

## RESEARCH ARTICLE

# Intraspecific scaling of chewing cycle duration in three species of domestic ungulates

Kristin K. Stover<sup>1</sup> and Susan H. Williams<sup>2,\*</sup>

<sup>1</sup>Department of Biological Sciences, Ohio University, Athens, OH 45701, USA and <sup>2</sup>Department of Biomedical Sciences, Ohio University College of Osteopathic Medicine, Athens, OH 45701, USA

\*Author for correspondence (willias7@ohio.edu)

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### SUMMARY

In mammals, chewing cycle duration (CCD) increases with various measures of size, scaling with body mass<sup>0.13–0.28</sup> and jaw length<sup>0.55</sup>. Proposed explanations for these scaling relationships include the allometry of body size, basal metabolic rate and tooth size, on the one hand, and pendular mechanics treating the jaw as a gravity-driven pendulum, on the other. Little is known, however, about the relationship between CCD and size within species. Recent research in dogs demonstrates altogether different scaling exponents and weaker correlations. This research suggests that breed-specific growth rates influence the maturation of the neural networks generating chewing rhythm, which may be altered because of changes in jaw mass during early postnatal growth. Here, we explored the intraspecific scaling of CCD within a sample of adult horses ranging from miniatures to draft breeds and an ontogenetic sample of goats and alpacas from infants to adults. In horses, CCD scales with body mass<sup>0.19</sup> and jaw length<sup>0.57</sup>, although in neither case is the correlation significant. In the ontogenetic samples of goats and alpacas, CCD is significantly correlated with body mass, scaling as  $CCD \propto \text{body mass}^{0.37}$  in both species. In goats, but not alpacas, CCD is also significantly correlated with jaw length, scaling as  $\text{jaw length}^{1.032}$ . As in dogs, the scaling of CCD in horses may reflect the influence of selective breeding on growth trajectories of different breeds, resulting in reduced body and jaw size differences among infants, when CCD is established, compared with adults. However, the allometric scaling of tooth size in horses of different breeds may be a potential influence on the scaling of CCD. The scaling of CCD with body and jaw size in goats, and to a lesser extent in alpacas, also suggests that the development of peripheral masticatory structures such as the teeth and occlusal relations may play a role in changes in CCD during the earliest stages of postnatal ontogeny.

Key words: mastication, chewing cycle duration, goat, alpaca, horse.

### INTRODUCTION

Rhythmic chewing is controlled at its most basic level by the masticatory central pattern generator (CPG) located in the pons and medulla of the brainstem (Dellow and Lund, 1971; Kogo et al., 1996; Lund and Kolta, 2006; Tanaka et al., 1999). The CPG can produce rhythmic movements without input from extrinsic sources but peripheral sensory receptors in the lips, oral mucosa, teeth and jaw muscles provide sensory feedback to modulate the final motor output (e.g. Appenteng et al., 1980; Goodwin and Luschei, 1975; Johansson et al., 1988; Lavigne et al., 1987; Trulsson, 2006; Trulsson and Johansson, 1994; Trulsson and Johansson, 1996a; Trulsson and Johansson, 1996b; Trulsson and Johansson, 2002; Turker, 2002; Turker and Jenkins, 2000). This modulation influences the electromyographic burst characteristics of the muscles controlling masticatory movements and the durations of the constituent phases (i.e. fast closing, slow closing, slow opening, fast opening) of individual chewing cycles (Schwartz et al., 1989; Thexton and Hiimae, 1997; Vinyard et al., 2008). Although there is significant intra-individual variation in chewing cycle length, with gender and age among humans being significant factors (Peyron et al., 2002; Peyron et al., 2004), the most pronounced differences in masticatory rhythm and chewing cycle length are evident between species with widely differing body sizes, suggesting that CPGs controlling masticatory rhythm are size-dependent (Druzinsky, 1993; Fortelius,

1985; Gerstner and Gerstein, 2008; Hiimae, 1978; Shipley et al., 1994).

All studies on the interspecific scaling of chewing rhythm have shown that chewing frequency decreases with increases in body size and jaw length. Small animals chew at a higher frequency and thus have a shorter chewing cycle duration (CCD) than larger animals (Druzinsky, 1993; Fortelius, 1985; Gerstner et al., 2010; Gerstner and Gerstein, 2008; Ross et al., 2010; Ross et al., 2009a; Ross et al., 2009b; Shipley et al., 1994). Several explanations have been proposed for the observed scaling of CCD with body mass and jaw length. With respect to body mass, the observed scaling of CCD is typically related to scaling relationships between basal metabolic rate, tooth size and the volume of food comminuted per chew, which would ultimately predict that CCD scales with body mass<sup>0.25</sup> (see Fortelius, 1985; Kay, 1985; Ross et al., 2009b). Most observations of the scaling of CCD and body mass provide slopes slightly lower than this predicted value, although the range of reported slopes – from 0.13 to 0.28 depending on the data set – is quite large (Druzinsky, 1993; Fortelius, 1985; Gerstner et al., 2010; Gerstner and Gerstein, 2008; Ross et al., 2010; Ross et al., 2009a; Ross et al., 2009b; Shipley et al., 1994). Notably, strepsirrhine primates exhibit a decrease in CCD with body mass (i.e. a negative slope) which may be related to their low basal metabolic rates (Ross et al., 2009a; Ross et al., 2009b). Finally, phylogenetically controlled

data sets yield altogether higher slopes of around 0.30 (Gerstner and Gerstein, 2008; Ross et al., 2009b).

