

Ontogeny of feeding function in the gray short-tailed opossum *Monodelphis domestica*: empirical support for the constrained model of jaw biomechanics

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Summary

The constrained model of masticatory function enables specific predictions of bite force potentials in skulls of differing craniodental configurations. In this study, empirical support for the constrained model is provided using maximum voluntary bite force data along Region I and II of the jaws of gray short-tailed opossums *Monodelphis domestica*. Then, growth series of *M. domestica* are used to assess how bite force potential changes with growth by evaluating craniodental changes using longitudinal sets of dorsoventral radiographs and by assessing maximal bite force potential at the Region I–II boundary of the jaw in juveniles (aged 70–80 days) and adults. Our findings show that, while juveniles and adults alike enclose at least three molariform teeth within Region

II (the area of highest bite force potential along the jaw), age-dependent elongation of the masticatory muscle resultant lever arm and narrowing of the palate relative to jaw length especially enhance the mechanical advantage of the adductor muscle resultant in adults. While maximal bite forces at the Region I–II boundary are absolutely greater in adults, these bite forces scale isometrically with body mass, which suggests that mass-specific forces exerted by jaw adductor muscles of larger (adult) opossums are disproportionately smaller than those exerted by smaller (juvenile) opossums.

Key words: bite force, ontogeny, gray short-tailed opossum, *Monodelphis domestica*.

Introduction

While juvenile and adult mammals are commonly confronted with similar functional challenges, body shape and size differences (and their physiological consequences) between age groups may necessitate the use of different strategies to deal with these challenges. For example, Carrier (1983, 1995) found ontogenetic limits on locomotion in jackrabbits *Lepus californicus*. Juvenile hares, which forage independently at a very young age, are able to accelerate more rapidly than adults, a feat accomplished in part by a greater mechanical advantage in the gastrocnemius muscle of juveniles. Conversely, the overall smaller size of juvenile hares negatively affects their locomotor stamina. Consequently, juvenile hares tend to avoid predation primarily by crypsis and, if detected, accelerating to another refuge rather than attempting to out-run their predators. In other words, allometric changes in the appendicular musculoskeletal system across postnatal ontogeny necessitate different locomotor behaviors in order to accomplish a similar outcome (avoiding predation).

Craniofacial structures also differ in juvenile and adult mammals. Compared with the adult masticatory apparatus, juveniles typically have absolutely smaller masticatory musculature, house fewer teeth in their jaws, and have

substantially distinct jaw configurations. For example, puma *Felis concolor* and spotted hyena *Crocuta crocuta* juveniles have short, wide jaws compared to their adult counterparts (Biknevičius, 1996), and this shape difference contributes to the reduced bite force production of juveniles (Binder and Van Valkenburgh, 2000). Functional inadequacies of the juvenile masticatory apparatus are initially counteracted by maternal provisioning of food (milk and then solids) to the offspring. This extended period of parental care allows more time for the development of the feeding apparatus, thereby ensuring that weaned juveniles are adequately equipped to compete effectively for meat, and thus increasing survival of offspring (Mills, 1990).

An extended period of parental care is not ubiquitous among mammals. Juveniles of many species must forage independently for food soon after weaning, as is the case for gray short-tailed opossums, *Monodelphis domestica*. Indeed, juvenile *M. domestica* may be directly competing with adults for similar foods as no resource-partitioning between age groups has been documented (Parker, 1977). The present study explores the configuration of the upper jaw of *M. domestica* in order to assess whether or not juvenile jaws display adaptations, allowing for bite force production, as in adults.

The analysis is based on the constrained model of lever mechanics of the jaws.

Constrained model of lever mechanics

A constrained model of lever mechanics was developed in the 1970s and is largely associated with the work of Walter Greaves (1978, 1982, 1988; see also Bramble, 1978; Spencer and Demes, 1993; Spencer, 1998, 1999). Three points of resistance ('triangle of support') occur during unilateral biting: one at each temporomandibular joint (TMJ) and one at the bite point (Fig. 1A). The side of the jaw where the bite occurs is known as the working (biting) side and the contralateral side is the balancing side. The model assumes that the adductor muscle resultant force (the bilateral sum of the adductor muscle forces, F_m) is positioned to limit distractive forces at the TMJ, as there is no evidence of regular loading of TMJs by large tensile stresses (Hylander, 1979). Accordingly, the muscle resultant is assumed to lie within the triangle of support and no further anterior than the distal margin of the caudalmost tooth (for more details, see Greaves, 1978; Spencer and Demes, 1993). Furthermore, the adductor muscle resultant force lies in the sagittal plane when jaw adductor muscles act bilaterally and equally.

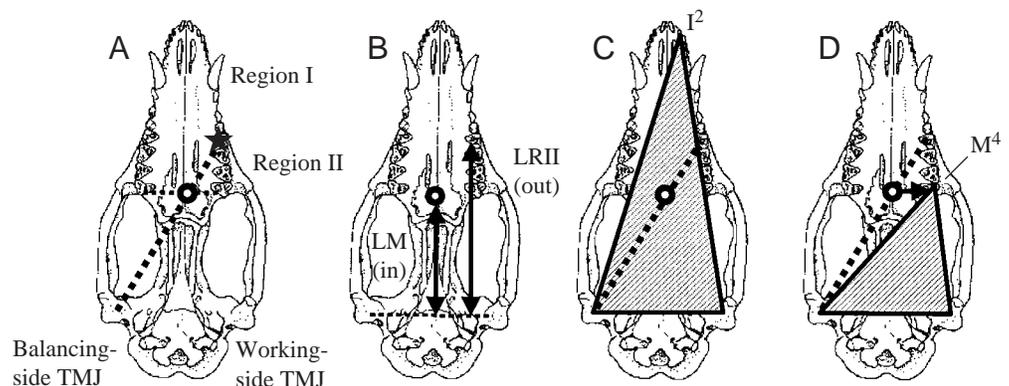
A line trajectory that originates at the balancing-side TMJ and passes through a point representing a midline muscle resultant will intersect the working-side tooththrow at the Region I–II boundary (Fig. 1A; Spencer and Demes, 1993). This intersection distinguishes the jaw into Region I anteriorly and Region II posteriorly. According to the constrained model, maximal bite force magnitudes obey different mechanical rules in Regions I and II.

