

RESEARCH ARTICLE

Accuracy of mandibular force profiles for bite force estimation and feeding behavior reconstruction in extant and extinct carnivorans

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ABSTRACT

Mandibular force profiles apply the principles of beam theory to identify mandibular biomechanical properties that reflect the bite force and feeding strategies of extant and extinct predators. While this method uses the external dimensions of the mandibular corpus to determine its biomechanical properties, more accurate results could potentially be obtained by quantifying its internal cortical bone distribution. To test this possibility, mandibular force profiles were calculated using both external mandibular dimensions ('solid mandible model') and quantification of internal bone distribution of the mandibular corpus obtained from computed tomography scans ('hollow mandible model') for five carnivorans (*Canis lupus*, *Crocota crocuta*, *Panthera leo*, *Neofelis nebulosa* and the extinct *Canis dirus*). Comparison reveals that the solid model slightly overestimates mandibular biomechanical properties, but the pattern of change in biomechanical properties along the mandible remains the same. As such, feeding behavior reconstructions are consistent between the two models and are not improved by computed tomography. Bite force estimates produced by the two models are similar, except in *C. crocuta*, where the solid model underestimates bite force by 10–14%. This discrepancy is due to the more solid nature of the *C. crocuta* mandible relative to other carnivorans. Therefore, computed tomography improves bite force estimation accuracy for taxa with thicker mandibular corpora, but not significantly so otherwise. Bite force estimates derived from mandibular force profiles are far closer to empirically measured bite force than those inferred from jaw musculature dimension. Consequently, bite force estimates derived from this method can be used to calibrate finite-element analysis models.

KEY WORDS: Beam theory, Mandible, Feeding behavior, Bite force, Carnivora, Computed tomography

INTRODUCTION

Feeding behavior and bite force are significant aspects of the ecology of a predator, as both play an important role in determining the type and/or size of prey hunted and the trophic position of the predator (Meers, 2002; Verwaijen et al., 2002; Wroe et al., 2005; Van Valkenburgh, 2007; see also Wiersma, 2001). Feeding behavior in extinct predators is usually inferred from the study of their craniomandibular characteristics and dental morphology, which can be interpreted as adaptations for capturing prey and

processing food. Various biomechanical approaches have been developed to investigate and compare the feeding behaviors and bite capabilities of extant and extinct mammalian predators, such as beam theory (e.g. Biknevicius and Ruff, 1992a; Therrien, 2005a,b; Organ et al., 2006), jaw musculature reconstructions (e.g. Christiansen and Adolfsson, 2005; Wroe et al., 2005; Christiansen and Wroe, 2007), and finite-element analysis (FEA) (e.g. McHenry et al., 2007; Slater et al., 2009, 2010; Tseng and Binder, 2010; Tseng and Wang, 2010; Tseng et al., 2011; Jones et al., 2013; Tseng, 2013; Wroe et al., 2013; Figueirido et al., 2014). Although most methods require exquisitely preserved specimens (i.e. complete or undistorted specimens) and/or extensive computational facilities [i.e. access to computed tomography (CT) scanners and bioengineering software], the mandibular force profile method is simpler and has the advantages of being easily reproducible, widely applicable to various taxa and requiring only access to isolated mandibles (e.g. Therrien, 2005a,b; Therrien et al., 2005; Christiansen, 2007; Blanco et al., 2011; Jasinski, 2011).

Mandibular force profiles apply beam theory to determine the biomechanical properties of mandibles, which reflect the loads and stresses endured by mandibles during life (Biknevicius and Ruff, 1992a; Therrien, 2005a,b; Therrien et al., 2005). This approach follows the assumption that bone has evolved to achieve maximum strength with a minimum amount of material and to remodel itself in response to the loads to which it is subjected. Reflecting this notion, both cortical thickness and bone shape will reflect the habitual loads experienced during life: elliptical shapes characterize bones that undergo higher bending stresses in one direction over another whereas greater cortical thickness characterizes bones subjected to high loads (see Wainwright et al., 1982; Lanyon and Rubin, 1985). Mandibular force profiles use the external dimensions of mandibles to model them as solid, elliptical beams composed of cortical bone that undergo bending loads during ingestion, here termed the 'solid mandible model' (Fig. 1; equivalent to the 'solid symmetrical model' of Biknevicius and Ruff, 1992b). However, mandibles modeled as solid ellipses may poorly reflect the mandible capacity to withstand bending stresses for three reasons: (1) the mandibular corpus contains porous cancellous bone, thus making it partly hollow, (2) the amount of cancellous bone in the mandibular cross-section varies along the mandible and between taxa, and (3) the cross-section of a mandible may differ from a perfect elliptical shape (see Biknevicius and Ruff, 1992b). As such, these divergences could lead to erroneous estimation of the biomechanical properties of the mandible, resulting in the misinterpretation of feeding behavior and bite force.

More accurate determination of mandibular biomechanical properties can potentially be achieved by quantifying the amount and distribution of cortical bone in the cross-section of the mandibular corpus through the use of X-ray imagery and CT scans (Biknevicius and Ruff, 1992b). To investigate the impact of X-ray imagery on the accuracy of mandibular force profiles,

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List of symbols and abbreviations

CA	cortical bone area in mandibular cross-section
FEA	finite-element analysis
I_x	second moment of area about the mediolateral axis
I_y	second moment of area about the dorsoventral axis
M_1	first molar (carnassial)
M_2	second molar
M_3	third molar
P_2	second premolar
P_3	third premolar
P_4	fourth premolar
TA	total area of mandibular cross-section
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, DC
Z_x	section modulus about the mediolateral axis
Z_x/L	dorsoventral mandibular force
Z_x/Z_y	relative mandibular force (or overall mandibular shape)
Z_y	section modulus about the dorsoventral axis

mandibles of extant and extinct carnivorans were CT scanned to quantify the internal distribution of cortical bone in the mandibular corpus in order to derive revised mandibular force profiles, an approach here termed the ‘hollow mandible model’ (Fig. 1). These results were compared with mandibular force profiles derived from external mandibular dimensions measured on the same CT data (i.e. ‘solid mandible model’) in order to determine: (1) whether feeding behavior interpretations differ between the two models, and (2) whether the hollow mandible model provides more accurate bite force estimates than the solid mandible model. As such, this study will determine whether the use of CT significantly affects paleoecological interpretations based on mandibular force profiles derived from external measurements.