Druzinsky (Druzinsky, 1993) and others (Ross et al., 2009a; Shipley et al., 1994) have also explored the relationship between CCD and jaw length, demonstrating that CCD scales with jaw length<sup>0.55</sup>, which is most consistent with a model that treats the jaw as an oscillating gravity-driven pendulum. In this model, the oscillating period of the pendulum is proportional to  $2\pi(l/g)^{0.5}$ , where  $l$  is the pendulum length and  $g$  is the acceleration due to gravity (Druzinsky, 1993; Ross et al., 2009a; Shipley et al., 1994). Another model has been proposed by Ross and colleagues (Ross et al., 2009a) in which the observed scaling of CCD with jaw length in primates is related to the spring properties of muscles as well as the mass-related inertial properties of the mandible. This model predicts a slightly higher scaling exponent than that observed for anthropoids and more generally for primates, but it is more biologically relevant than the simple gravity-driven pendulum model.

Despite the wealth of information on the interspecific scaling of masticatory rhythm and chewing frequency, the scaling of CCD within a species has received little attention. This is likely due to the reduced body mass variation within species. However, domesticated species bred for different body sizes offer one potential avenue for exploring the issues of the scaling of CCD. Recently, Gerstner and colleagues (Gerstner et al., 2010) utilized the domestic dog in one such study, sampling CCD in breeds ranging in body mass from 2 kg to 50 kg. They showed that, within dogs, CCD scales with body mass<sup>0.07</sup> and jaw length<sup>0.20</sup>, but that there is no correlation between the CCD and either of the morphological variables. Because a non-canid sample matching the sizes of the individual dog breeds yields scaling exponents similar to those obtained from previous interspecific studies, Gerstner and colleagues (Gerstner et al., 2010) propose that the limited size range sampled among the dogs is not a confounding factor in the analysis. More importantly, they argue that the lack of correlation between body size and CCD has a developmental basis. Specifically, early changes in CCD within an individual may occur because of changes in jaw mass that elicit a response from immature neural networks underlying the CPG. However, once the CPG controlling masticatory rhythm has matured, an individual's CCD can no longer increase with additional growth (Gerstner et al., 2010). There are two lines of evidence to support this hypothesis. First, adult rats in which the jaw mass is artificially increased demonstrate no additional increases in the duration of oral behaviors (Carvalho and Gerstner, 2004). Second, anodontic mice in which the teeth fail have comparable CCDs to mice with occluding postcanine dentitions (Kobayashi et al., 2002).

In this study, we used two approaches to further investigate the intraspecific scaling of CCD in mammals, focusing on three species of domesticated herbivores. The first approach complements the study by Gerstner and colleagues (Gerstner et al., 2010) on dogs and utilizes the horse (*Equus caballus* L.) as a model system for determining the scaling of CCD in a domesticated species exhibiting a large size range due to artificial selection. Whereas dogs of different breeds exhibit major differences in the shape of the head and face, horses of different breeds are remarkably similar, offering a more constrained test of a species-specific chewing cycle rate *versus* size-dependent changes in CCD within species. Published data for equids, including donkeys (*Equus asinus*), are mostly from small to medium-sized individuals, ranging from approximately 140 kg to 300 kg (Druzinsky, 1993; Fortelius, 1985; Gerstner and Gerstein, 2008; Gross et al., 1993; Mueller et al., 1998; Ross et al., 2007). These studies give a range of CCDs from approximately

720 ms to 813 ms. In the present study, we extended the upper end of the body size range to approximately 800 kg.

The second approach utilizes an ontogenetic sample of goats (*Capra hircus* L.) and alpacas (*Lama pacos* L.). Published CCD data from goats, including infants, weanlings and adults, can be extracted from chewing data from a handful of studies. For example, Hooper and Welch (Hooper and Welch, 1983) report kid goats chewing at approximately 95–96 chews min<sup>-1</sup> whereas 9 month old weaned goats chewed at 86 chews min<sup>-1</sup>. This is equivalent to CCDs of approximately 631 ms in the infants and 697 ms in the weaned animals. CCDs for standard (i.e. non-pygmy) adult goats weighing 40 kg are around 600 ms (Gerstner and Gerstein, 2008; Ross et al., 2007). CCDs for adult alpacas range from 460 ms to 570 ms (Gerstner and Gerstein, 2008; Ross et al., 2007; Williams et al., 2010a). Despite having a fairly representative sample of CCD data from goats and alpacas, we know little about the ontogenetic scaling of chewing frequency. Because goats and alpacas exhibit similarities in chewing orbit characterized by significant mediolateral deviations of the jaw and a transverse power stroke, and both have selenodont dentitions, we expected that the two species would exhibit similar ontogenetic scaling patterns.

## MATERIALS AND METHODS

### Subjects

The horse data set consists of 17 dentally mature individuals (i.e. all premolars and molars erupted and in occlusion) from a variety of breeds including miniatures and draft horses. Horses were housed at local farms and all data were collected on-site at these farms. The ontogenetic data sets were acquired from 15 goats, aged 1 month to 8 years, and 15 alpacas, aged 3 months to 9 years. Some of the younger individuals of both species in the study were utilized multiple times throughout ontogeny. Because of the wide size range of different goat breeds, we used goats from the larger breeds, specifically Nubian, Boer and La Mancha. Goats and alpacas were housed at the Ohio University Large Animal Research Facility for the duration of the study. This study was conducted under the supervision of the Ohio University Institutional Animal Care and Use Committee (protocol no. U06-09).