Bite force magnitudes in Region I follow simple lever mechanics, that is, bite forces are inversely proportional to the leverage of the bite force but directly proportional to both the muscle resultant force and its leverage. Because the triangle of

support is large, masticatory muscles can contract bilaterally and maximally when biting with teeth located in Region I. The muscle resultant is, therefore, located sagittally and no further anterior than the caudalmost molars. Bite force magnitudes are expected to increase caudally along Region I in response to decreases in mechanical advantage of the lever system (ratio of in-lever to out-lever, with the in-lever measured as the distance from the interglenoid line to F_m and the out-lever as the distance from the interglenoid line to the bite; Fig. 1B). Maximal bite force values are obtained at the Region I–II boundary.

Different mechanics control bite force magnitudes in Region II. According to the constrained model's original conception, bite forces do not continue to increase caudally across Region II, but rather are equal in magnitude to the maximal value obtained at the Region I–II boundary (Greaves, 1978). This is because a midline muscle resultant would be excluded from the triangle of support when biting with Region II teeth, and repositioning it within the triangle of support necessitates a reduction in balancing-side muscle activity (shifting the vector laterally toward the working-side jaw; Fig. 1C). While maximal muscle resultant forces are lower in Region II than in Region I, high bite forces are maintained across Region II because lower muscle forces are paired with reduced out-lever lengths. More recent work has challenged the expectation of equal and maximal bite force within Region II. While electromyographic (EMG) data of jaw adductor muscles in humans show the ratio of balancing-side-to-working-side activity fell within Region II (as expected to keep the muscle resultant within the smaller triangle of support), activity levels of both working- and balancing-side activity levels fell when biting with more posterior teeth, suggesting that bite force magnitudes may actually decrease caudally within Region II (Spencer, 1999). Mathematical modeling for estimating bite force magnitudes also anticipate a posteriorly decreasing bite

Fig. 1. The constrained lever model of the masticatory apparatus illustrated on the ventral skull of *Monodelphis domestica*. (A) The Region I–II boundary (indicated by the star) is located where the trajectory from the balancing-side temporomandibular joint (TMJ) intersects the working-side jaw after passing through the midline muscle resultant (midline circle). Region I and Region II are those parts of the dental array rostral and caudal to the Region I–II boundary, respectively. (B) The in-lever and out-lever are measured as the perpendicular distance from the interglenoid line to the muscle resultant (LM) and to the bite point (shown here at the Region I–II boundary, LR_{II}), respectively. (C) Biting with Region I teeth. The triangle of support (hatched area) is defined by the working- and balancing-side TMJs and the bite point (shown here as the I²). Because a midline muscle resultant is enclosed within the triangle of support, jaw adductor muscles may contract maximally and bilaterally. (D) Biting with Region II teeth. The triangle of support shrinks as bites are produced with teeth located caudal to the Region I–II boundary (bite point shown here is the M⁴). The muscle resultant vector must shift laterally toward the working side jaw in order to remain within the triangle of support (illustrated by the arrow); this accomplished *via* a reduction in the contractile force of the balancing-side musculature.



force within Region II (Kieser et al., 1996). This is precisely the pattern found in one study of bite forces in humans (Pruim et al., 1980), although other human studies found increasing bite forces posteriorly (Mansour and Reynick, 1975; van Eijden, 1991).

One of the appeals of the constrained model of masticatory function is that it enables specific predictions of bite force potentials in skulls of differing configurations, as might occur during ontogeny. Bite force potential at the Region I–II boundary is of great interest because this represents the highest bite forces potential across the jaw (Greaves, 1978; Kieser et al., 1996; Spencer, 1999). Mechanical advantage, or the ratio of the lever arm length of the muscle resultant (in-lever) to that of the bite point at the Region I–II boundary (out-lever), strongly influences bite force maxima. While certain changes in craniofacial dimensions have straightforward affects on mechanical advantage (e.g. a shortened out-lever to the bite point increases mechanical advantage), others are more complicated. For example, simply elongating the muscle resultant lever arm (broken lines in Fig. 2A) does not improve mechanical advantage because it is accompanied by a proportionately equivalent elongation of the Region I–II boundary lever arm (see Discussion and Appendix I). Mechanical advantage may also be affected by differential widening of the skull components. Increasing interglenoid width (by shifting laterally the glenoid fossae; broken lines in Fig. 2B) will shorten the leverage to the Region I–II boundary because this configurational shift drives a more acute trajectory to the working-side jaw (W. S. Greaves, personal communication; Spencer, 1999). By contrast, the out-lever length to the bite point will decrease if the cheek teeth move medially (narrowing the palate; broken lines in Fig. 2C)

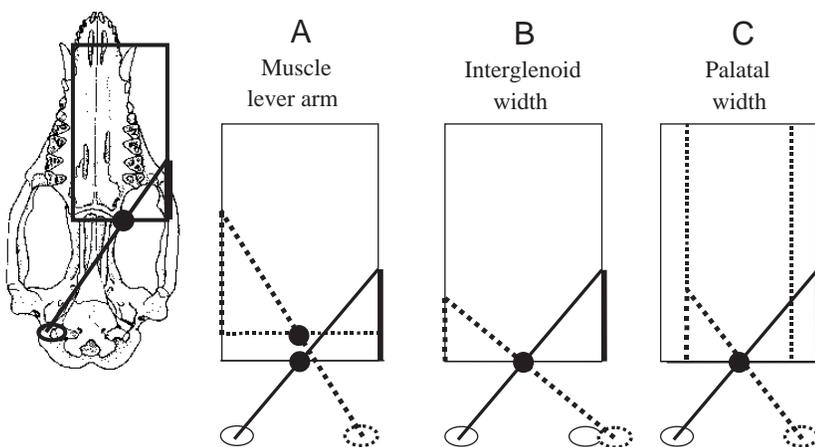


Fig. 2. Effect of changing craniofacial configurations on mechanical advantage. The inset illustrates the simplification of the palate as a rectangle, the glenoid fossae as ovals, and the midline muscle resultant as the filled circles. The solid lines portray a baseline condition for comparison with the altered condition (indicated by the broken lines), illustrating three different means by which mechanical advantage may be enhanced: (A) elongation of the masticatory muscle resultant lever arm (not effective; see Appendix I), (B) widening interglenoid width and (C) palatal widening.

because the shorter trajectory from the balancing-side TMJ will intersect the working-side tooth row more caudally. Narrowing the palate also has the effect of allowing higher bite force magnitudes within Region II as a relatively smaller reduction in balancing-side muscle activity is adequate to move the muscle resultant back into the triangle of support when biting with the caudalmost teeth (Spencer and Demes, 1993).

