	-0.163
ϵ_1 unloading rate	-0.263
ϵ_2 loading rate	0.400
ϵ_2 unloading rate	0.304
ln chewing cycle vs. in body mass	0.518*
ln chewing frequency vs. in body mass	-0.694** (slope: -0.110; y-int: 0.870)

^aCorrelation significance levels: * $P < 0.10$; ** $P < 0.05$; others not significant.

variance in one independent variable not accounted for by the other independent variable(s). A low tolerance value indicates that a variable contributes little to the model independent of the other variables, which is an indicator of multicollinearity between independent variables. As there was a significant correlation between independent variables in all three sets of comparisons, multiple regression analyses were performed with and without interaction terms so as to determine a model that explains the highest proportion of the variance in the respective dependent variable.

RESULTS

Interspecific correlation and regressions were used to evaluate a series of predictions from three hypotheses regarding relationships between masticatory loading parameters and body mass as well as two hypotheses regarding associations between loading rate, loading time, principal-strain magnitudes, and chewing frequency.

Scaling of Masticatory Loading Parameters

Of the series of bivariate correlations between masticatory loading parameters and body size, only four significant comparisons are observed (Table 3). Loading time of maximum and minimum principal strain increases significantly with body size, and as reported on the basis of kinematic data (Druzinsky, 1993; Gerstner and Gerstein, 2008; Ross et al., 2009a), chewing cycle duration increases with size. That is, chewing frequency scales negatively versus body mass (Fig. 3).

The remaining loading parameters demonstrate no significant change with body mass (Table 3). Occlusal duty factor is similar over a range of sizes, as predicted by comparison with locomotor data (cf., Biewener, 1983). Principal- and shear-strain magnitudes do not vary with body mass (Table 3), supporting predictions regarding the similarity of peak strains across a spectrum of body sizes (Rubin and Lanyon, 1984; Lanyon and Rubin, 1985; Biewener, 1991, 1993).

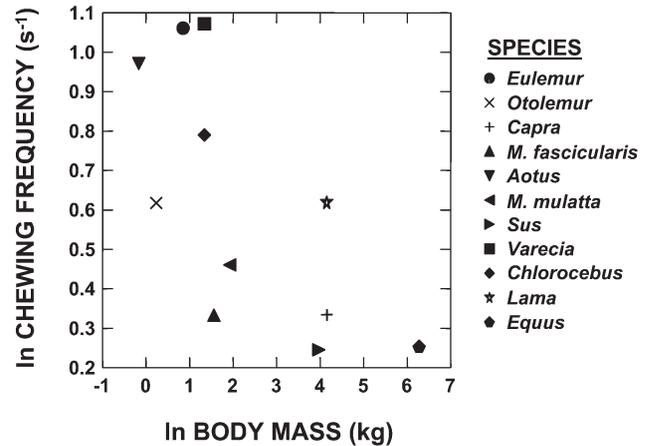


Fig. 3. Interspecific scaling of chewing frequency. The significant negative allometry indicates that larger-bodied mammals exhibit lower chewing rates (see Table 3).

Chewing Frequency versus Loading Rate and Time

Using loading parameters related to maximum principal strain, chewing frequency is positively correlated with loading rate (0.541, $P < 0.10$) and negatively correlated with loading time (-0.795 , $P < 0.01$). However, the influence of loading rate on chewing frequency disappears in a multiple regression analysis including loading time (not shown, $P = 0.647$). This underscores the strength of the predicted relationship between chewing frequency and loading time.

Given the link between chewing frequency and body size noted earlier (Table 3), a multiple regression model was constructed with loading time for ϵ_1 and body mass as the independent variables. A model including an interaction term between loading time and body mass best explains variation in chewing frequency, accounting for 73.4% of the observed interspecific variation (Table 4). This represents about a 7% increase in the amount of variance explained by loading time and body mass without the inclusion of interaction terms. Given the higher partial correlation and differentially higher tolerance for loading time, this suggests that size-related decreases in chewing frequency variation are associated with factors influencing the allometry of loading time.

Peak-Strain Magnitude versus Loading Rate and Time

Maximum principal-strain magnitude is positively correlated with loading rate, and to a lesser extent, negatively correlated with loading time (Fig. 4a; Table 5). Similarly, minimum principal-strain magnitude is positively correlated with loading rate, and to a lesser degree, positively correlated with loading time (Fig. 4b; Table 5). This mirrors intraspecific findings regarding *in vivo* modulation of bite force magnitude being determined by variation in loading time, and especially, loading rate (Ross et al., 2007a).