MATERIALS AND METHODS**Samples**

Dentaries of five carnivoran species [*Panthera leo* (Linnaeus 1758), *Neofelis nebulosa* (Griffith 1821), *Crocuta crocuta* (Erxleben 1777), *Canis lupus* Linnaeus 1758 and the extinct *Canis dirus* Leidy 1858], each represented by two large adult specimens (Table 1), were scanned on a Siemens Somatom CT

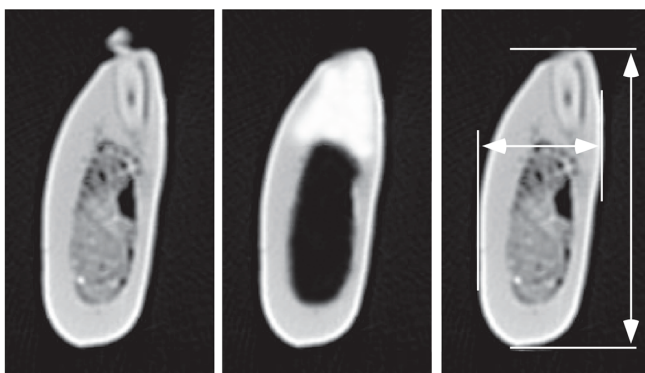


Fig. 1. Use of computed tomography (CT) scans to calculate the biomechanical properties of carnivoran mandibles. (A) Raw CT slice. (B) Alteration of CT slice to remove cancellous bone/tooth crown and fill cortical bone/tooth alveolus to determine biomechanical properties following the hollow mandible model. (C) External linear measurements of mandibular corpus used to determine biomechanical properties following the solid mandible model. The CT slice illustrated is the M_2M_3 interdental gap of *Canis dirus* (USNM 8305).

scanner (slice thickness 1 mm, pixel dimension 0.2 mm, energy and current levels were not recorded but presumably close to the standards of 120 kV and 200 mA; see Ridgely and Witmer, 2006) in the Department of Anthropology at the National Museum of Natural History, Washington, DC, USA. The ramus was oriented in life position and CT scans were selectively made at each individual interdental gap in the coronal plane, perpendicular to the neutral axis (which is approximated by the central axis) of the mandible (Fig. 2). At the canine, CT scans were taken diagonally from the lingual aspect of the symphysis through the posterior margin of the canine alveolus so the CT slices were taken perpendicular to the neutral axis of the mandible. The distance between each interdental gap and the middle of the articular condyle (L) was measured with calipers.

Individual CT slices were saved as IMA files and analyzed using the software ImageJ v. 1.40g (National Institutes of Health, Bethesda, MD, USA). Mandibular depth and width, defined as the greatest diameter of the mandibular corpus in the vertical and horizontal planes, respectively, were measured on each CT slice with the ImageJ measuring tool (Fig. 1). A few CT slices were edited in ImageJ to better define the extent of cortical bone (with white paintbrush tool), erase cancellous bone and tooth crowns (with black paintbrush tool), and fill tooth alveoli for analytical purposes (with white paintbrush tool). When the distinction between cortical bone and medullary cavity was difficult to

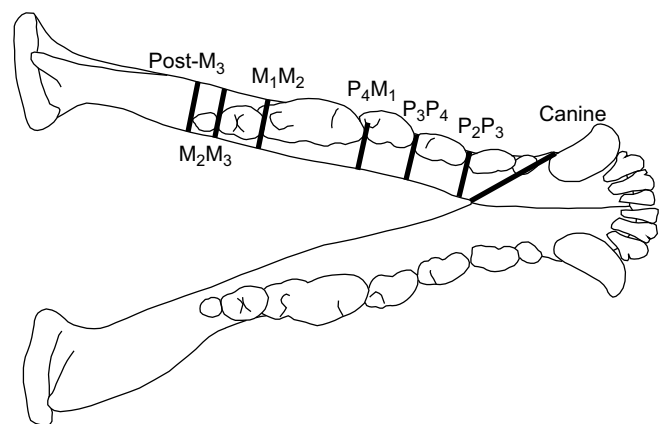
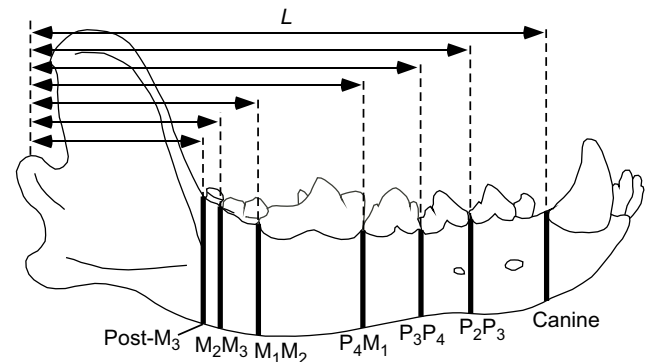


Fig. 2. Orientation of CT slices taken at interdental gaps along the mandible. The mandibular ramus was oriented in life position and CT scans were taken at each interdental gap in the coronal plane, perpendicular to the central axis of the mandible. At the canine, CT scans were taken diagonally from the lingual aspect of the symphysis through the posterior margin of the canine alveolus. Distance of each interdental gap to the articular condyle (L) was also measured (double-headed arrows).