### Body mass and jaw length measurements

Goats and alpacas were weighed to the nearest 0.1 kg using a large animal scale. Animals were weighed each time data on chewing frequency or muscle activity patterns were collected. Body masses (kg) of horses were estimated using a standard horse weight tape. These were compared against estimates taken from the literature for the large horses, given the potential inaccuracy of mass estimates using the weight tape in the largest animals. Jaw length was measured to the nearest 0.1 cm with calipers (goats and infant and juvenile alpacas) or to the nearest 0.5 cm with a measuring tape (adult alpacas, horses) from the mandibular condyle to the gingival margin at the incisors. As with body mass, jaw length was measured each time CCD data were collected.

### CCD data collection

CCD was determined from either video sequences of rhythmic chewing or electromyographic recording of the jaw muscles. For both types of data sets, the animals were chewing a standard hay mix containing alfalfa, timothy grass and other grasses. Animals were allowed to feed *ad libitum* during recording sessions. Kinematic CCD was determined from video recorded with a Sony Handycam at 60 Hz. Chewing sequences were selected from the videos for analysis. For each animal, at least three chewing sequences

containing multiple same-side chews were selected. Data for left and right chews were averaged as there were no obvious differences associated with chewing side. However, chews bracketing a side-shift within a sequence were excluded from analysis as it appeared that there were changes in CCD associated with the shift and movement of the food bolus. As there were many sequences in which maximum gape could not be reliably determined because of head movements, CCD was calculated in milliseconds as the duration of chewing sequence length divided by the number of complete rhythmic chews from maximum gape of the first chew to maximum gape of the last chew of the sequence.

CCDs based on electromyograms (EMGs) were calculated as the time in milliseconds between successive peaks of working-side superficial masseter EMG during a rhythmic chewing sequence with multiple chews on the same side (Fig. 1). EMG data collection and quantification procedures are described elsewhere (Williams et al., 2010a). Briefly, EMGs from the superficial masseters were acquired using finewire bipolar electrodes. EMGs were amplified and filtered (bandpass, 100–3000 Hz; Grass Model P511, West Warwick, RI, USA) and recorded at 10,000 Hz per channel using Labview 8.0 (National Instruments, Austin, TX, USA). Raw EMGs were transformed into a single, positive waveform by calculating the root mean square (r.m.s.) using a 42 ms time constant in 2 ms intervals (Hylander and Johnson, 1994). Exclusion criteria associated with side shifts were similar to those for the kinematic CCD data set. CCDs from each sequence were averaged to create single chewing cycle mean and standard deviation for each individual. In the case of the ontogenetic data sets of single individuals, a single chewing cycle mean and standard deviation was calculated for an individual at a specific body mass or jaw length.

#### Data analysis

All data were log transformed prior to analysis. In order to investigate the scaling relationship of CCD with body mass and jaw length, we conducted standardized major axis (SMA) regressions using SMATR (Falster et al., 2006) individually for each species. We also calculated 95% confidence intervals (CIs) for the SMA slopes. For SMA regressions exhibiting a significant correlation between CCD and either body mass or jaw length, SMA slopes for CCD–body mass regressions were tested against predicted slopes from the literature of 0.25 for body mass and 0.50 for jaw length (e.g. Druzinsky, 1993; Fortelius, 1985). This is done in SMATR by

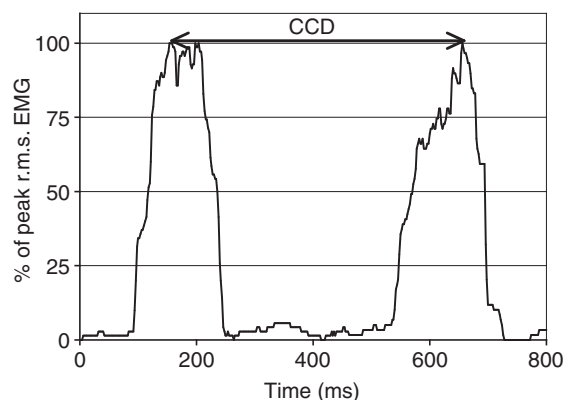


Fig. 1. Calculation of chewing cycle duration (CCD) from integrated electromyograms (EMGs). The EMG waveforms from the working-side superficial masseter during two consecutive chews are shown. CCD is calculated as the time between successive peak EMGs of this muscle.

determining whether there is a correlation ( $F$ -test) between residual and fitted axis scores when a line with the predicted slope is fitted to the data. Although not a major focus of this study, interspecific comparisons of SMA slopes were also conducted to determine whether goats and alpacas exhibited similar ontogenetic trajectories for CCDs and, together, whether they differed from the horses. Tests for a common slope among the groups were conducted in SMATR, which uses a likelihood ratio test and compares it with a chi-squared distribution. In cases where there were common slopes between groups, tests for shifts in the elevations or shifts along the axis were conducted by comparing residual axis and fitted axis scores, respectively, using the Wald statistic (Warton et al., 2006). If no common slope could be fitted to the three groups, then *post-hoc* pairwise comparisons were conducted to determine which groups differed from each other. Details of these procedures are provided elsewhere (Warton et al., 2006).

## RESULTS

Individual means for each variable are provided in Table 1. The smallest horses were approximately 1/6th the body masses of the largest horses with jaws about half the length. The difference in the body masses among the goats was more pronounced, with the largest goats weighing approximately 8 times more than the smallest goats. Differences in jaw lengths were less pronounced but, like the horse, the jaws of the smallest goats were just over half the length of those of the largest individuals. In the alpacas, there was only a fourfold increase in body mass but jaw length differed by 50% between the smallest and largest individuals. Chewing cycle duration among the individuals differed by 290 ms in the horses, 430 ms in the goats and 334 ms in the alpacas.