As loading rate and loading time for both principal strain magnitudes are correlated with one another, a series of multiple regression models was constructed so as

TABLE 4. Interspecific Multiple Regressions for Chewing Frequency, Body Mass, and Loading Time for ϵ_1

Variable	Adjusted r^2	Variable	Beta	Bivariate correlation	Partial correlation	Tolerance
ln chewing frequency	0.662/0.734	ϵ_1 load time	-9.061***	-0.811***	-0.691	0.242
		ln body mass	-0.234**	-0.694**	-0.459	0.058
		ϵ_1 load time vs. ln body mass	1.362*	0.588**		

The first adjusted r^2 is moderately high, indicating that it explains much of the variation in chewing frequency. The second adjusted r^2 is higher, reflecting the significant positive effect of the interaction between load time and body mass in explaining variation in chewing frequency (vs. the simpler model with a lower r^2). Significance levels: * $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$.

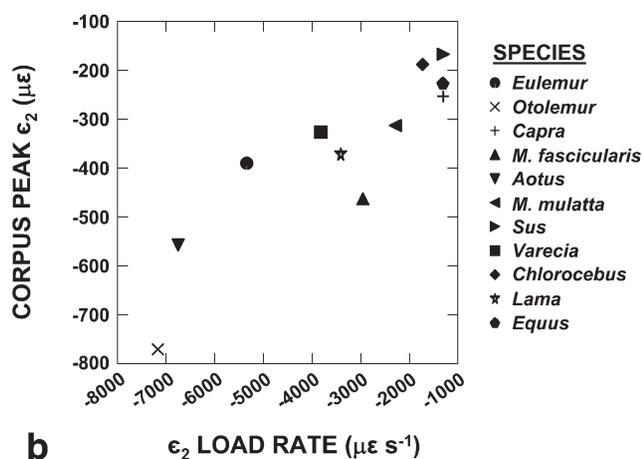
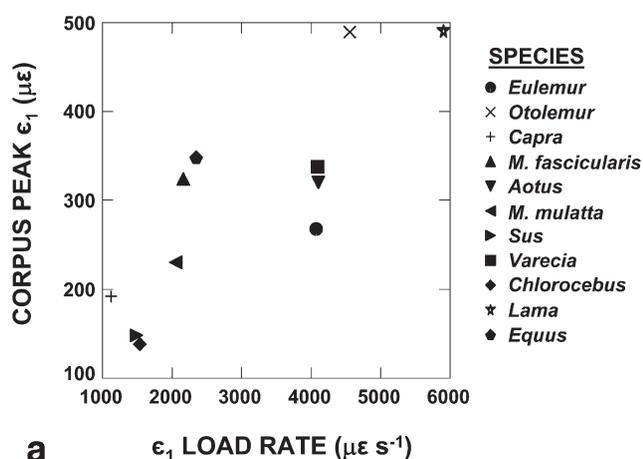


Fig. 4. Interspecific regressions of corpus peak-strain levels vs. load rate (a: ϵ_1 ; b: ϵ_2). Note the significant positive correlations between maximum (ϵ_1) and minimum (ϵ_2) principal strains and their respective loading rates. This demonstrates that the generation of larger peak bone-strain magnitudes, and corresponding bite forces occurs in part by increasing loading rate (see Fig. 1; Table 4).

to fully model the relative influence of these parameters on the generation of peak strains during biting and chewing (Table 5). In terms of both maximum and minimum principal strain, a model that accounts for the significant interaction between loading rate and loading

time explains a large proportion of the interspecific variation in strain magnitudes, respectively, accounting for 98.1% and 96.6% of the variation in peak-strain magnitude during postcanine biting and chewing. In both cases, this represents $\sim 10\%$ increase in the amount of variance explained by loading rate and loading time without the inclusion of interaction terms. In multiple regression models explaining variation in principal-strain magnitudes, the partial correlations are higher for loading rate, with the influence of loading time being more independent of loading rate in the generation of maximum principal strain (Table 5).