Table 1. Mandibular dimensions and biomechanical properties of carnivorans

Specimen/interdental gap	Depth (cm)	Width (cm)	L (cm)	Solid model		Hollow model		CA (cm ²)	TA (cm ²)
				Z _x (cm ³)	Z _y (cm ³)	Z _x (cm ³)	Z _y (cm ³)		
<i>Canis dirus</i>									
(USNM 8305, jaw length=19.23 cm)									
Post-M ₃	4.68	1.82	5.85	3.91	1.52	3.58	1.29	4.83	6.65
M ₂ M ₃	4.34	1.84	6.75	3.40	1.44	2.98	1.37	4.40	6.17
M ₁ M ₂	4.07	1.84	7.7	2.99	1.35	2.72	1.37	5.00	6.12
P ₄ M ₁	3.89	2.13	11.06	3.16	1.73	2.39	1.36	4.20	6.02
P ₃ P ₄	3.43	2.03	12.65	2.34	1.39	1.80	1.03	3.76	4.92
P ₂ P ₃	3.41	2.09	–	2.39	1.46	1.70	0.92	3.43	4.76
Canine	3.64	3.53	16.86	4.59	4.45	3.58	3.42	8.23	8.34
<i>Canis dirus</i>									
(USNM 8307, jaw length=21.1 cm)									
Post-M ₃	4.56	1.84	6.03	3.76	1.52	3.20	1.22	4.85	5.97
M ₂ M ₃	4.45	1.86	6.6	3.62	1.51	2.95	1.07	4.36	5.70
M ₁ M ₂	4.07	1.86	7.88	3.02	1.38	2.75	1.14	5.18	5.65
P ₄ M ₁	3.8	1.95	11.4	2.76	1.42	2.19	1.25	4.60	5.63
P ₃ P ₄	3.28	1.8	13.34	1.90	1.04	1.44	0.79	3.28	4.31
P ₂ P ₃	3.12	1.72	–	1.64	0.91	1.37	0.69	3.01	3.93
Canine	3.16	2.88	18	2.82	2.57	2.28	1.90	6.07	6.07
<i>Canis lupus</i>									
(USNM 274487, jaw length=20.2 cm)									
Post-M ₃	4.21	1.22	6.31	2.12	0.62	1.92	0.53	2.75	4.05
M ₂ M ₃	4.14	1.22	6.91	2.05	0.60	1.93	0.49	2.72	4.01
M ₁ M ₂	3.95	1.3	8.3	1.99	0.66	1.89	0.64	3.44	4.25
P ₄ M ₁	3.91	1.75	11.05	2.63	1.18	2.07	0.88	3.61	4.93
P ₃ P ₄	3.34	1.64	13.05	1.80	0.88	1.43	0.67	2.78	3.89
P ₂ P ₃	2.99	1.46	–	1.28	0.63	1.01	0.52	2.57	3.19
Canine	3.18	2.72	17.68	2.70	2.31	1.82	1.63	5.13	5.50
<i>Canis lupus</i>									
(USNM 274942, jaw length=est. 19.7 cm)									
Post-M ₃	4.07	1.57	5.87	2.55	0.98	2.00	0.72	2.91	4.80
M ₂ M ₃	3.97	1.59	6.61	2.46	0.99	1.87	0.63	2.70	4.59
M ₁ M ₂	3.74	1.61	7.64	2.21	0.95	1.66	0.77	3.45	4.67
P ₄ M ₁	3.38	1.89	10.73	2.12	1.19	1.85	1.06	4.12	4.87
P ₃ P ₄	2.91	1.74	12.54	1.45	0.86	1.22	0.75	2.83	3.76
P ₂ P ₃	2.74	1.68	–	1.24	0.76	0.95	0.61	2.81	3.24
Canine	2.87	2.79	17.1	2.26	2.19	1.69	1.58	5.18	5.26
<i>Crocuta crocuta</i>									
(USNM 368502, jaw length=18.5 cm)									
Post-M ₁	5.31	1.4	5.75	3.88	1.02	3.71	0.74	4.61	5.36
P ₄ M ₁	4.51	1.78	8.83	3.55	1.40	2.88	0.89	4.53	5.44
P ₃ P ₄	4.14	1.84	11.1	3.10	1.38	2.74	1.21	5.19	5.82
P ₂ P ₃	4.14	2.16	14	3.63	1.90	2.87	1.75	5.11	6.83
Canine	3.86	2.64	15.8	3.86	2.64	3.07	2.11	6.88	6.93
<i>Crocuta crocuta</i>									
(USNM 181524, jaw length=18.43 cm)									
Post-M ₁	4.82	1.32	6.3	3.01	0.82	3.00	0.76	4.25	4.91
P ₄ M ₁	3.86	1.53	9.35	2.24	0.89	2.21	0.84	4.21	4.68
P ₃ P ₄	3.32	1.7	11.38	1.84	0.94	1.74	0.92	4.25	4.40
P ₂ P ₃	3.43	2.06	14.5	2.38	1.43	1.72	1.23	4.08	5.08
Canine	3.45	2.34	15.95	2.73	1.85	2.14	1.49	5.46	5.49
<i>Neofelis nebulosa</i>									
(USNM 49974, jaw length=12.10 cm)									
Post-M ₁	2.24	0.99	4.98	0.49	0.22	0.48	0.19	1.34	1.76
P ₄ M ₁	2.22	1.18	6.37	0.57	0.30	0.48	0.26	1.77	2.01
P ₃ P ₄	2.33	1.12	7.81	0.60	0.29	0.57	0.29	1.90	2.09
P ₂ P ₃	2.51	1.14	–	0.71	0.32	0.57	0.26	1.55	2.23
Canine	2.83	1.66	10.55	1.31	0.77	1.29	0.75	3.65	3.72
<i>Neofelis nebulosa</i>									
(USNM 196600, jaw length=10.96 cm)									
Post-M ₁	1.99	0.89	4.5	0.35	0.15	0.34	0.14	1.16	1.40
P ₄ M ₁	1.89	0.99	6.04	0.35	0.18	0.34	0.18	1.43	1.52
P ₃ P ₄	1.93	1.01	7.46	0.37	0.19	0.32	0.16	1.32	1.45
P ₂ P ₃	2.04	0.97	–	0.40	0.19	0.34	0.17	1.13	1.59
Canine	2.39	1.45	9.58	0.81	0.49	0.87	0.55	2.83	2.85

Continued

Table 1. Continued

Specimen/interdental gap	Depth (cm)	Width (cm)	L (cm)	Solid model		Hollow model		CA (cm ²)	TA (cm ²)
				Z _x (cm ³)	Z _y (cm ³)	Z _x (cm ³)	Z _y (cm ³)		
<i>Panthera leo</i>									
(USNM 162913, jaw length=est. 22.7 cm)									
Post-M ₁	5.6	2.29	10.8	7.05	2.88	5.79	1.84	6.81	9.57
P ₄ M ₁	5.02	2.27	13.5	5.62	2.54	4.45	2.21	6.31	8.81
P ₃ P ₄	4.43	2.23	16.1	4.30	2.16	3.51	2.03	6.36	7.62
P ₂ P ₃	4.47	2.14	—	4.20	2.01	3.14	1.69	4.89	7.35
Canine	5.31	3.65	21.2	10.10	6.95	7.45	5.35	12.41	12.79
<i>Panthera leo</i>									
(USNM 181569, jaw length=21.97 cm)									
Post-M ₁	5.12	2.02	10.06	5.20	2.05	4.61	1.28	5.66	7.70
P ₄ M ₁	4.69	2.06	12.99	4.45	1.95	3.53	1.84	5.49	8.03
P ₃ P ₄	4.33	2.12	15.32	3.90	1.91	3.12	1.89	6.05	7.20
P ₂ P ₃	4.23	2.15	—	3.78	1.92	2.67	1.66	4.33	7.22
Canine	4.96	3.38	19.48	8.16	5.56	5.88	4.24	10.51	11.23

L is the distance separating the articular condyle from the specified interdental gap. Jaw length was estimated for two specimens based on comparison with the conspecific individual. Section moduli (Z) for the 'solid mandible model' were calculated from the depth and width of the mandibular corpus measured on CT slices. Section moduli for the 'hollow mandible model', cortical area (CA) and total area (TA) were calculated with the MomentMacro in ImageJ. USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC.

determine in a CT slice, comparison with the CT slice for the same interdental gap in the second individual of the same species was made in order to delineate the extent of the cortical bone. Biomechanical properties (see below), total surface area (TA) of the mandibular corpus cross-section, and surface area represented by cortical bone (CA) in the mandibular corpus cross-section were quantified in each CT slice using the MomentMacro version 1.3 (freely available at http://www.hopkinsmedicine.org/FAE/mm_macro.htm) run within ImageJ.