The constrained model has been used to explain the adaptive significance of orofacial configurations as varied as Neandertals and Inuits (Spencer and Demes, 1993) and carnivorous marsupials (Werdelin, 1987). And while it has also been used to evaluate age-dependent craniofacial changes in carnivorans (Biknevicius, 1996) and to explain the great bite-force potential in ferrets *Mustela putorius* (Dessem and Druzinsky, 1992), the constrained model has never been rigorously tested in non-human mammals. Therefore, the first objective of the present study is to provide empirical support for the constrained model of jaw mechanics using voluntary bite force data in adult gray short-tailed opossums *Monodelphis domestica*. Then, ontogenetic changes in the jaw of *M. domestica* are documented in order to explain differences in maximal bite force potential in *M. domestica* juveniles and adults.

Materials and methods

Verification of the constrained model of jaw mechanics

Bite force data were collected from eight adult (four females and four males) gray short-tailed opossums *Monodelphis domestica* (Wagner 1842). Adults were well over 100 days old and ranged in body mass from 61 to 125 g (mean 90 g) (Parker, 1977; Maunz and German, 1996), therefore, this study does not include early postnatal development of the marsupial's skull (Smith, 1994).

Bite force transducers were designed after the models of Binder and Van Valkenburgh (2000) and McBrayer and White (2002). The transducers were composed of two parallel steel plates (tines) that were cantilevered to a brass handle. Four foil strain gauges were firmly bonded on each surface of each tine at the cantilevered end, and these were configured into a full Wheatstone bridge. The tips of the tines were tapered so to allow specificity of tooth use. The distal end of each tine was also covered with a rubber coating to protect the teeth of the opossums during forceful biting (Rubberize-It!, Rhodes American, Chicago, IL, USA). Two bite force transducers were built, each differing only in the dimensions of the tines: the distal end of the smaller transducer (including the rubber coating) was 3.2 mm in width whereas the larger transducer was 4.8 mm wide. Biting on the force transducer caused the tines to bend toward one another and thus altered the voltage output of the Wheatstone bridge. Analog outputs were

amplified (National Instruments SCXI 1000 and 1121, Austin, TX, USA) and then converted to a digital format (National Instruments NB-M10-16L). Voltage changes were recorded with a LabView 5.0 (National Instruments) virtual instrument data acquisition program (designed by S. M. Reilly, Ohio University, USA). Data were collected at 500 Hz for 20 s. The transducers were calibrated each trial day by simultaneously loading the tines with known weights (0.05–0.5 kg); the resulting voltage outputs were then regressed against weight (in N) to determine the calibration factor between the variables (McBrayer and White, 2002).

The opossums either readily bit on the bite force transducers or were induced to bite by pinching the nape of their necks (which caused them to open their jaws). Only unilateral bites were recorded. The position of the transducer along the jaw was determined videographically using a 60 Hz Hi-8 camcorder (Sony CCD-TR400). Three bite locations were identified: incisor or canine, premolar (excluding the deciduous premolar in juveniles), and Region II (molars plus deciduous premolar in juveniles; Fig. 3A). The tines of the smaller bite force transducer were sufficiently narrow to localize bite forces from individual molars within Region II in the adult opossums (M^1 , M^2 and M^3 only; the caudalmost molar was difficult to visualize).

Bite force data were captured during multiple trials over several days, but only the maximal voluntary bite force record for each bite location from each individual was used in the analysis because the constrained model predictions are based on maximal force production. We assumed that bite force transducer results provide a good proxy for the initial puncture-crushing phase of mastication; indeed, in teiid lizards *Tupinambis teguixin* motor activity patterns of adductor muscles during high bite force development on a

force transducer were similar to those developed during initial capture bites and crushing bites (McBrayer and White, 2002). Unfiltered bite force data were analyzed. Due to the problem of interdependence that is inherent in collecting multiple measurements from a given animal, repeated-measures analysis of variance (ANOVA) was used to determine position variation in maximal bite force using SYSTAT 9 (Wilkinson, 1998). This was followed by a Bonferroni pairwise comparison where significant variation was determined.

Morphological sample

Linear measurements of the upper jaws were obtained from longitudinal sets of dorsoventral radiographs of *Monodelphis domestica* in order to assess how geometric differences in the orofacial complexes of juveniles and adults arise. These radiographs represented eleven individuals from three different litters (Maunz and German, 1996). The animals were weaned at 48 days of age, similar to the time of weaning in the wild (50 days of age; Parker, 1977). The animals were radiographed at 2-day intervals starting from 50 days of age until 160 days old, after which radiographs were taken every 10–20 days until the animals reached 395 days of age. Although *M. domestica* stops gaining weight at around 250 days of age (Maunz and German, 1996), periodic radiography continued through 395 days to ensure that skeletal growth was complete.