DISCUSSION

Although behavioral sources of stresses acting on the mandible are quite different from those affecting the limbs (Hylander, 1985), a comprehensive *in vivo* analysis of interspecific variation in mammalian masticatory loading parameters is lacking. For instance, while there is emerging consensus regarding the scaling of chewing rate (Druzinsky, 1993; Gerstner and Gerstein, 2008; Ross et al., 2009a), similar interspecific analyses of strain similarity and occlusal duty factor have yet to be performed. The surprising lack of basic information on the patterning of masticatory stresses within and across organisms can undermine interpretations of allometric variation in mammalian craniomandibular form and function (Emerson and Bramble, 1993). This hinders an understanding of basic principles of musculoskeletal design, information fundamental to evolutionary and translational research on myriads aspects of bone biology.

Information on how loading parameters, which in turn affect skeletal modeling and remodeling, vary predictably with body size is important for identifying fundamental constraints on skeletal design, which apply broadly to diverse clades. To date, more is known regarding the scaling of locomotor loading patterns versus similar evidence concerning variation in masticatory loading parameters. One goal of this study was to conduct novel analyses to address the interspecific allometry of masticatory loading patterns and to compare the scaling of jaw loading with similar allometric analyses of the loading of locomotor elements. Another aim was to investigate the correspondence between intra- and interspecific patterns of bite-force modulation in mammals. In performing such analyses, we sought to identify questions and/or problems worthy of future investigation.

TABLE 5. Interspecific Multiple Regressions for Peak Tensile (ϵ_1) and Compressive (ϵ_2) Strains

Peak-strain magnitudes	Adjusted r^2	Variable	Beta	Bivariate correlation	Partial correlation	Tolerance
ϵ_1	0.899/0.981	Load rate	0.107***	0.835***	0.956	0.419
		Load time	2287.058**	-0.331 ^{NS}	0.857	0.419
		Load rate vs. load time	0.965***	-0.762**		
ϵ_2	0.849/0.966	Load rate	0.104***	0.893***	0.912	0.359
		Load time	1935.150*	0.544*	-0.633	0.359
		Load rate vs. load time	1.330***	0.801**		

The first adjusted r^2 is high for both models, indicating that each explains most of the variation in respective peak-strain levels. The second adjusted r^2 for each comparison is more pronounced, reflecting the significant positive effect of the interaction between load rate and load time in explaining variation in peak principal strains (vs. simpler models with a lower r^2). Significance levels: * $p < 0.10$; *** $p < 0.05$; **** $p < 0.01$; NS = not significant.

Scaling of Masticatory Loading Parameters

Interspecific analyses of mandibular strain patterns indicate that much as observed in mammal limb elements (Biewener, 1982, 1983, 1993; Rubin and Lanyon, 1982, 1984; Lanyon and Rubin, 1985), peak-strain magnitudes are similar in the corpus across mammals of highly disparate body sizes (Table 6). This corresponds and greatly extends the implications of earlier research in primates (Hylander, 1985; Hylander et al., 1998; Vinyard and Ravosa, 1998; Ross and Metzger, 2004), which had supported the presence of stress and strain similarity in the mandible within and across species. However, comparison of mammalian corpus shear strains with similar postcranial data for tetrapods indicates that the latter experience significantly larger peak values, with mean γ_{\max} for locomotor elements almost four times larger than that for the corpus (Table 6 and references therein). Indeed, among the highly diverse taxa using aerial, arboreal, and terrestrial locomotion, only γ_{\max} values for alligators and iguanas fall within the range of corpus shear strains for mammals (i.e., upper third—Table 6); higher safety factors in alligators and iguanas appear linked to a sprawling gait and corresponding axial torsion (versus parasagittal bending) of the limbs (Blob and Biewener, 1999).

One explanation for routinely higher safety factors of cranial elements, such as the corpus is that in contrast to the postcranium, safety factors in the skull and feeding complex may not as closely track loading regimes related to the ontogenetic process of functional adaptation. In this scenario, safety factors for limb elements are posited to reflect the fact that failure occurs during loading regimes that may not vary appreciably from routine locomotor stresses (Lanyon and Rubin, 1985; Hylander et al., 1991; Hylander and Johnson, 1997; Ravosa et al., 2000a,c). Thus, to minimize the risk of fracturing cranial elements due to traumatic nonmasticatory forces and associated atypical loading patterns, it is posited that cranial and perhaps especially neurocranial elements are under strong selection to maintain higher safety factors (Hylander and Johnson, 1997). Compared to locomotor elements, this would result in craniofacial structures that are variably overbuilt relative to peak strains experienced during normal biting and chewing (Tables 7 and 8). Our findings for the corpus are consistent with such an interpretation suggesting that it applies to sites along the upper and lower facial skulls.