Mandibular force profiles

Following the principles of beam theory, mandibles can be modeled as cantilevers undergoing bending loads during food ingestion (for reviews of the methodology and equations, see Therrien, 2005a; Therrien et al., 2005). Biomechanical properties of the mandible are calculated based on the dimensions of the mandibular corpus and the distribution of cortical bone within it (Biewener, 1992; Biknevicius and Ruff, 1992a). In this study, the second moment of area (I), a measure of bone distribution around a given axis, is evaluated in two different ways: (1) using measurements of the vertical (i.e. dorsoventral) and horizontal (i.e. labiolingual) diameters of the mandibular corpus, which assumes that the latter has a solid elliptical cross-section (*sensu* the solid mandible model, see Fig. 1); and (2) through quantification (via the MomentMacro) of cortical bone distribution in the mandibular corpus based on CT scan images, which takes into consideration the actual shape of the mandibular corpus cross-section (i.e. any deviation from a perfect elliptical cross-section) and the presence of cancellous bone in the corpus (*sensu* the hollow mandible model, see Fig. 1). Because the hollow mandible model takes into consideration the actual shape of and the internal distribution of cortical bone in the mandibular corpus, its results are considered to represent the true biomechanical properties of the mandible (see Biknevicius and Ruff, 1992b).

From the second moment of area, the following properties were evaluated for both solid and hollow mandible models at each interdental gap. (1) Z_x , the section modulus or maximum bending strength about the mediolateral axis: for the solid ellipse model, $Z_x = \pi \times (\text{mandibular width}/2) \times (\text{mandibular depth}/2)^2/4$ and for the hollow mandible model, $Z_x = I_x / (\text{mandibular depth}/2)$, where I_x is

the second moment of area determined by MomentMacro. (2) Z_y , the section modulus or maximum bending strength about the dorsoventral axis: for the solid ellipse model, $Z_y = \pi \times (\text{mandibular depth}/2) \times (\text{mandibular width}/2)^2/4$ and for the hollow mandible model, $Z_y = I_y / (\text{mandibular width}/2)$, where I_y is the second moment of area determined by MomentMacro. (3) Z_x/L , the dorsoventral mandibular force. By assuming constancy of bone material property and safety factor in the vertebrate mandible, the flexure formula of Timoshenko and Gere (1972) can be modified to show that the applied force on a structure can be expressed as the ratio of the section modulus over the moment arm length (for details, see Therrien, 2005a). As such, Z_x/L is a measure of the maximum force applied in the dorsoventral plane at an interdental gap, where L is the distance separating the interdental gap studied from the articular condyle. (4) Z_x/Z_y , the relative mandibular force (or overall mandibular shape) at a given point. (5) CA/TA , the ratio of cortical bone area to total surface area of the mandibular corpus cross-section; a measure of the 'hollowness' of the mandible at a given interdental gap.

Species means were calculated for each of the aforementioned variables. For the hollow mandible model, species means were calculated from the values produced by MomentMacro. For the solid mandible model, linear measurements (mandibular depth, mandibular width, and distance to interdental gaps) of both individuals of a given species were averaged prior to calculating the mandibular biomechanical properties. The graphic representation of variations in biomechanical properties, namely, bending force (Z/L) and relative mandibular force (Z_x/Z_y), along the mandible are called mandibular force profiles and have been shown to reflect differences in feeding behavior among predators (Therrien, 2005a,b; Therrien et al., 2005; Christiansen, 2007; Blanco et al., 2011; Jasinski, 2011).

Bite force estimation

Following the approach of Therrien (2005a), Z_x/L values at the carnassial (P₄M₁ and M₁M₂ or post-M₁ in felids and *C. crocuta*), where maximum bite force is theoretically achieved in carnivorans (Greaves, 1983, 1985), were used as a bite force proxy for each taxon. The Z_x/L values of each taxon were compared with those of *P. leo*, providing a 'relative bite force' estimate expressed as a percent value of the bite force of the lion (Table 2).

Table 2. Comparison of bite force estimates produced by various methods

Taxon	Z _x /L (present study)			Therrien (2005b) P ₄ M ₁ solid	Christiansen and Adolfsen (2005) Carn. (N)	Wroe et al. (2005, supplementary data) Cam. (N)	Christiansen and Wroe (2007) Cam. (N)	Thomason (1991) corrected bite force	Experimentally determined bite force
	Post-M ₁ hollow	P ₄ M ₁ hollow	Post-M ₁ solid						
<i>Canis dirus</i>	0.35 (70%)	0.20 (68%)	0.39 (66%)	0.22 (64%)	–	1577 (51%) corrected 3479.4	–	–	–
<i>Canis lupus</i>	0.22 (45%)	0.18 (60%)	0.26 (45%)	0.17 (50%)	1262.3 (37%) corrected 2786.5	1033 (33%) corrected 2281.7	773.9 (38%) corrected 1711.2	1412.2 (34%)	2000 ^a (49%)
<i>Crocuta crocuta</i>	0.56 (112%)	0.28 (93%)	0.57 (98%)	0.35 (104%)	1421.6 (42%) corrected 3137.2	1569 (51%) corrected 3461.8	985.5 (49%) corrected 2177	–	4500 ^b (108%)
<i>Panthera leo</i>	0.50 (100%)	0.30 (100%)	0.58 (100%)	0.34 (100%)	3405.4 (100%) corrected 7505	3085 (100%) corrected 6800	2023.7 (100%) corrected 4462.9	4167.6 (100%)	–
<i>Neofelis nebulosa</i>	0.09 (17%)	0.07 (22%)	0.09 (15%)	0.06 (19%)	587.8 (17%) corrected 1301.5	1051 (34%) corrected 2321.3	544.3 (27%) corrected 1205.7	–	–

Values in parentheses are relative bite force (i.e. expressed relative to the bite force of *Panthera leo*). For the bite force derived from the jaw musculature method, both published values and corrected values (if not published) are listed. 'Cam.' stands for estimates provided at the carnassial without precision of the exact position.

^aN. L. Denton, Purdue University, personal communication.

^bBinder and Van Valkenburgh (2000; their fig. 3A).

To assess the accuracy of bite force estimates derived from mandibular force profiles, values were compared with bite force estimates derived from measurements of cross-sectional areas and lever arms of major jaw adductor muscles (the 'dry skull' method of Thomason, 1991) and empirical *in vivo* bite force measurements (Table 2). Because the bite force values from the various methods could only be compared if expressed in relative terms (i.e. relative to the lion bite force), we limited our search to studies that evaluated both the bite force of *P. leo* and of other taxa considered in our study in order to insure consistency of methodology and bite force estimates. Empirically measured bite forces, reported in absolute terms (i.e. Newtons), were expressed relative to Thomason's (1991) bite force estimate for *P. leo*. Although an empirically derived bite force for the lion would have been preferable, this estimation method has been considered a reliable proxy in felids in the absence of empirical data (Sakamoto et al., 2010).