The radiographs were imported into the computer by either downloading digital images captured with a Kodak DC265 digital camera or scanning the radiographs directly into the computer using a Hewlett Packard ScanJet HDF scanner; these techniques produced equivalent results. Nine landmarks were identified along the skull, primarily on the upper jaw (Fig. 3B, Table 1). Of the nine, five were homologous landmarks on the juvenile and adult skulls (landmarks 1, 7, 3, 5 and 4). The remaining landmarks were influenced by dental eruption. The caudal borders of the distalmost molars (landmarks 2 and 6)

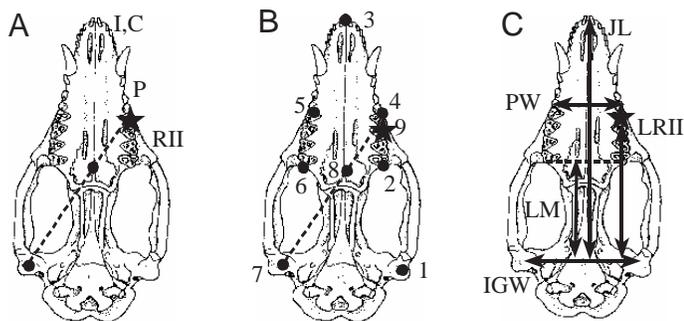


Fig. 3. Ventral view of the skull of a *Monodelphis domestica* adult. (A) Maximal bite forces were measured from three locations along the jaw: incisors or canines (I,C), premolars (P) and molars (M) and deciduous premolar (dP; juveniles only) located in Region II (RII). The first two locations are in Region I. The oblique broken trajectory intersects the left jaw at the Region I–II boundary. (B) Landmarks digitized on radiographs (see Table 1). (C) Linear measurements produced for the reduced major axis and Gompertz regressions: IGW, interglenoid width; JL, jaw length; LM, lever arm of resultant adductor muscle force (in-lever); LR II, lever arm to the Region I–II boundary (out-lever); PW, palatal width. Stars indicate the bite point.

Table 1. Craniodental landmarks shown in Fig. 3B and their use in each analysis

Landmarks	Analyses	
	RMA	Gompertz
1,7 Geometric center of the left and right TMJ	X	X
2,6 Buccodistal corner of left and right distalmost molar	X	
4,5 Left and right P ³ –M ¹ interdental gap	X	X
3 I ¹ –I ¹ interdental gap	X	X
8 Adductor muscle resultant vector ^a	X	
9 Region I–II border on the left jaw	X	

RMA, repeated-measures analysis; TMJ, temporomandibular joint.

^aAdductor muscle resultant vector when biting with the teeth located at the Region I–II boundary is assumed to lie at a sagittal position (midline), immediately posterior to the distalmost erupted molar.

X indicates use in analyses.

necessarily shift caudally with successive molar eruption. Consequently, the assumed location of the midline muscle resultant (landmark 8), determined by landmarks 2 and 6, also shifts caudally with dental eruption. Finally, an oblique line was drawn from the right TMJ (landmark 7), through the midline muscle resultant; the intersection of this trajectory with the contralateral tooth row determines the location of the Region I–II boundary (landmark 9, or the location of maximal bite force potential).

Landmarks were digitized using the Thin Plate Spline digitizing program (TPS dig) and were used to define the following linear measurements (Fig. 3C). Palatal width was calculated as the width of the palate distal to P³. A baseline axis was drawn between the centroids of the glenoid fossae, the length of which was used as the interglenoid width. Jaw length was calculated as the perpendicular distance from the baseline axis to the I¹–I¹ interdental gap. The resultant adductor muscle force lever arm (in-lever) and the Region I–II lever arm (out-lever) were calculated as the perpendicular distances from the baseline axis between the glenoid fossae to landmarks 8 and 9, respectively.

Morphometric analyses

Reduced major axis regressions were run on log₁₀-transformed variables using the SYSTAT 9 statistics package (Wilkinson, 1998). The first set of regressions explored the relationship between skull width measurements and jaw length. The second set evaluated the relationship among lever arms and jaw length. This latter analysis was complicated because caudal tooth eruption caused a punctuated change in the lengths of the both lever arm (see Fig. 5B). Therefore, the data were split into two samples according to eruption pattern (those with a fully erupted M³, i.e. adults, *versus* those without, i.e. juveniles and sub-adults) and separate regression coefficients were calculated for each age group. Significant allometric patterns were identified by inspection of the 95% confidence intervals for each regression slope (isometry indicated by a slope of 1).

Ontogenetic growth patterns for jaw length, palatal width and interglenoid width were established by plotting raw values of each variable against age (days) and using the Gompertz non-linear curve-fitting equation (Maunz and German, 1996; Lammers et al., 2001):

$$Y = Ae^{-be^{-kt}}, \quad (1)$$

where Y represents the variable measured, A is the asymptote of Y , b is onset of rapid growth of the measured variable, k describes its rate of growth decay, and t is age. Additionally, the rate of instantaneous growth (I) was calculated by multiplying b with k . The time of growth cessation (T_f) was described as the time at which growth slows to 5% of its maximal rate (modification of Lammers et al., 2001) and was calculated as:

$$T_f = [-\ln(0.05/b)]k^{-1}. \quad (2)$$

Gompertz parameters were determined for jaw length,

palatal width and interglenoid width for each individual *M. domestica*. Significant differences between these Gompertz parameters were quantified by running one-way ANOVAs; patterns of variation were confirmed with the Tukey *post-hoc* test using the NCSS statistics package (Hintze, 1998). Parameters were identified as being significantly different from each other if $P < 0.05$.

Maximal masticatory force potentials for *M. domestica* juveniles and adults

Bite force data were also collected from eight *M. domestica* juveniles (all female) that were 70–80 days of age, i.e. these animals were weaned but were still anatomically and reproductively immature (Parker, 1977; Maunz and German, 1996). These juveniles were unrelated to the opossums used to obtain the adult bite force sample. Body mass range was 30–40 g, mean 35.5 g. As with the adults, bite force data were captured during multiple trials over several days, but only the maximal voluntary bite force recorded for incisor/canine, permanent premolars and Region II teeth (including the deciduous premolar) from each individual was used in the analysis. Unfortunately, the smaller mouths of juveniles provided limited visibility for discriminating Region II teeth, therefore only pooled data on bites from Region II are reported. Bite force data for juveniles were compared with those obtained for adults, with position and age-related variation in maximal bite force determined *via* repeated-measures ANOVA followed by Bonferroni pairwise comparisons using SYSTAT 9 (Wilkinson, 1998).