The presence of strain similarity along the mammalian corpus likewise implies that bony tissues of the mandible do experience significant functional adaptation during the lifetime of an organism (also Bouvier and Hylander, 1981, 1982, 1984, 1996; Vinyard and Ravosa, 1998; Ravosa et al., 2007, 2008a,b). Taken a step further, similarity of peak-strain levels and corresponding safety factors over a diverse range of organisms would appear to be an epiphenomenon of the maintenance of a common strain environment during the ontogeny of the members of a species (Rubin and Lanyon, 1982, 1984; Lanyon and Rubin, 1985; Biewener, 1991, 1993; Vinyard and Ravosa, 1998). However, while strain similarity may characterize locomotor and masticatory elements over a wide spectrum of sizes, safety factors for the corpus are notably greater. This variability suggests that strain-mediated, site-specific osteogenic thresholds may exist throughout the skeleton (Goodship et al., 1979; Rawlinson et al., 1995; Hylander and Johnson, 1997). Indeed, as masticatory elements such as the mandibular symphysis and anterior zygoma, exhibit peak strains within the range of values for locomotor elements (Hylander, 1984, 1985; Hylander and Johnson, 1997), safety factors appear to vary within the feeding apparatus (Tables 7 and 8). Whether strain similarity is characteristic of other cranial elements must await experimental sampling of additional skeletal sites in more disparate species, both in an ontogenetic and interspecific context. Presently, there is tentative support for strain similarity in the mandibular symphysis (Hylander, 1985; Vinyard and Ravosa, 1998), but an apparent lack of such a pattern in the circumorbital region (Ravosa et al., 2000a,b). Further analyses are particularly important as adult intra- and interspecific loading patterns may not characterize the entirety of postweaning ontogeny (Herring et al., 2005; Main and Biewener, 2007; Williams et al., 2009).

Chewing frequency in mammals is inversely correlated with body size (Druzinsky, 1993; Gerstner and Gerstein, 2008; Ross et al., 2009a), a pattern that also characterizes the scaling of locomotor stride frequency across a mouse-to-horse size series (Heglund et al., 1974; Biewener and Taylor, 1986; Heglund and Taylor, 1988). Indeed, allometric coefficients for stride frequency at the trot-gallop transition (-0.150: Heglund and Taylor, 1988) are remarkably similar to those for chewing frequency based on corpus strains (-0.110: Table 3) and jaw kinematics (-0.150: analyzing data in Ross et al., 2009a). However, the y -intercept of the bivariate

TABLE 6. Interspecific Comparison of Mandibular and Appendicular Peak Shear Strains

Species and element	γ_{\max} mean	Source of data
Brown lemur corpus	644	This study
Ruffed lemur corpus	660	This study
Greater galago corpus	1254	This study
Owl monkey corpus	873	This study
Vervet monkey corpus	325	This study
Crab-eating macaque corpus	783	This study
Rhesus macaque corpus	535	This study
Goat corpus	439	This study
Pig corpus	311	This study
Alpaca corpus	860	This study
Horse corpus	586	This study
Mammal corpus mean (SD)	661 (275) ^a	
Macaque ulna	1784	Demes et al. (1998)
Macaque tibia	2512	Demes et al. (2001)
Gibbon humerus	1911	Swartz et al. (1989)
Gibbon radius	2384	Swartz et al. (1989)
Gibbon ulna	2691	Swartz et al. (1989)
Dog tibia	3300	Rubin and Lanyon (1982)
Goat radius	2806	Biewener and Taylor (1986)
Sheep tibia	2097	Lanyon and Bourn (1979)
Sheep radius	3500	Lanyon and Baggott (1976); Rubin and Lanyon (1984)
Horse tibia	5550	Rubin and Lanyon (1982)
Bat humerus	3,050	Swartz et al. (1992)
Bat radius	3,083	Swartz et al. (1992)
Pigeon humerus	3,500	Biewener and Dial (1995)
Chicken femur	1,464	Carrano and Biewener (1999)
Turtle femur	1,975	Butcher et al. (2008)
Iguana femur	869	Blob and Biewener (1999)
Alligator femur	973	Blob and Biewener (1999)
Alligator tibia	752	Blob and Biewener (1999)
Tetrapod limb mean (SD)	2,456 (1166) ^a	