Statistical analyses

To compare the degree of hollowness of the various carnivorous mandibles, the CA/TA ratios at post-canine interdental gaps were compared for all specimens by performing a one-way ANOVA with *post hoc* tests for multiple comparison on samples where equal variance is not assumed using the software IBM SPSS Statistics 22.0.

RESULTS

Comparison of solid and hollow mandible models

Comparison via bivariate plots reveals that the solid and hollow mandible models follow similar trends but differ in absolute values, the magnitude of difference varying between species and as a function of the location along the mandible.

The solid mandible model generally overestimates the true biomechanical properties (as expressed by the hollow mandible model) of mandibular strength (Z_x ; Fig. 3) and mandibular force (Z_x/L ; Fig. 4). Posterior to P₃P₄, the solid mandible model overestimates Z_x and Z_x/L in canids and *P. leo* (by 10–31%), but significantly less so in *C. crocuta* and *N. nebulosa* (<12%). At P₂P₃, the solid ellipse model overestimates Z_x by approximately 30% in canids and *C. crocuta*, 37% in *P. leo*, and 17% in *N. nebulosa*. (Because the distance from the articular condyle to P₂P₃ was only available for *C. crocuta*, Z_x/L values could only be calculated for this species and are overestimated by 29% by the solid ellipse model.) At the canine, the solid mandible model overestimates Z_x and Z_x/L in all carnivorans (by 25–41%), except *N. nebulosa*, where these values are slightly underestimated (by 4%).

In estimating the relative mandibular force (Z_x/Z_y), the solid ellipse model generally provides values close to those of the hollow mandible model (Fig. 5). Among canids, the Z_x/Z_y values produced by the two models are usually within 10% of each other, although the solid model consistently underestimates the values in the post-carnassial region. This underestimation of Z_x/Z_y values in the post-carnassial region is due to the fact that Z_y values are overestimated to a greater extent (proportionally speaking) than Z_x values by the solid model (see Table 1). In *C. crocuta*, the Z_x/Z_y values produced by the two models are within 17% of each other and nearly identical at P₃P₄ and at the canine. In *N. nebulosa*, the Z_x/Z_y values produced by the two models are nearly identical along the entire tooth row, except behind the carnassial, where the solid ellipse model underestimates the Z_x/Z_y value by 11%. The greatest divergence is observed in *P. leo*, where the solid ellipse model overestimates Z_x/Z_y values by 5–20% along the entire tooth row, except behind the carnassial, where it underestimates values by 25%.

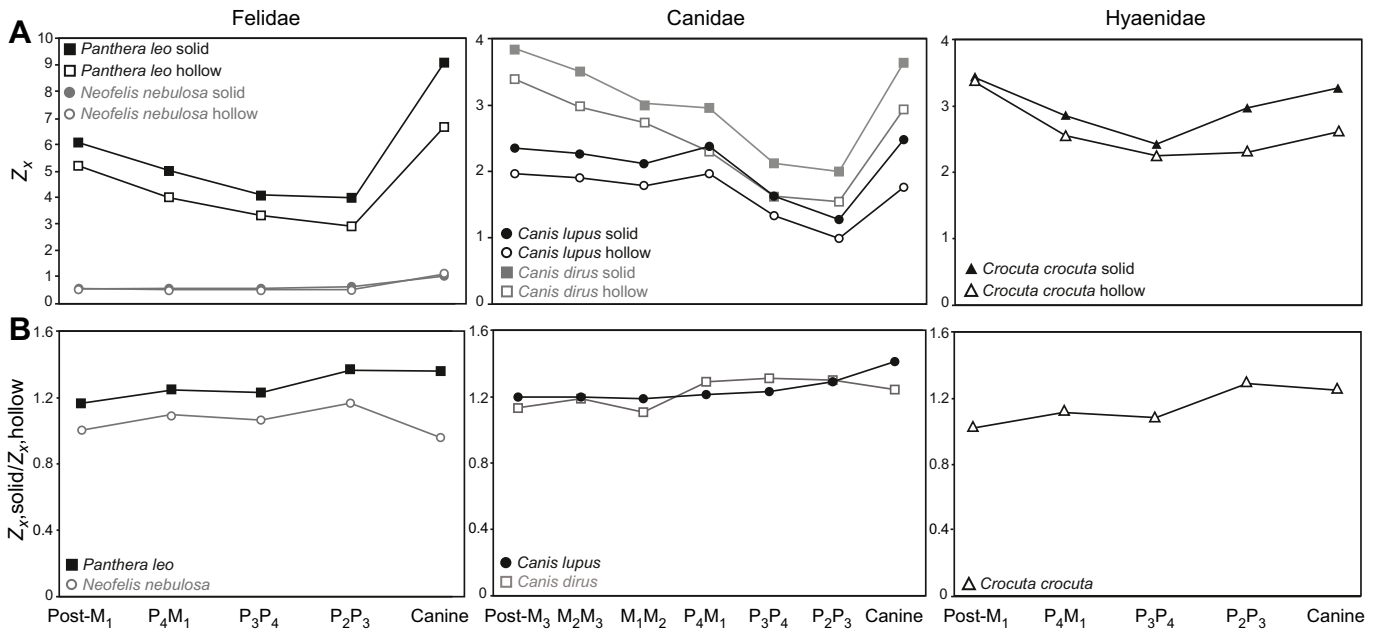


Fig. 3. Comparison of section modulus (Z_x) values produced by the solid mandible and hollow mandible models for studied carnivorans. (A) Profiles of Z_x values along the mandible. The pattern of change in Z_x along the mandible is nearly identical in the two models, but the values for the solid model slightly exceed those for the hollow model. (B) Ratios of Z_x values produced by the solid mandible and hollow mandible models. The solid model slightly overestimates Z_x values produced by the hollow model, generally by ~20% (i.e. ratio close to 1.2), except in *Neofelis nebulosa* and *Crocota crocuta*, where Z_x values are more similar (i.e. ratio closer to 1.0). The solid model overestimates Z_x at the canine in all carnivorans except in *N. nebulosa*, where it is slightly underestimated.