In order to further compare bite force potentials of juveniles and adults, it was assumed that biting at the Region I–II boundary represented a functionally equivalent event in juveniles and adults, because this is where the greatest maximal voluntary bite forces are expected to be generated according to the constrained model of jaw mechanics. Mechanical advantage, or the ratio of lever arm of the muscle resultant to that of the tooth located at the Region I–II boundary, was determined using dorsoventral radiographs of juvenile and adult *M. domestica*; animals were first anesthetized by isoflurane inhalation prior to radiography in order to minimize movement artifacts. Finally, scaling coefficients of mechanical advantage and bite force against body mass (M_b) were determined by reduced major axis regression. A slope of 0 meets the expectation of geometric similarity for mechanical advantage. Because muscle force is proportional to the cross-sectional area of the muscle, isometry expectations are met when muscle and bite forces scale with $M_b^{0.67}$.

Results

Location of Region I–II boundary

The Region I–II boundary in *M. domestica* was located at dP³ (deciduous premolar 3) in juveniles and at either M¹ or M² for adults. Because dP³ is molariform, Region II always encloses only molariform ('grinding') teeth in all age groups. Furthermore, Region II always contains at least three teeth:

Table 2. Maximal voluntary bite forces in *M. domestica* juveniles and adults using the incisors or canines (I,C), Region I premolars (P), Region II teeth (which include the deciduous premolar in juveniles), and, for the adult sample only, M¹, M² and M³ within Region II

	Bite force (N)				Age-group comparisons
	Region I		Region II		
	I,C	P			
Adults (N=8)	20.78±0.75	25.12±0.76	31.26±1.20	I,C<P<RII*	
Juveniles (N=8)	10.25±0.75	12.38±0.76	17.24±1.20	I,C=P<RII†	
Adult/juvenile comparison‡	J<A	J<A	J<A		

	Molars within Region II			Within Region II
	M ¹	M ²	M ³	
	Adults (N=7)	31.20±2.27	31.72±2.52	

Values are means ± S.E.M.

*P-values for comparisons of bite locations within adults: between P and RII, $P<0.018$; for all other comparisons, $P<0.001$ (except between molars in adults, which were not significant).

†P-values for comparisons of bite locations within juveniles: between I,C and P, $P<0.27$ (not significant); between P and RII, $P<0.001$; between I,C and RII, $P<0.002$.

‡P-values for comparisons between adults and juveniles within each bite location: $P<0.02$.

dP³ through M² in juveniles and M¹ or M² through M⁴ in adults.

Variation of bite force along the jaw in adult *M. domestica*

Maximal voluntary bite forces varied significantly with respect to tooth position in *M. domestica* (Fig. 4; Table 2). Among adults, bite force magnitudes of Region II teeth were,

on average, greater than those of Region I ($P<0.002$). Within Region I, bites generated with the premolars were stronger than those with the incisors or canines ($P<0.02$). By contrast, maximal bite forces did not vary significantly within Region II, so that bites with M¹, M² or M³ were equivalently strong ($P>0.17$).

Craniofacial allometry

The longitudinal growth series revealed that both palatal width and interglenoid width scale with negative allometry relative to jaw length in *M. domestica* (Fig. 5A; Table 3). Furthermore, palatal width scales with negative allometry with respect to interglenoid width. Therefore, skull widths (particularly palatal widths) become relatively narrower as *M. domestica* develop.

Scaling relationships for either the muscle resultant lever arm or Region I–II lever arm length against jaw length consistently demonstrated positive allometry in both juvenile and adult age-groups (Fig. 5B; Table 3). In other words, older individuals (within each age group and across both groups) exhibit relatively longer lever arms. Additionally, positive allometry was found for the regression of muscle leverage against bite point leverage, indicating that the elongation of Region I–II lever arm falls behind that of the muscle resultant through ontogeny.

Finally, positive allometry was found for regression of lever arm lengths on cranial width in both the juvenile and adult sample (Table 3). Consequently, compared with juveniles, adult orofacial proportions emphasize length over width.

Ontogenetic trajectories

Growth curves for jaw length, palatal width and interglenoid width obtained from the longitudinal growth series are shown

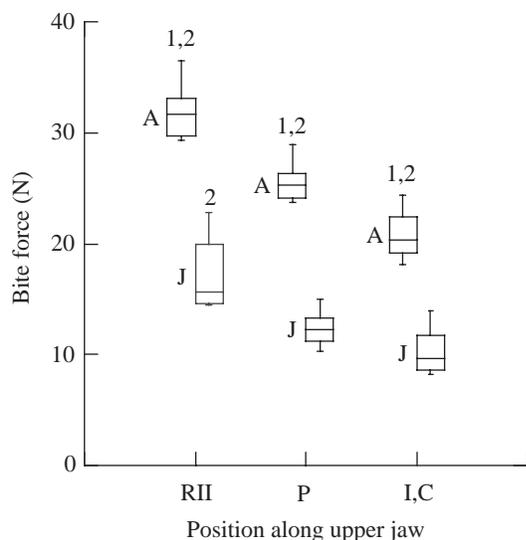


Fig. 4. Box plots of bite forces collected from *Monodelphis domestica* juveniles (J) and adults (A) at three locations along the dental arcade: Region II (RII, including molars and, in juveniles, deciduous premolar), premolar (P) and incisors or canines (I,C). Significant differences within the sample: 1, $P<0.02$ between age groups within a single dentary region; 2, $P<0.001$ between tooth positions within an age group.