^aANOVA of mammal corpus vs. tetrapod limb γ_{\max} means is significantly different ($P < 0.001$).

regression equation for stride frequency at the trot-gallop transition (4.19: Heglund and Taylor, 1988) is significantly higher than that for chewing frequency determined herein (0.870: Table 3) or with jaw-kinematic data (1.203: using data in Ross et al., 2009a). This means that for a given body size, an organism will exhibit a higher stride versus chewing frequency, which in turn suggests that limbs are routinely loaded at a higher frequency than masticatory elements. For instance, comparing data for two species in common between this study and Heglund and Taylor's (1988), both taxa are observed to exhibit higher stride versus chewing frequencies (goat: 2.505 vs. 1.398 s⁻¹; horse: 1.969 vs.

TABLE 7. Summary of crab-eating macaque peak shear-strain levels during forceful biting and chewing

Gage location	γ_{\max} mean ($\mu\epsilon$)	Largest γ_{\max} ($\mu\epsilon$)
WS dorsal orbit	101	270
BS dorsal orbit	144	372
Dorsal interorbit	216	651
Rostral interorbit	98	270
WS anterior zygomatic arch	985	2,256
BS anterior zygomatic arch	903	1,899
WS infraorbit	835	1,655
BS infraorbit	522	1,033
WS mandibular corpus	724	1,679
BS mandibular corpus	501	1,119
Anterior mandibular symphysis	691	2,612

Note the significant disparity or strain gradient between upper facial values in the top four rows versus those for the midface and mandible in the bottom seven rows. For the most part, there is little disparity between values from the working and balancing sides of the upper and lower facial skulls (compiled from Hylander, 1984; Hylander et al., 1991, 1998; Hylander and Johnson, 1997).

TABLE 8. Summary of Greater Galago Peak Shear-Strain Levels During Biting and Chewing

Gage location	γ_{\max} mean ($\mu\epsilon$)	Largest γ_{\max} ($\mu\epsilon$)
WS postorbital bar	534	1,320
BS postorbital bar	174	587
Dorsal interorbit	420	1,221
WS mandibular corpus	1,197	2,653
BS mandibular corpus	216	746

Note the strain gradient between upper facial values in the top three rows and those for the mandible in the bottom two rows. In addition, there is a significant disparity between values from the working and balancing sides of the upper and lower facial skulls (from Ravosa et al., 2000a,b).

1.297 s⁻¹). The significance of this observation is that in all of the species examined here, the mandible is shorter in length than the limbs, yet is moved at a lower frequency. This difference likely reflects fundamental differences in design criteria of locomotor and feeding systems of mammals. In the locomotor system, the speed of limb movement is an important performance criterion related, albeit indirectly, to the speed of movement of the animal's center of mass. Thus, the locomotor system might better reflect selection for enhanced power. In contrast, the performance of the masticatory system has been suggested to be improved if the frequency of mandibular movement is kept relatively constant, around the natural frequency of the system (Ross et al., 2007b, 2009a). Moreover, the feeding system may be optimized for parameters other than power, such as precise control of displacement and force during the power stroke, or coordination of tongue and jaw during chewing. Arguably, the implications of this disparity for adaptive modeling and remodeling will only be more fully understood via recourse to detailed comparisons of mandibular and limb

kinematics, analyses of internal patterns of cortical bone distribution and skeletal inertial properties, as well as additional behavioral data on locomotor and feeding bouts in the wild. Further comparisons of the design of feeding and locomotor systems are clearly needed.

Several explanations exist for the scaling of chewing rate and frequency. Some argue that size-related decreases in chewing rate reflect allometric variation in jaw-adductor contractile properties, with larger forms exhibiting a greater proportion of slow-twitch fibers (Maxwell et al., 1979; Nakata, 1981; Dechow and Carlson, 1990). Others posit that as jaw-adductor lever-arm arrangements and physiological cross-sectional area scale negatively versus dentary mass, chewing rate is constrained to decrease with body size (Druzinsky, 1993; Reilly, 1995; Richard and Wainwright, 1995; Wainwright and Richard, 1995). A study of the morphological determinants of chewing frequency in primates suggests that chewing frequency in anthropoids, but not strepsirrhines, can be predicted relatively well by a forced mass-spring system incorporating empirical estimates of the scaling of muscle cross-sectional areas and lever arms (Ross et al., 2009a). Observed subtle allometric increase in loading time would be consistent with this explanation for size-related decrease in chewing frequency and this is likely to be related to factors outlined in the forced mass-spring model. Further refinement of this model may benefit from analyses of the role of jaw-adductor contractile properties in explaining variation in chewing rate. Moreover, given the presence of ontogenetic variability in jaw-adductor fiber types (Maxwell et al., 1979; Langenbach et al., 2008; Ravosa et al., 2010a), architecture (Herring and Wineski, 1986; Herring et al., 1991; Taylor et al., 2006) and mechanical advantage (Ravosa, 1991b; Ravosa and Daniel, 2010; Ravosa et al., 2010b), the relative contribution of such factors to understanding postnatal variation in chewing frequency likewise remains to be fully explored.