CA/TA ratio

The hollowness of the mandible, expressed by the CA/TA ratio, varies along the mandible and between species (Fig. 6). All species have a nearly solid mandibular corpus at the canine (CA/TA ~95–

99%) but differ in the posterior portion of the mandible. The mandibles of canids and *P. leo* are moderately solid (CA/TA ~73–86%), except in the postcarnassial region of *C. lupus* and at P₂P₃ in *P. leo*, where they are more hollow (CA/TA ~63–64%). In contrast,

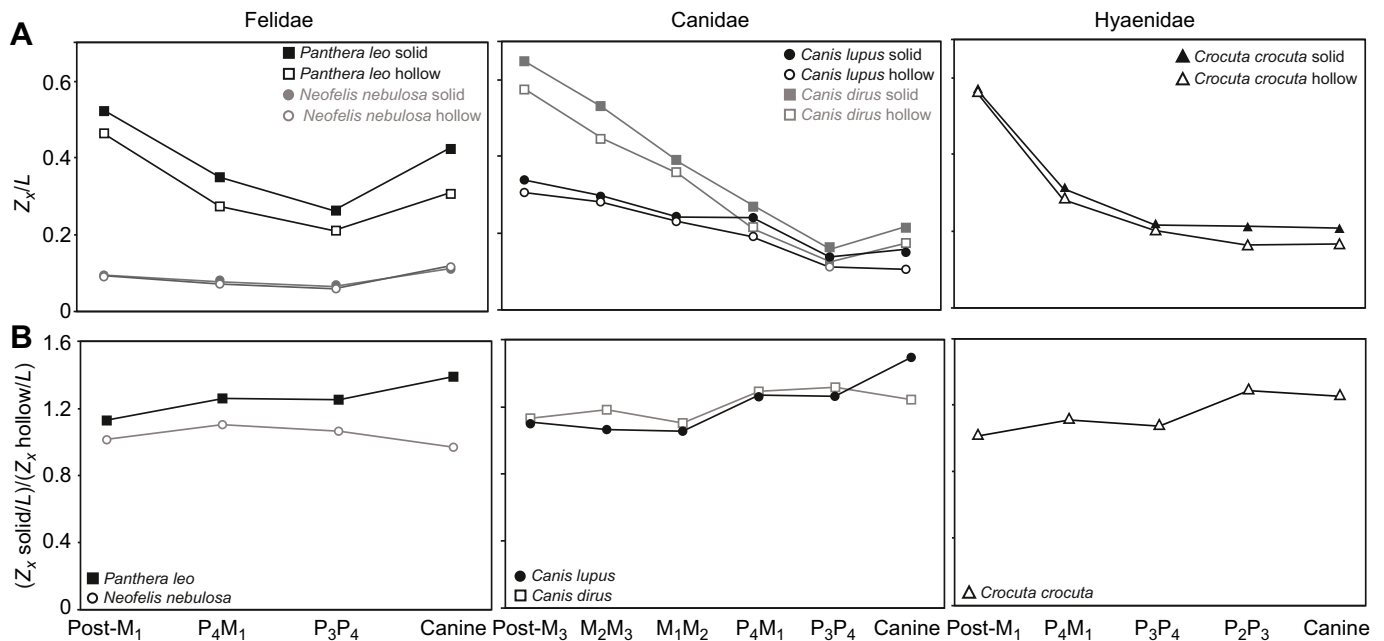


Fig. 4. Comparison of dorsoventral mandibular force (Z_x/L) values produced by the solid mandible and hollow mandible models for studied carnivorans. (A) Profile of Z_x/L values along the mandible. The pattern of change in Z_x/L along the mandible is nearly identical in the two models, but the values for the solid model slightly exceed those for the hollow model. (B) Ratios of Z_x/L values produced by the solid and hollow mandible models. The solid model slightly overestimates Z_x/L values produced by the hollow model, generally by ~10–30% (i.e. ratio varying between 1.1 and 1.3), except in *N. nebulosa* and *C. crocuta*, where Z_x/L values are more similar (i.e. ratio closer to 1.0). The solid mandible model overestimates Z_x/L at the canine in all carnivorans except in *N. nebulosa*, where it is slightly underestimated.

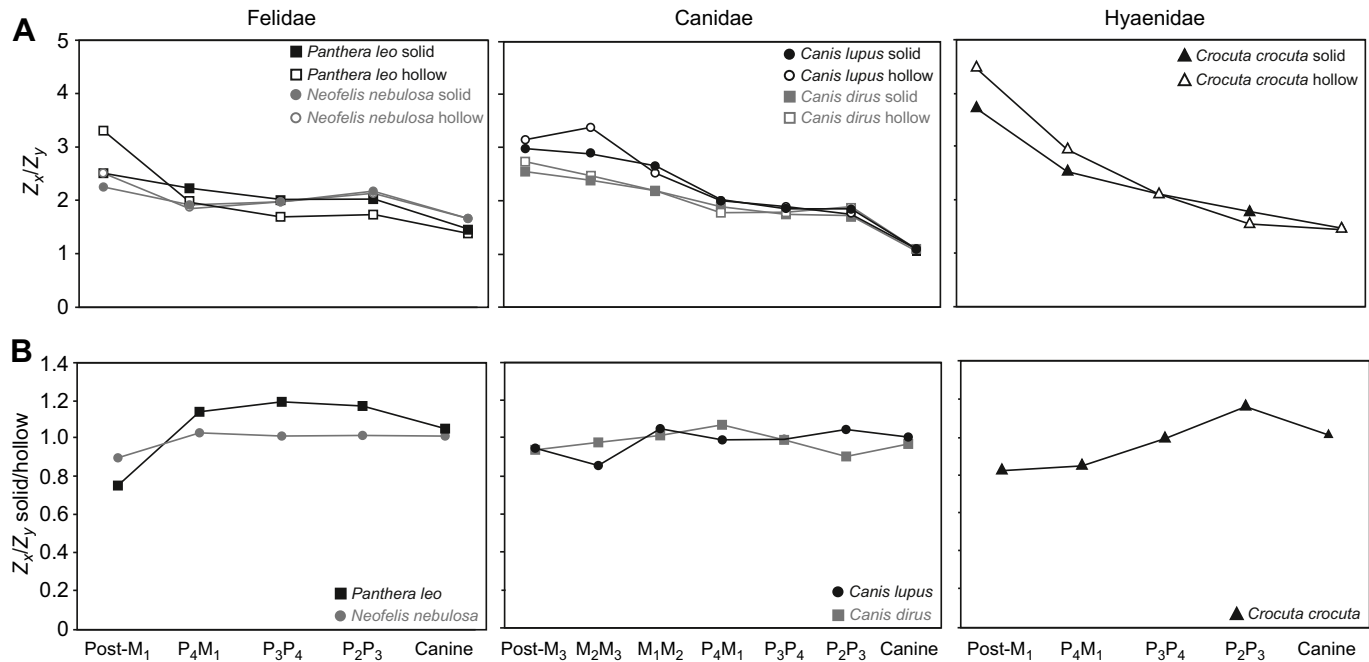


Fig. 5. Comparison of Z_x/Z_y values produced by the solid mandible and hollow mandible models for studied carnivorans. (A) Profile of Z_x/Z_y values along the mandible. The pattern of change in Z_x/Z_y along the mandible is nearly identical in the two models. (B) Ratios of Z_x/Z_y values produced by the solid mandible and hollow mandible models. The solid mandible model generally provides values close to those of the hollow mandible model. Among canids, the two models are usually within 10% of each other, although the solid model consistently underestimates the values in the post-carnassial region. In *C. crocuta*, the two models are within 17% of each other and are nearly identical at P₃P₄ and at the canine. In *N. nebulosa*, the two models are nearly identical along the entire tooth row, except behind the carnassial, where the solid mandible model underestimates Z_x/Z_y by 11%. In *Panthera leo*, the solid mandible model overestimates Z_x/Z_y values by 5–20% along the entire tooth row, except behind the carnassial, where it underestimates values by 25%.