Table 3. Reduced major axis slopes and 95% confidence intervals

Dependent variable	Independent variable	RMA slope	95% CI	Allometry
Cranial widths				
PW	JL	0.518	0.501–0.535	N
IGW	JL	0.832	0.813–0.852	N
PW	IGW	0.622	0.603–0.642	N
Lever arm lengths				
LR _{IIJ}	JL	1.750	1.603–1.897	P
LR _{IIA}	JL	1.391	1.335–1.447	P
LM _J	JL	1.853	1.710–1.995	P
LM _A	JL	1.487	1.427–1.547	P
LM	LR _{II}	1.047	1.022–1.071	P
LR _{IIJ}	IGW	2.259	1.944–2.574	P
LR _{IIA}	IGW	1.575	1.489–1.661	P
LM _J	IGW	2.392	2.091–2.692	P
LM _A	IGW	1.684	1.598–1.710	P
LR _{IIJ}	PW	2.997	2.549–3.444	P
LR _{IIA}	PW	2.522	2.351–2.694	P
LM _J	PW	3.173	2.707–3.638	P
LM _A	PW	2.697	2.516–2.878	P

RMA, reduced major axis; CI, confidence intervals.
 PW, palatal width; JL, jaw length; IGW, interglenoid width; LM, muscle resultant lever arm; LR_{II}, lever arm to Region I–II boundary.
 Samples: A, adult; J, juvenile.
 Allometry: N, negative; P, positive.

in Fig. 6; Table 4 lists the associated Gompertz parameters. Palatal width at the onset of rapid growth (b) is significantly smaller ($P < 0.001$), indicating an earlier onset of rapid growth for palatal width but delays in rapid growth of jaw length and interglenoid width. The instantaneous rate of growth (I) of jaw length is significantly larger than either width measurement. There was no significant difference between the measurements in the rate of growth decay (k). However, the time of growth cessation (T_t) was significantly earlier in palatal width. Therefore, while palatal width has an earlier onset of rapid growth it also ceases growth earlier than either interglenoid width or jaw length. Furthermore, although growth of interglenoid width and jaw length is delayed, both parameters have faster initial rates of growth in comparison to palatal width.

Age-based differences in masticatory forces

As was found in the adult sample, bite force magnitudes of Region II teeth were significantly greater than those of Region I teeth in *M. domestica* juveniles ($P < 0.002$; Table 2; Fig. 4); however, juveniles did not display caudally increasing bite forces within Region I because there were no significant differences in bite forces obtained in the incisor/canine region versus the non-Region II premolars.

Maximal bite forces in adults exceeded juvenile values when comparable dental regions were examined ($P < 0.001$; Table 2). Scaling relationships of maximal bite forces generated by

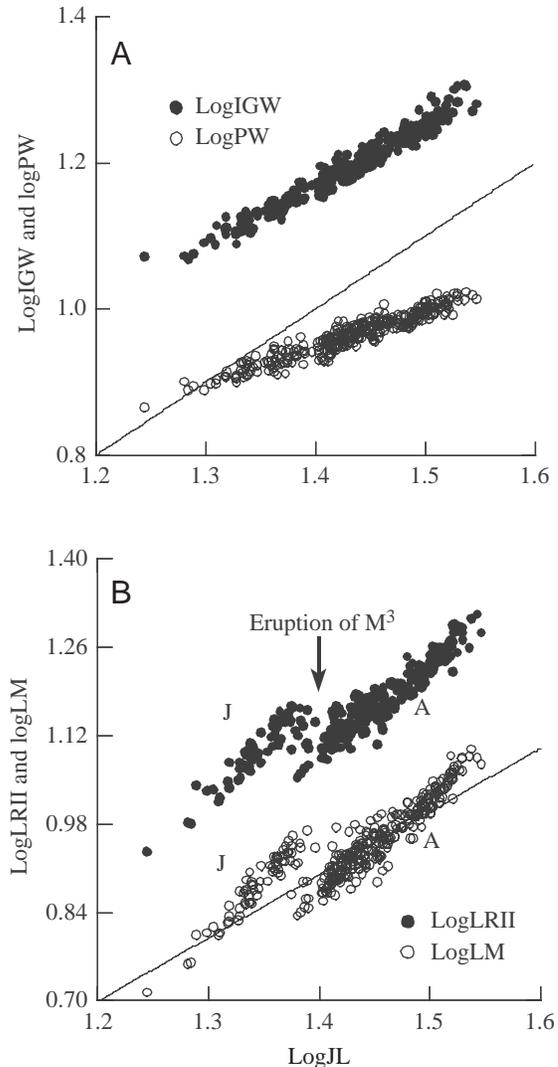


Fig. 5. Scaling of (A) interglenoid and palatal widths and (B) lever arms to the Region I–II boundary and the muscle resultant against jaw length. The solid line represents isometry. All length measurements are in mm. The reduced major axis regression slopes and 95% confidence intervals listed in Table 3. Abbreviations as in Fig. 3.

Region II teeth fit isometric expectations ($M_b^{0.77}$, 95% confidence interval ± 0.20). By contrast, mechanical advantage for biting at the Region I–II boundary scales with positive allometry ($M_b^{0.34}$, 95% confidence interval ± 0.26).

Discussion

Constrained model of jaw lever mechanics

Maximal voluntary bite force data from *M. domestica* adults provide the first unequivocal empirical support for the pattern of bite force potential predicted by the constrained lever model. Not only are bite forces recorded for Region II teeth significantly stronger than those applied by Region I teeth but maximal voluntary bites produced within Region II (M^1 – M^3)

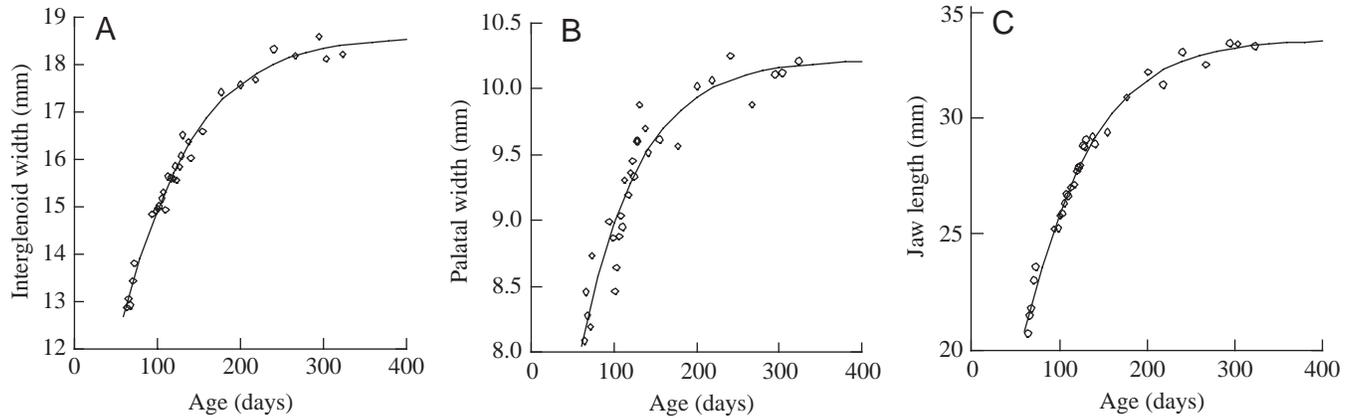


Fig. 6. Growth in cranial length and width for *M. domestica*, with the best-line fit by the Gompertz model: (A) interglenoid width, (B) palatal width and (C) jaw length.