Our data demonstrate that in a mammalian sample across 2.5 orders of magnitude in body size where variation in dietary properties is minimized relative to variation in the wild, occlusal duty factor does not differ. This mirrors ontogenetic analyses of jaw-adductor muscle duty factor in alpacas (Williams et al., 2010) and interspecific results for the locomotor system (Biewener, 1983). Of particular interest is that mean occlusal duty factor from this study is equivalent to that for mean locomotor duty factor (0.44 ± 0.07 vs. 0.42 ± 0.03 from Biewener, 1983; Blob and Biewener, 1999). In the context of mandibular corpus strain similarity and the negative allometry of chewing frequency, the finding of constant occlusal duty factors across a range of body sizes suggests that in mammals loading rate in the mandible also scales negatively.

Peak-Strain Magnitude versus Loading Rate and Time

In our interspecific analyses, peak-strain magnitude is positively correlated with loading time and especially loading rate, which resembles the pattern observed within individuals of each of the mammalian species examined herein (Ross et al., 2007a). The prior study concluded that the modulation of peak strain during a chewing cycle occurs primarily via alterations in loading

rate (Ross et al., 2007a). The current study extends these results to interspecific comparisons, suggesting that variation in loading rate, loading time, and peak strains is an epiphenomenon of loading patterns experienced within members of a given species.

However, the allometric increase in loading time for principal strains suggests the presence of subtle variation in the modulation of strain magnitudes in mammals of different body sizes. One explanation for this trend is that the relatively bigger and more fracture-resistant foods ingested by larger organisms (Anderson et al., 1979; Scapino, 1981; Kiltie, 1982; Ravosa, 1991a; Ravosa and Hylander, 1994; Ravosa and Hogue, 2004; Vinyard et al., 2008) might require longer power strokes which, in the context of constant duty factors, results in slower chewing frequencies. In turn, greater stresses associated with processing more resistant and/or tough foods may be mitigated by a lower chewing, and consequently loading, frequency. Given the influence of food properties on jaw-adductor activity patterns (Herring and Scapino, 1973; Gorniak and Gans, 1980; Thexton et al., 1980; Weijs and Dantuma, 1981; Hylander et al., 1987, 1992, 2000; Weijs et al., 1989) as well as cyclical loading and cranial plasticity (Bouvier and Hylander, 1981, 1982, 1984, 1996; Ravosa et al., 2007, 2008a,b), comparative field data on food properties, bolus size and the amount of time spent during daily feeding bouts (Wright, 2005; Wright et al., 2008; Nakagawa, 2009; Vinyard et al., 2008, 2009; Yamashita et al., 2009) would be highly beneficial to a more integrative perspective on the scaling of masticatory loading parameters (Ross et al., 2009b).

Additional Loading Parameters Unique to the Feeding Apparatus

Although our analyses focus on WS corpus strains, an additional factor worthy of discussion is the role of variation in WS versus balancing-side (BS) peak-strain magnitudes along the masticatory complex. For instance, in primates it is well known that anthropoids with fused mandibular symphyses recruit relatively larger levels of BS jaw-adductor muscle force and corresponding elevated BS strain levels versus strepsirrhines with unfused joints (Hylander, 1979a,b; Hylander et al., 1987, 1991, 1998, 2000; Ross and Hylander, 1996; Ravosa et al., 2000a,b; Ravosa and Hogue, 2004) (compare Tables 7 and 8). Likewise, mammals experience relatively greater BS jaw-adductor activity during unilateral mastication of fracture-resistant diets (Herring and Scapino, 1973; Gorniak and Gans, 1980; Thexton et al., 1980; Weijs and Dantuma, 1981; Weijs et al., 1989; Hylander et al., 1992). Therefore, the pattern of masticatory stresses along the working and balancing sides of the skull will differ in organisms that routinely process tougher diets and/or vary in the degree of symphyseal fusion (Ravosa et al., 2000b). Indeed, this WS/BS discrepancy appears to be reflected in the presence of relatively larger mandibular cross-sectional dimensions in anthropoids versus strepsirrhines as well as in mammals with more resistant or tougher diets (Hylander, 1979b; Ravosa, 1991a,b; Ravosa and Hylander, 1994; Ravosa and Hogue, 2004; Ravosa and Daniel, 2010). Given the presence of size-related variation in dietary properties and/or relative bolus size across the members of many mammalian clades (Anderson et al., 1979;