the mandibles of *C. crocuta* and *N. nebulosa* are generally far more solid (CA/TA ~86–92%), except at P₂P₃, where they are in the range observed among canids (70–77%). These results indicate that the medullary cavity in the mandibles of *C. crocuta* and *N. nebulosa* is much smaller than in other carnivorans, usually occupying only 8–14% of the mandibular cross-section as opposed to 14–37% in other carnivorans (see also Tseng and Binder, 2010). A statistical comparison of CA/TA values for all post-canine interdental gaps reveals that the mandibular corpus of *C. crocuta* is significantly more solid than that of *C. lupus* and *P. leo* ($P < 0.027$) and *C. dirus* ($P = 0.097$), but similar to that of *N. nebulosa* ($P > 0.957$).

Relative bite force estimates

Relative bite force estimates derived from the solid ellipse and hollow mandible models are generally consistent (within 4%) among most taxa, with the solid model usually underestimating bite force values produced by the hollow model (Fig. 7, Table 2). The reason why the solid model produces lower bite force estimates

when it generally overestimates Z_x and Z_x/L values is due to the fact that the lion mandible is more hollow at the carnassial than that of other taxa, resulting in a greater discrepancy of Z_x/L values between solid and hollow models in that reference taxon than in other taxa. The two models differ the most in *C. crocuta*, where the solid mandible model underestimates relative bite force values by 10–14%. These results are largely consistent with Therrien’s (2005a) bite force estimates based on the solid model (Fig. 7, Table 2), the slight incongruences most likely due to differences in sample size, i.e. mean of seven individuals in Therrien (2005a) versus mean of two individuals in the present study. Interestingly, relative bite force estimates calculated anterior (at P₄M₁) and posterior (at M₁M₂ or post-M₁) to the carnassial differ by 4–15%, except in *C. crocuta*, where the difference is much greater (15–19%).

DISCUSSION

Our study demonstrates that mandibular force profiles are a reliable approach to document the biomechanical properties of carnivoran

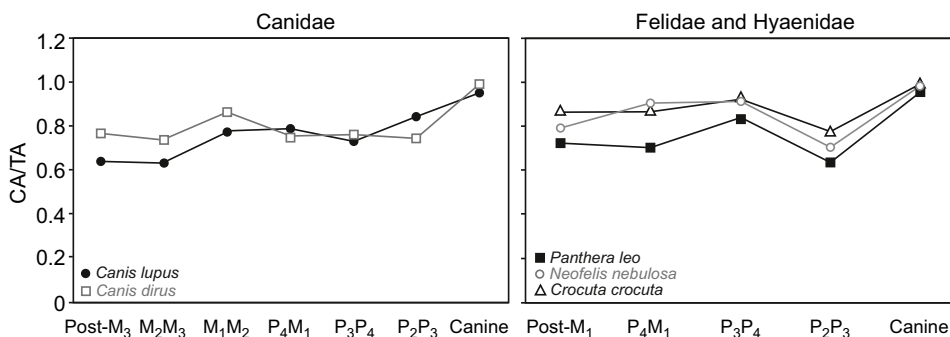


Fig. 6. Comparison of CA/TA values (the ratio of cortical bone area to total surface area of the mandibular corpus cross-section) for studied carnivorans. The mandibles of canids and *P. leo* are moderately solid (73–86%), except in the postcarnassial region of *C. lupus* and at P₂P₃ in *P. leo* where they are more hollow (~63%). The mandibles of *C. crocuta* and *N. nebulosa* are generally far more solid (86–92%), except at P₂P₃, where they are in the range observed among canids (70–77%). All species have nearly solid mandibles at the canine (95–99%).

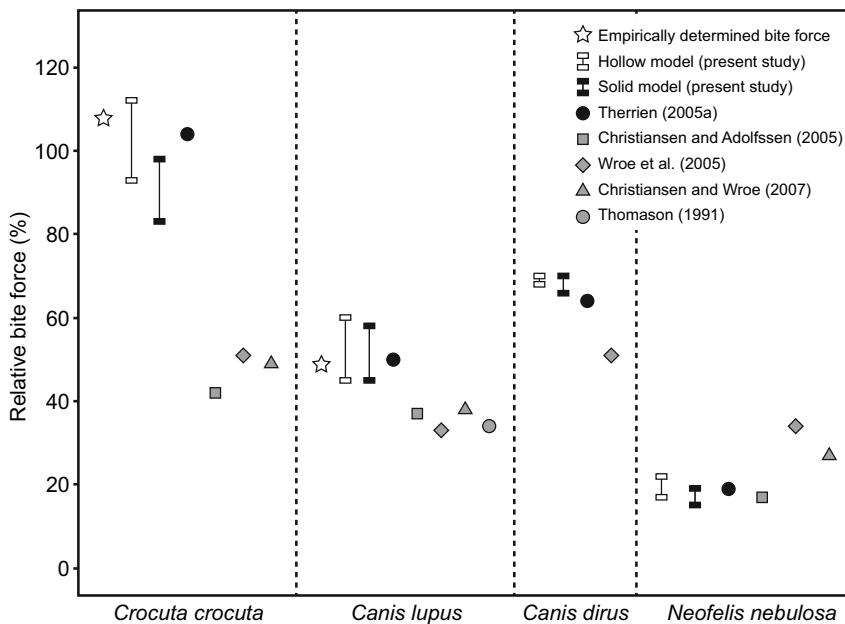


Fig. 7. Comparison of bite force estimates obtained from various methods. Each bite force estimate is reported relative to the bite force value of *P. leo* obtained by the same estimation method. Estimates derived from mandibular force profiles (solid and hollow models) are generally higher and closer to empirically determined bite force (star) than those derived using Thomason's (1991) jaw musculature method (gray symbols). Only in *N. nebulosa* are bite force estimates derived from mandibular force profiles lower or equal to those derived from the jaw musculature method.