#### Scaling of CCD with body mass and jaw length

In horses, there was a very slight trend towards increases in CCD with body mass and jaw length (Fig. 2). However, this trend was not significant as there was no correlation between CCD and either variable (Table 2). In goats and alpacas, there was a significant and positive correlation between CCD and body mass (see Table 2; Fig. 2). The SMA slopes in both species differed from the predicted slope of 0.25 (goats:  $F=10.373$ ,  $P=0.005$ ; alpacas:  $F=4.727$ ,  $P=0.041$ ). CCD was significantly correlated with jaw length in goats but not in horses or alpacas (see Table 2). In goats, the RMA slope of 1.032 was significantly higher than the predicted slope of 0.5 ( $F=35.428$ ,  $P<0.001$ ).

#### Interspecific comparisons of species SMA slopes

The individual SMA regression of CCD on body mass yielded common slopes characterizing all three species. Slope estimates for CCD on body mass indicated a shift both in elevation (Wald statistic=12.267, d.f.=2;  $P=0.002$ ) and along a common axis (Wald statistic=138.396, d.f.=2;  $P<0.001$ ). *Post-hoc* pairwise comparisons identified the horse data set as driving both shifts. Comparisons of residual axis scores between horses and the other two species were significant, signifying a shift in elevation (horses transposed above both other species) (horse *versus* goat,  $P=0.001$ ; horse *versus* alpaca,  $P=0.006$ ) due to their longer CCDs. Likewise, the fitted axis scores also differed between horses and the other two species, reflecting the larger body size in the former (horse *versus* goat,  $P<0.001$ ; horse *versus* alpaca,  $P<0.001$ ). Fitted and residual axis scores for goats and alpacas did not differ significantly from each other. For the SMA regressions of CCD on jaw length, no common slope fitted all three species ( $P<0.041$ ). *Post-hoc* tests for heterogeneity of slopes revealed significant differences between species, with goats having

Table 1. Sample sizes and descriptive statistics for variables in the study

Species	No. of chewing cycles	Body mass (kg)	Jaw length (cm)	CCD (ms)	
				Mean	s.d.
Horse	3	590	47.0	659.7	84.6
	3	540	47.0	887.7	91.3
	1	520	43.2	800.0	–
	3	567	49.5	754.1	40.4
	1	640	51.0	810.0	–
	1	600	47.0	833.3	–
	3	435	41.9	879.6	73.2
	3	168	35.6	702.9	9.5
	3	794	56.0	890.0	87.2
	1	513	48.3	600.0	–
	2	540	45.7	721.8	77.6
	2	620	57.0	801.6	54.3
	3	145	33.0	785.0	45.1
	5	140	32.0	737.5	34.7
	4	160	34.0	686.6	28.0
	8	215	30.5	871.0	42.8
8	250	35.6	839.0	46.1	
Goat	2	52.0	21.0	412.2	36.9
	3	45.0	21.5	486.6	22.2
	4	11.0	13.0	323.8	6.9
	2	15.2	13.5	366.0	31.3
	3	17.0	14.0	439.3	121.1
	3	13.4	13.5	413.0	2.4
	2	52.0	22.0	493.9	10.4
	3	10.8	12.5	354.1	27.4
	2	16.4	12.5	324.7	6.7
	2	47.5	20.5	499.9	17.8
	5	47.5	20.5	597.4	99.5
	6	74.1	23.0	675.8	35.7
	5	89.8	26.0	647.6	61.8
	4	71.6	21.5	758.6	47.0
	3	52.0	22.0	733.3	63.9
	4	14.8	13.5	386.4	64.3
7	23.8	14.5	386.0	45.4	
7	25.2	16.0	388.0	19.4	
11	12.4	12.0	397.6	41.0	
Alpaca	3	61.2	24.5	567.8	84.4
	3	68.0	26.0	474.1	34.0
	3	24.8	20.0	481.7	31.9
	2	32.0	21.0	397.3	32.1
	2	62.0	25.5	458.1	2.7
	3	51.4	24.5	527.0	41.7
	2	53.5	24.0	418.3	82.5
	4	64.2	25.0	628.5	86.7
	3	23.0	20.5	397.0	61.8
	4	23.8	14.5	438.2	78.5
	5	31.2	16.0	468.9	22.9
	6	40.4	17.0	480.7	6.7
	7	30.0	15.3	481.6	6.6
	6	29.0	15.1	418.4	4.4
	10	34.0	16.9	493.6	14.4
	5	29.0	13.4	552.8	20.9
5	31.2	13.5	463.2	11.9	
5	19.8	13.2	448.8	157.4	
6	46.2	23.0	457.2	2.4	
10	61.2	25.0	638.1	56.7	
13	54.5	24.0	530.3	44.8	
11	72.0	25.0	731.0	78.5	
23	73.0	26.0	449.9	64.0	

Each line represents the average recorded for one individual at a particular body mass or jaw length.  
 CCD, chewing cycle duration.  
 s.d., standard deviation.