Scapino, 1981; Kiltie, 1982; Ravosa, 1991a; Ravosa and Hylander, 1994; Ravosa and Hogue, 2004; Vinyard et al., 2008; Yamashita et al., 2009), WS/BS variation in cranial stresses is another factor to be integrated into analyses of the scaling of masticatory loading parameters.

SUMMARY AND CONCLUSIONS

Similarities and differences in the design constraints of the locomotor apparatus and masticatory complex have long been of interest to myriad researchers (e.g., English, 1985; Lanyon and Rubin, 1985). For example, in contrasting the loading environments of postcranial and cranial elements, Hylander (1985, p. 325) noted that "...primates do not routinely transmit body weight or locomotor stress through their faces." Although the behaviors underlying forces acting on the skull are distinct from those affecting locomotor elements, a comprehensive interspecific analysis of mammalian masticatory loading patterns was heretofore lacking, particularly as regards interspecific analyses of corpus strain similarity and occlusal duty factor. In contrast, our understanding of loading parameters affecting adaptive modeling and remodeling of locomotor elements within and across vertebrates is fairly extensive. To fill this gap, bone-strain data from the mandibular corpus were used to characterize masticatory loading parameters for diverse mammals ranging in body size by over 2.5 orders of magnitude.

In many respects, the scaling of mandibular loading parameters is surprisingly similar to those for the postcranium. Peak-strain levels and duty factors do not vary across body sizes for masticatory and locomotor elements, while stride and chewing frequency both scale negatively. However, additional comparisons indicate that similar-sized organisms exhibit both higher mandibular corpus safety factors and lower loading rates. These findings highlight the presence of global as well as site-principles of skeletal design and functional adaptation relevant to myriad research on the evolution, biomechanics, and bioengineering of masticatory and locomotor systems. Such evidence is beneficial for computer-based models of craniomandibular form as well as for understanding functional constraints on fossil taxa. Taken a step further, this allows one to speculate that certain aspects of the genetic and epigenetic control of cellular responses to strain-mediated osteogenesis also may be similar between locomotor and masticatory elements.

Nonetheless, our analyses identify areas of inquiry regarding the mechanobiology of cranial and limb elements that remain to be more fully investigated. Site-specific variability in skeletal safety factors requires additional experimental analysis, as does a hypothesis of strain similarity in other masticatory elements. Explanations for the allometry of mammalian loading patterns, most notably chewing frequency, require further attention in terms of the underlying basis of observed ontogenetic patterns. Interspecific and ontogenetic data on the scaling of jaw-muscle fiber types would also benefit our understanding of chewing rate based on a forced mass-spring model. Our interspecific sample did not include representatives from a number of mammalian clades with unique behaviors (e.g., carnivorans), thus the findings herein would be greatly bolstered by the con-

sideration of such taxa. Although chewing and stride frequency scale negatively, locomotor loading rate is higher in similar-sized mammals perhaps due to relatively longer limb lengths. Given this disparity as well as the lack of support for the pre-eminence of an optimal strain environment in explaining skeletal form, our research underscores the need to document a broader suite of osteogenic factors for understanding the evolutionary morphology of the skeleton, that is, daily cycles, cycle rate, peak strains, loading rate, and duty factor (Goodship et al., 1979). In the masticatory system, such evidence can be sought in more naturalistic studies of feeding behavior across a size spectrum of organisms that account for food properties, bolus size, and feeding duration (Vinyard et al., 2008; Wright et al., 2008; Ross et al., 2009b; Yamashita et al., 2009). By integrating ecomorphological data on a range of locomotor loading parameters, it will be possible to develop a more global perspective on the allometry of musculoskeletal adaptations of mammals and other vertebrates.

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