attained equivalent strength. Previous analyses in humans yielded more mixed results. One study reported posteriorly increasing bite forces within Region II at a rate consistent with a decrease in adductor muscle force (Mansour and Reynik, 1975), whereas another found much greater rates of posteriorly increasing bite forces, as predicted by the simple lever model (van Eijden, 1991). Yet a third study of human bite force production noted posteriorly decreasing bite forces within Region II (Pruim et al., 1980), precisely the pattern implied by an EMG study of human jaw adductor muscles in which activity levels of both working- and balancing-side masticatory muscles peaked when biting at M1 and then decreased when biting on more posterior teeth (Spencer, 1998). Reduced bite force potential across Region II was also inferred by mathematical modeling (Kieser et al., 1996).

Reduced bite force potential when biting with M¹–M³ in humans may be due to the decline in tooth root surface area and complexity, which may limit the ability of the posteriormost teeth to withstand high occlusal loads (Spencer, 1998). Opossums may circumvent these constraints because overall tooth size increases from M¹ to M³, potentially enabling *M. domestica* adults to maintain fairly high activity levels of the working-side musculature and therefore avoid the caudal decline in bite forces across Region II found in humans. While the caudalmost molar of *M. domestica* is substantially smaller than the other molars, we were unable to unequivocally verify

bite forces with this tooth and thus could not provide data to empirically test Spencer's dental complexity hypothesis.

Age-based differences in masticatory function

Based on theoretical (Greaves, 1978; Kieser et al., 1996) and empirical (Spencer, 1998; this study) grounds, bite force magnitudes using teeth located at the Region I–II boundary are likely to represent the greatest values across all teeth. Maximal bite forces are directly affected by the adductor muscle resultant force (its magnitude and lever arm) and are inversely related to the lever arm to the Region I–II boundary. If maximizing bite forces provide animals with some selective advantage then jaws should be configured with a high mechanical advantage for biting with teeth located at the Region I–II boundary. Yet the present study shows that *M. domestica* juveniles do not compensate for their absolutely smaller masticatory muscles by enhancing their adductor muscles' mechanical advantage as mechanical advantage was found to increase with body size ($M_b^{0.34}$) and, hence, with age.

Improvements in mechanical advantage with age in *M. domestica* can not be explained by simple increases in the leverage of the jaw adductor muscle resultant. The constrained lever model specifies that any rostral shift of the muscle resultant will necessarily drive the Region I–II boundary even further rostrally as the trajectory from the balancing-side TMJ becomes less acute (Fig. 2A). The resulting proportionate elongation of the bite point lever arm should negate any lengthening of the muscle resultant lever arm (Appendix I). In other words, simple changes to the in-lever length alone can not improve mechanical advantage. A review of other ontogenetic changes of the orofacial complex reveals that relative palatal narrowing has a potent effect on masticatory leverages in *M. domestica* adults (Appendix II). Specifically, the trajectory from the balancing-side TMJ intersects a narrower palate more caudally than in a wider palate, resulting in a more caudal Region I–II boundary and, thus, a reduced out-lever length (Fig. 2C). Therefore, the relatively narrow palatal widths of adults help to temper elongation of the out-

Table 4. Average Gompertz parameters

Measurements	Gompertz parameters			
	<i>b</i>	<i>I</i>	<i>k</i>	<i>T_f</i>
Interglenoid width	0.798*	0.012	0.013	211.73
Palatal width	0.571*	0.008	0.015	164.13*
Jaw length	0.999*	0.016*	0.014	214.68

*Significant differences at $P < 0.001$, based on ANOVA and Tukey's *post-hoc* test.

b, onset of rapid growth; *I*, instantaneous growth rate; *k*, rate of growth decay; *T_f*, time of growth cessation.

lever to the bite point that necessarily accompanies any increase in muscle lever arm length. This combination of elongated muscle leverage with a disproportionately smaller elongation of the bite point leverage results in an enhanced mechanical advantage for biting with the Region I-II teeth in *M. domestica* adults.

The increase in mechanical advantage with size (and age) reported here for the jaw adductor muscle resultant of *M. domestica* concurs with scaling relationships found for the superficial masseter and internal pterygoid muscles in *Rattus norvegicus* (although the mechanical advantages of other craniomandibular muscles in rats were not found to change significantly with growth; Hurov et al., 1988). What implications do lower mechanical advantages have on juvenile animals? The present study has shown that bite forces scale isometrically in *M. domestica* so that the poor leverage of the juvenile masticatory systems must be compensated for by relatively greater muscular effort. Indeed, jaw adductor resultant muscle force in *M. domestica* is proportional to $M_b^{0.43}$ (bite force/mechanical advantage = $M_b^{0.77}/M_b^{0.34}$), falling below $M_b^{0.67}$ expected for geometrically-similar animals.

While the scaling of maximal bite forces with body mass provides a window into understanding the physiological (muscular) cost of generating bite forces, it is absolute bite force values that determine, to a large degree, feeding performance. Data reported here verify that juvenile opossums have absolutely weaker bite forces than adults. It is also unarguably true that the components of the orofacial complex are absolutely smaller in juveniles. Paradoxically, absolutely narrower palates may provide juveniles with some functional bonus, i.e. narrow jaws have been associated with smaller reductions in balancing-side muscle activity when biting with the teeth located in Region II (Spencer and Demes, 1993; Spencer, 1995). If balancing-side activity need not drop as much in narrow jaws then muscle resultant forces and bite forces for Region II teeth are correspondingly enhanced. Hence, bite force magnitudes of *M. domestica* juveniles might actually be even weaker if their dental arcades were absolutely wider.