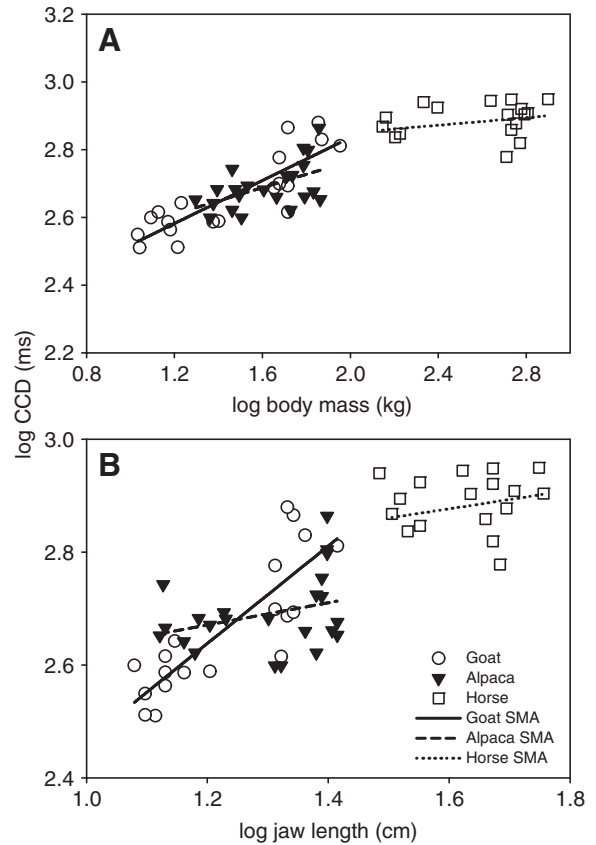


Fig. 2. Bivariate plots of standardized major axis (SMA) regression of CCD on (A) body mass and (B) jaw length.

a significantly higher slope estimate than either horses ( $P=0.047$ ) or alpacas ( $P=0.043$ ). However, the slope estimate for alpacas did not differ significantly from that for horses ( $P=0.891$ ).

**DISCUSSION**

**Scaling of CCD in equids**

In horses, the lack of correlation between CCD and body mass and CCD and jaw length found here is generally consistent with the study of Gerstner and colleagues on dogs (Gerstner et al., 2010). Although we could not sample over as large a size range as in the dog study, the results of the present study clearly demonstrate that chewing rhythm in adults of the same species does not exhibit the same allometric scaling trends as chewing rhythm in adults of different species. As argued by Gerstner and colleagues (Gerstner et al., 2010), one reason for these differences may be the different growth curves for breeds within species as compared to size-matched adults from different species. If CCDs can only respond to changes in jaw mass during development due to the plasticity of CPG networks, scaling coefficients should arguably be tied to the growth curves for specific breeds in intra-specific studies (see Gerstner et al., 2010). As in dogs, adult body masses of horses of different breeds span a smaller range than those of breed-matched foals and weanlings. Although quantitative data on the birth masses of each breed are scarce, birth masses of smaller breeds (e.g. Shetland ponies, ~175 kg adult mass) are approximately 13% of the adult body mass. In contrast, larger breed foals (e.g. Shires, ~1000 kg adult mass) are typically only ~7% of the adult body mass. Medium-sized foals at birth (400–500 kg adult mass) are typically 8–10% of adult body

Table 2. Results of the RMA regressions

Species	<i>N</i>	<i>R</i> <sup>2</sup>	<i>P</i>	Slope	Lower 95% CI	Upper 95% CI	Intercept	Lower 95% CI	Upper 95% CI
CCD–body mass									
Horse	17	0.029	0.653	0.187	0.111	0.314	2.407	2.144	2.671
Goat	19	0.721	<0.001	0.374	0.286	0.488	2.119	1.969	2.270
Alpaca	23	0.281	0.009	0.370	0.254	0.539	2.094	1.864	2.325
CCD–jaw length									
Horse	17	0.003	0.834	0.570	0.337	0.963	1.963	1.452	2.473
Goat	19	0.701	<0.001	1.032	0.783	1.360	1.395	1.039	1.752
Alpaca	23	0.101	0.139	0.620	0.408	0.941	1.887	1.539	2.234

CI, confidence interval.

mass (National Research Council US Subcommittee on Horse Nutrition, 1989). Thus, the low adult horse scaling coefficients relating CCD and body mass or jaw length may be indicative of the relatively narrow time frame when maturation of the CPG occurs in response to changes in jaw size. As foals of different breeds are more similar in size compared with their adult counterparts, they would be expected to exhibit roughly similar CCDs. Thus, the horse data offer a second line of support for the hypothesis of Gerstner and colleagues (Gerstner et al., 2010) that the unique developmental trajectories of domesticated breeds account for the difference in the scaling of CCD with size when compared with interspecific studies.

Although our results are consistent with the recent data from dogs, there are some notable differences between horses and dogs that should be considered. For example, horses of all breeds and sizes have very similarly shaped skulls whereas the facial skeleton and mandible of dogs can differ markedly among breeds of the same size (e.g. the highly curved jaw of Pekingese associated with brachycephaly *versus* the long jaws of the similar-sized Italian greyhound). While Gerstner and colleagues (Gerstner et al., 2010) do not account for these differences, they do acknowledge that jaw growth likely varies among breeds. Thus, given the similarities in jaw morphology among horses we interpret the low scaling exponents in the present study as providing an even more rigorous test of the hypothesis that CCDs mature early beyond which subsequent jaw growth has little influence on chewing rhythm.

Because we do not have ontogenetic chewing data for horses, we must also consider other aspects of masticatory morphology that may influence CCDs and account for the lack of a correlation between CCD and size in horses. For example, selective breeding for size may not result in proportionate changes in tooth size and other components of the masticatory apparatus, all of which may influence CCD. Anecdotal evidence comes from the veterinary dental literature documenting that miniature horse breeds, in particular, are prone to dental crowding and uneven tooth wear associated with disproportionately large teeth (Pence and Mitz, 2002). More quantitative evidence comes from a study by Radinsky (Radinsky, 1984) (see also Williams, 1955) on the scaling of the skull and teeth in horses. He showed that tooth row length scales with negative allometry relative to braincase length in adult horses. Moreover, he showed that the distance between the condyle and the anterior surface of the lower first molar scaled with isometry in the same sample because of the positive allometry of the mandibular angle length (i.e. the distance between the back of the mandibular condyle and the back of the posterior surface of the last molar). This means that small adult horses have relatively long teeth for the skull size, a finding that is consistent with patterns observed in non-domesticated clades exhibiting evolutionary changes in body size (e.g. clades with ‘dwarf’ representatives) (Gould, 1975; Maglio, 1972). Assuming that the length of the tooth row has important

implications for feeding efficiency, the negative allometry of tooth size in domesticated horses may also contribute to the lack of size-related changes in chewing cycle length. Without specific data on tooth size in the individuals in this study, however, we cannot tease apart the influence of the allometry of tooth size *versus* jaw mass-related changes in CCDs in horses. Nonetheless, both factors highlight the influence of domestication on masticatory function caused by the effects of selective breeding on growth in different breeds. In our view, however, the present study provides additional compelling evidence that selective breeding has altered the relationship between CCD and jaw mass observed in interspecific studies due to differences in jaw growth among breeds.

#### Ontogenetic scaling of CCD in goats and alpacas

The ontogenetic analyses yielded mixed results for the scaling of CCD and body mass and CCD and jaw length in goats and alpacas. In both species, there were significant and positive correlations between CCD and body mass. The comparison of residual and fitted axis scores derived from the CCD–body mass SMA regression revealed no differences between the two species. Thus, among closely related species, there is a similar and strong relationship between CCD and body mass during ontogeny. In both species, the SMA slopes involving CCD and body mass were significantly higher than the predicted slope of 0.25 and also the phylogenetically controlled slopes of approximately 0.30 found in interspecific analyses (Gerstner and Gerstein, 2008; Ross et al., 2009b). These results also differ from the intraspecific analyses in horses (this study) and dogs (Gerstner et al., 2010) both of which showed no correlation between CCD and body mass.

One potential interpretation of our results is related to the maturation of the dentition and the development of occlusion. Although there are limited data, ontogenetic changes in CCDs have been observed in other herbivorous species, with mature individuals chewing more slowly than their infant and weanling counterparts. Research on rabbits demonstrates that adults have longer CCDs than infant animals, with this difference being attributed to natural wear processes that shape or ‘prepare’ the occlusal surfaces for processing tough foods (Weijts et al., 1989). Like rabbits, goats and alpacas require precise occlusion and occlusal wear to expose shearing ridges to process tough foods such as hay. Both species also exhibit prolonged periods of dental development, with the full complement of permanent postcanine teeth coming into occlusion around 4 years of age in goats and slightly later in alpacas (Fowler, 1998; Navarre et al., 2002).

In the present study, we included dentally mature individuals with full occlusion and dentally immature individuals lacking fully erupted teeth. In general, however, the alpacas represented a slightly more dentally mature group than the goats, which exhibited more selectivity in their feeding behavior, often chewing only a few strands of hay at a time. Gross comparisons between dentally mature

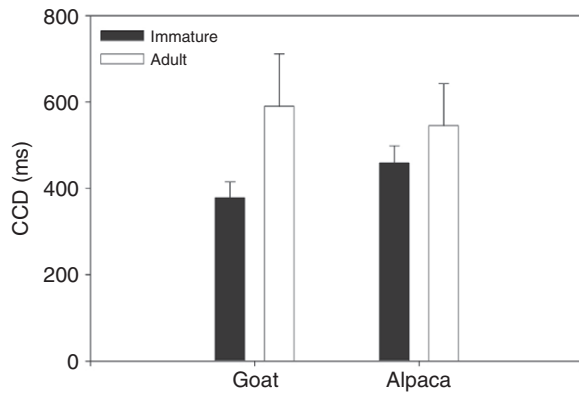


Fig. 3. Bar graphs of mean CCDs for the juvenile (i.e. dentally immature) and adult goats and alpacas used in this study.

and immature individuals in both species demonstrate differences in CCDs (Fig. 3). This is consistent with a previous study in alpacas by Williams and colleagues (Williams et al., 2010a), showing no difference between CCDs of weanlings prior to and following the occlusion of the first molars but a significant increase in CCDs at later stages of occlusion development (Williams et al., 2010a). Lack of functional occlusion may necessitate the extreme selectivity observed in the goats and may also explain the lower CCDs in infants. In alpacas, we have also observed some changes in muscle coordination and chewing motor patterns that may be related to changes in occlusion during ontogeny (Williams et al., 2010a). These too may be an important factor influencing the differences in CCDs between immature and mature individuals in both species. Therefore, it is difficult to interpret the changes in CCDs during ontogeny observed in the two species as direct evidence for the continuing development of the neural networks producing the chewing rhythm. Furthermore, we would predict that maturation of the CPG probably occurs fairly rapidly within the time frame sampled in the present study despite continued growth. This would be represented by a fairly rapid increase in CCDs in the youngest animals (smallest) and then a plateau in CCD as size increases. This is not what we observed in either species. As we could not follow all individuals through the same ontogenetic time frames and our data on the very young animals were limited, we take a more conservative interpretation of our observations, which is that they reflect the inherent flexibility in modulating the CCD in the face of developing occlusal relations and changes in masticatory performance.