Although absolutely weaker bite forces of *M. domestica* juveniles may appear to place younger animals at competitive disadvantage relative to adults when feeding on similar foods, it is important to remember that force magnitudes alone are unlikely to adequately reflect the ability of animals to comminute food. Because crack development in foods is, in large part, a function of the stress applied to the surface of the food, and because stress is determined by the quotient of bite force and area of force application (Lucas and Luke, 1984), the unworn cusps and shearing crests of newly erupted teeth may enhance stress development in juveniles. In other words, the topography of the newly erupted molariform teeth may partially compensate for the lower absolute bite forces in juveniles. Other characteristics of masticatory behavior may also help equilibrate juvenile and adult feeding performance (e.g. several rapid bites may cause food fracture quickly even if each bite is of weaker force). Finally, it is also possible that *M. domestica* age groups partition foods by choosing items of

different sizes or toughness (e.g. grubs *versus* adult insects) even if they customarily choose similar types of foods (e.g. invertebrates), as has been demonstrated in other taxa (Dumont, 1999; Strait, 1993).

Appendix I

Effects of elongating muscle resultant lever arm length on mechanical advantage

The rectangular shape in Fig. AI represents the palate in *Monodelphis domestica* juveniles (j, solid lines) and adults (a, broken lines). The adult condition is shown with a relatively longer muscle resultant lever arm (LM); palatal width (PW) and interglenoid width (IGW) are assumed to be constant in this simplification. Because of the less acute trajectory from the balancing-side TMJ through the midline muscle resultant in the adult condition, the lever arm to the Region I-II boundary (LRII) is longer in adults. In the juvenile condition, $\tan\theta = LM_j / (\frac{1}{2}IGW) = LR_{IIj} / (\frac{1}{2}IGW + \frac{1}{2}PW)$ so that the juvenile mechanical advantage $(LM_j / LR_{IIj}) = IGW / (IGW + PW)$.

Similarly, in the adult condition, $\tan\theta + k = LM_a / (\frac{1}{2}IGW) = LR_{IIa} / (\frac{1}{2}IGW + \frac{1}{2}PW)$, resulting in an adult mechanical advantage of $(LM_a / LR_{IIa}) = IGW / (IGW + PW)$.

In other words, simply elongating the muscle resultant lever arm does not improve mechanical advantage because it is accompanied by a proportionately equivalent elongation of the Region I-II boundary lever arm.

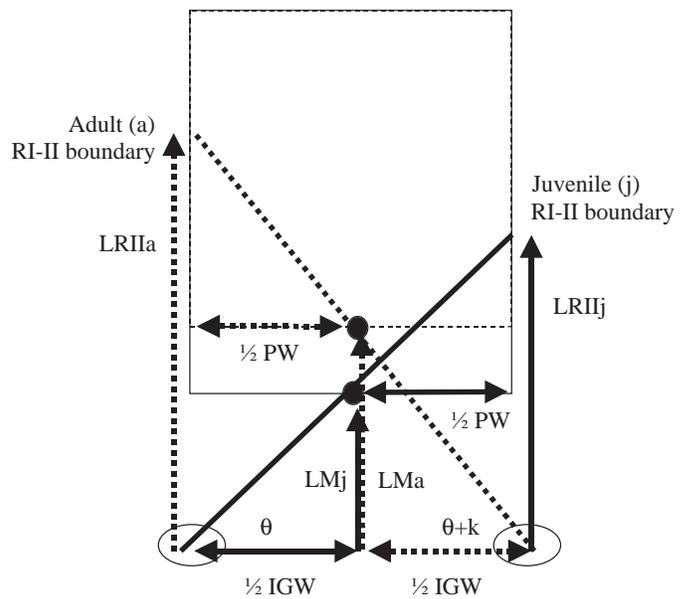


Fig. AI

Appendix II

Effects of both elongating muscle resultant lever arm length and narrowing palatal width on mechanical advantage

Fig. AII differs from Fig. AI in that the adult palate (broken line) is relatively narrow compared with the juvenile condition.

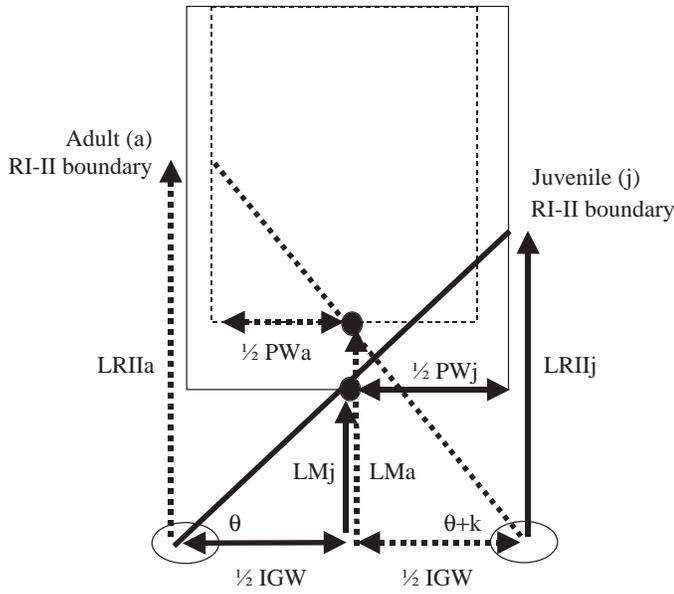


Fig. AII

The lever arm for the muscle resultant is still assumed to be relatively longer in adults, but the interglenoid width is assumed to be equivalent.

A key difference in the equations describing mechanical advantage is that palate widths differ among juveniles and adults so that:

$$\text{Juvenile mechanical advantage is } (LM_j/LRII_j) = \text{IGW}/(\text{IGW}+PW_j)$$

and

$$\text{Adult mechanical advantage is } (LM_a/LRII_a) = \text{IGW}/(\text{IGW}+PW_a).$$

Because $PW_j > PW_a$, then the mechanical advantage of biting at the Region I–II boundary is expected to be greater in the adult condition compared with that of juveniles.

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