Perhaps the most compelling evidence suggesting that we are not necessarily documenting the maturation of the CPG comes from the analyses of the relationship between CCDs and jaw length in alpacas. In alpacas, CCD and jaw length are not correlated, a finding that is also true of strepsirrhine (but not anthropoid) primates (see Ross et al., 2009a). Ross and colleagues (Ross et al., 2009a) argue that differences in jaw mass between lemurids and lorisids may account for the lack of correlation between the two variables in strepsirrhines. However, similar arguments cannot be made for alpacas. We had several animals with very similar jaw lengths (e.g. 25.0 cm and 26.0 cm) and overall body sizes (e.g. 72 kg versus 73 kg) that had markedly different CCDs (e.g. 731.0 ms versus 449.9 ms) (see Table 1 and Fig. 2). Furthermore, there is no reason to believe that these inter-individual differences in CCDs represent differences in the timing of maturation of neural networks underlying chewing rhythm relative to jaw growth between individuals. Individuals within a species have clear similarities in the development of many aspects of the feeding

apparatus (e.g. age of weaning and tooth eruption) so any pronounced inter-individual differences in neural maturation seem highly unlikely as well. Rather, we may be documenting marked inter-individual variability that may exist in CCDs that is often not apparent in interspecific studies. Of course, we have not considered the role that muscles and other components of the chewing apparatus may play in governing CCD. For example, there is preliminary evidence of inter-individual differences in myosin isoform distribution within the jaw muscles of alpacas (P. Starkey, S.H.W., K.K.S. and P. J. Reiser, unpublished data). It remains to be seen whether these differences influence muscle function to the extent that such pronounced differences in chewing rhythm exist between individuals.

In contrast to alpacas, in the goat, CCD and jaw length are highly correlated but scaling exponents are significantly higher than the slope of 0.5 predicted by pendulum models and supported by interspecific regressions (e.g. Druzinsky, 1993; Ross et al., 2009a). Given this high slope and that pendulum models assume the jaw is a gravity-driven pendulum, which it is not, we reject this interpretation of the results for goats. The high slope and significant correlation between CCD and jaw length in goats but not alpacas may be due to differences in the ontogenetic time frame sampled in the two studies. The goats represented a longer ontogenetic 'snapshot' than the alpacas because of the inclusion of younger individuals in the present study, and there was a greater increase in overall jaw growth compared with that of the alpaca. The fact that the SMA slopes differed between goats and alpacas and goats and horses, but not between alpacas and horses, further suggests that larger increases in jaw length are driving the correlation between CCD and jaw length in goats.

We cannot rule out the possibility that the youngest goats are not in the period of neural flexibility allowing for alterations in CCDs in association with changes in jaw size. However, we would expect this period to be fairly rapid, as long bouts of rhythmic chewing become a significant proportion of their behavior early on in development. This is because goats develop rumination very early during ontogeny, which involves a significant amount of time spent chewing per day. Hooper and Welch (Hooper and Welch, 1983) showed that by 3 months of age, kid goats spend 3.9 h per day ruminating, resulting in approximately 38,000 chews day<sup>-1</sup>. Despite prolonged periods of dental and motor pattern immaturity, CPGs should be sufficiently developed to coordinate highly rhythmic chewing by the time the animals begin ruminating at around 2 months of age. If this is the case, we may be observing the maturation of the CPG underlying changes in the CCD in association with jaw growth in the smallest individuals but also the subsequent period when changes in muscle activation in response to changes in food properties may be more important in altering the CCD during ontogeny (see Gerstner et al., 2010).

#### Inter-individual and intra-individual variation in CCDs

Our results are generally consistent with CCDs reported in previous studies. For horses, our data extend the lower and upper limits of published CCDs by over 100 ms and approximately 80 ms, respectively. For infant and weanling goats, our CCDs are approximately 50% shorter than those estimated from data in Hooper and Welch (Hooper and Welch, 1983). However, our results for medium-sized adults weighing 40–55 kg are similar to the reported estimates for size-matched individuals in Gerstner and Gerstein (Gerstner and Gerstein, 2008). At the other end of the size spectrum, our CCDs for the larger adults weighing 70–90 kg are longer by as much as ~250 ms. In alpacas, there is more inter-individual variation in CCDs among the adults compared with the younger animals. For example, two of our largest animals with similar body masses had

Table 3. Comparison of CCDs derived from individually recorded masseter EMGs, and simultaneously recorded masseter EMGs and mandibular corpus bone strains

Species	Animal	EMG only		Simultaneous EMG and bone strain			
		EMG	s.d.	EMG	s.d.	Strain	s.d.
Horse	Animal 1	686.6	28.0	822.4	57.2	826.6	60.7
	Animal 2	737.4	34.7	789.4	64.4	789.1	66.3
Goat	Animal 1	675.8	35.7	645.9	54.3	647.4	48.5
	Animal 2	647.6	61.8	593.5	69.7	593.2	66.1
Alpaca 1	Animal 1	503.0	47.1	626.0	29.2	623.0	31.6
	Animal 2	657.6	58.4	584.9	14.2	581.3	16.8
	Animal 3	668.9	27.0	690.0	58.3	658.5	77.8
	Animal 4	479.0	44.8	422.4	10.2	425.1	12.1

CCD values are in milliseconds.

All data come from the working-side superficial masseter and working-side mandibular corpus following methods outlined in the present study and in Williams et al. (Williams et al., 2009).

CCDs of 731 and 450ms, the latter being more similar to that reported for a much larger (100kg) individual (Gerstner and Gerstein, 2008).

Intra-specific variation in chewing CCDs can be due to several factors. First, despite similarities in chewing behaviors, we cannot rule out the influence that experimental conditions have on CCDs when comparing across studies or even within studies using different data collection techniques. Previously reported CCDs for goats, alpacas and horses are based on kinematic (e.g. Druzinsky, 1993; Fortelius, 1985; Gerstner and Gerstein, 2008), EMG (Williams et al., 2010a) and mandibular corpus bone strain data (e.g. Ross et al., 2007), all of which require different levels of manipulation of the animal, which in turn may influence chewing behavior, including chew duration. For example, Thompson and colleagues (Thompson et al., 2007) found that the anesthesia required for strain gauge implantation in bone strain studies and electrode implantation in EMG studies on primates results in significantly lower CCDs (based on kinematics) than when the animals had no experimental manipulations and were allowed to move freely in their cages.

Although we cannot replicate this analysis exactly with our data, we can evaluate the extent to which experimental conditions of EMG and combined EMG and bone strain data collection protocols influence CCD values within the same individuals using previously recorded data for several adult individuals per species. We compared CCDs based on masseter EMG data with those based on independently and simultaneously recorded mandibular corpus bone strains data from the same individuals (Table 3). Whereas EMG-only experiments require no or mild sedation for electrode implantation, experiments with simultaneously recorded EMG and bone strain data require full anesthesia for the implantation procedures (see Williams et al., 2007; Williams et al., 2008; Williams et al., 2009). Simultaneously recorded EMG and bone strain data are expected to yield similar CCD values whereas

individually recorded data may not. As expected, for all three species, we found nearly identical EMG and bone strain CCDs when calculated from simultaneously recorded data. Sequence averages and species means were nearly identical, differing usually by less than 10ms with only one exception (see Table 3). When compared with simultaneously recorded EMG or bone strain data, CCDs derived from EMG-only experiments on the same individual were lower in most, but not all, cases. In general, however, they were very similar. While these subtle differences may be due to the effects of sedation *versus* anesthesia or the implantation protocols, they more likely represent the inherent intra-individual variation in CCDs, which is readily apparent when CCDs from multiple EMG-only experiments on adult individuals. These intra-individual differences make the similarities in independently derived EMG and bone strain CCDs within and across studies even more remarkable.

Finally, in ruminants a major source of intra-individual variation in CCDs is the different types of chewing behaviors. Specifically, our previous research on goats and published data for other species show that ingestive chewing and rumination chewing CCDs can differ by as much as 33% (Table 4) (Fortelius, 1985; Williams et al., 2010b). Both studies show that CCDs during rumination are typically longer than those during ingestive chewing. Consequently, across species, rumination CCDs regressed against body mass yield a slightly higher slope than those for ingestive CCDs (Druzinsky, 1993). This intra-individual variation in CCD during chewing likely reflects differences in bolus consistency and the mechanics of breaking down fresh forage *versus* cud. Given the differences in CCDs for the two behaviors, the CPG governing rhythmic chewing appears to be highly plastic, being influenced substantially by the peripheral nervous system to alter temporal parameters of chewing. For the purposes of CCD comparisons across individuals and studies, these differences highlight the need to ensure that the two behaviors

Table 4. Comparison of CCDs during ingestive and rumination chewing

Species	Ingestion CCD (ms)	Rumination CCD (ms)	%Increase	Body mass (kg)
<i>Capra hircus</i> *	602	739	23	45–52
<i>Capra ibex</i>	597	821	38	40
<i>Capra falconeri</i>	581	657	13	64
<i>Hemitragus jemlahicus</i>	471	628	33	50
<i>Oreamnos americanus</i>	780	846	8	60
<i>Bos grunniens</i>	872	880	10	250
<i>Camelus bactrianus</i>	912	1172	29	500

\*Data are from Williams et al. (Williams et al., 2010b). All other data are from Fortelius (Fortelius, 1985).

are not conflated, particularly in studies where the experimental conditions cannot be rigorously controlled.

### CONCLUSIONS

The present study investigated the intraspecific scaling of CCD with body mass and jaw length in three species of domesticated mammals with the goal of testing biomechanical and developmental hypotheses for the scaling of chewing rhythm in mammals. The intraspecific scaling of CCD with body mass and jaw length within species of domestic ungulates differs from that observed between species. The results of the analyses on the three different species suggest that multiple factors are involved in the observed scaling relationships of CCDs with body mass and jaw length. In adult horses, the differences may reflect CPG development in response to jaw mass properties and reduced size variation in foals. However, as with goats and alpacas, we cannot rule out the effect of other aspects of growth and development during later ontogeny, particularly in the masticatory apparatus. Additional and more controlled studies on single individuals from the earliest stages of postnatal ontogeny are necessary for teasing apart these factors underlying flexibility in the CPG during ontogeny.

The focus of this paper on intraspecific CCDs in ungulates also highlights the range and potential sources of inter- and intra-individual variation inherent in timing parameters relating to rhythmic chewing. In addition to the myriad experimental conditions that can influence CCDs within individuals, animals also have the ability to modulate their chewing behavior to alter chew duration. Ongoing research on ruminants will investigate one example of this ability to modulate rhythmic mastication by comparing chewing cycle kinematics and phase durations during ingestion *versus* rumination chewing within individuals.

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