mandibles and, consequently, to infer the feeding behavior and bite force of extant and extinct taxa. Although the solid mandible model does not record the 'true' biomechanical properties of the mandible (as represented by the hollow mandible model), the two approaches produce comparable results. While the solid ellipse model tends to overestimate mandibular strength (Z_x) and mandibular force (Z_x/L), it generally closely reflects relative mandibular force (Z_x/Z_y). Similar conclusions were reached by Biknevičius and Ruff (1992b) in their comparison of various approaches to calculate the second moment of area (I) of carnivoran mandibles. Although the difference between the solid and hollow mandible models is not always consistent between interdental gaps, which could raise concerns about the validity of the solid mandible model, this discrepancy is generally $\leq 20\%$ (see Figs 3–5). While this discrepancy may appear large in relative terms, its absolute magnitude (0.04–0.12 for Z_x/L and 0.4–0.8 for Z_x/Z_y) is so small that it often falls within the range of intraspecific variation (i.e. values between two similar-sized individuals of a given species can differ by as much as the solid model discrepancy, see Table 1). As such, the solid model discrepancy is minimal and does not alter the interpretation of the results. Given the primary purpose of mandibular force profiles to infer feeding behavior, it is the relative pattern of change in biomechanical properties (primarily Z_x/L and Z_x/Z_y ratios) along the mandible that is of relevance. The only instances where the actual value of a biomechanical property is used to infer feeding behavior are: (1) the Z_x/Z_y value at the canine (i.e. to infer the method of prey capture) and (2) the Z_x/L values at the carnassial (i.e. to infer bite force) (see Therrien, 2005a). In the first case, the solid and hollow models are shown to produce nearly identical Z_x/Z_y values at the canine (ratio of the two models is ~ 1.0 ; see Fig. 5). In the second case, Z_x/L values at the carnassial are shown to be nearly identical between the solid and hollow models (see Accuracy of bite force estimates derived from mandibular force profiles, below). Consequently, the solid mandible model is a reliable approach to reconstruct feeding behavior. However, if one seeks to determine the exact values of the biomechanical properties of the mandible (e.g. to infer peak stress the mandible can withstand), the hollow mandible model should preferably be applied.

From an ecological and behavioral perspective, the general pattern of change in biomechanical properties along the mandible is consistent between the solid and hollow models (Figs 3–5), resulting in identical feeding behavior interpretations for the carnivorans studied. Furthermore, the fact that the magnitude of change in biomechanical properties exceeds the aforementioned solid–hollow model discrepancy and intraspecific variation confirms the validity of mandibular force profile analysis for feeding behavior reconstructions. The much lower Z_x/L values at the canine than at the carnassial seen in canids and *C. crocuta* reflect their pack hunting behavior, where individuals deliver numerous shallow canine bites to weaken prey (e.g. Kruuk, 1972; Ewer, 1973; Biknevičius and Ruff, 1992a; Therrien, 2005a). The higher Z_x/L values at the canine and steeper increase in Z_x/L values along the tooth row observed in the extinct *C. dirus* presumably reflect mandibular adaptations to subdue large Pleistocene herbivores (Therrien, 2005a; see also Anyonge and Baker, 2006). In contrast, the high Z_x/L values at the canine relative to the carnassial observed in felids reflect the powerful, canine killing bite these solitary hunters deliver to subdue prey (Kruuk and Turner, 1967; Schaller, 1972; Ewer, 1973; Therrien, 2005a).

Mandibular force profiles also provide insight into the bone-cracking abilities of carnivorans (see Therrien, 2005a). Although pre-carnassial (i.e. P_4M_1 and P_3P_4) Z_x/Z_y values remain constant in felids and canids, reflecting the fact that this region of the mandible is used for slicing flesh, they increase posteriorly in *C. crocuta*. This increase in Z_x/Z_y values over the pre-carnassial corpus reflects a species that cracks bone with the premolars (Rensberger, 1995; Van Valkenburgh, 1996). By contrast, canids crush bones with their post-carnassial molars (M_1 – M_3 ; Ewer, 1973) and, in these species, the increase in Z_x/Z_y values occurs posterior to M_1 . The more anteriorly situated bone-processing location in hyaenids allows them to break larger bones but requires (1) relatively larger bite forces because of the reduced mechanical advantage induced by cracking bones at a greater distance from the jaw joint (Greaves, 1985) and (2) deeper mandibular corpora (i.e. posteriorly increasing Z_x/Z_y values) to sustain stresses associated with this behavior (Biknevičius and Ruff, 1992a). The post-carnassial Z_x/Z_y values of canids, including the extinct *C. dirus*, are lower than those of *C. crocuta*, as originally noted by Therrien (2005a), which indicate

poorer adaptations for bone processing. Although both canids have less cortical bone in their mandibular cross-section than hyaenids (Fig. 6), the post-carnassial mandibular corpus of *C. dirus* is characterized by slightly thicker (9–13%) cortical bone than that of *C. lupus* (Fig. 6), resulting in greater mandibular bending strength (Z_x) values in the extinct canid, approaching values observed in *C. crocuta* (Fig. 3). Nevertheless, the lower Z_x/Z_y values produced by hollow mandible models confirm that dire wolves were not as adept bone crushers as modern gray wolves and clearly lacked the adaptations for osteophagy of hyaenids (Van Valkenburgh and Koepfli, 1993; Therrien, 2005a; Anyonge and Baker, 2006; contra Meehan and Martin, 2003). Indeed, extant canids are considered unspecialized for osteophagy (Biknevicius and Ruff, 1992a) and tend to crush bones rather than crack them like hyaenids (Werdelin, 1989). Despite having a mandible characterized by a very thick layer of cortical bone like that of *C. crocuta*, *N. nebulosa* does not display any biomechanical mandibular adaptations associated with osteophagy (i.e. the Z_x/Z_y profile remains constant over the cheek teeth, indicative of a slicing function). Furthermore, its highly specialized dentition, characterized by a blade-like carnassial, absence of postcarnassial teeth, and narrowed premolars, is indicative of a hypercarnivorous diet without bone-cracking abilities (Holliday and Stepan, 2004). Thus the thickened cortical bone layer of this felid is not an adaptation to withstand bending stresses associated with bone cracking. *Neofelis nebulosa* is known for hunting prey both smaller (e.g. small primates, birds) and far larger than itself (e.g. large primates, deer, wild boars), which it dispatches with a powerful bite to the back of the neck (see Banks, 1949; Prater, 1971; Payne et al., 1985; Rabinowitz et al., 1987; Grassman et al., 2005; Chiang, 2007). Thus the greater cortical bone thickness of the mandibular corpus in *N. nebulosa* may be an adaptation to deliver powerful bites to capture large prey. Interestingly, this mandibular condition is also observed in sabertoothed predators (Akersten, 1985; Biknevicius and Van Valkenburgh, 1996; McHenry et al., 2007), adding to the list of convergences between *N. nebulosa* and these extinct predators (Therrien, 2005b; Christiansen, 2005, 2008).

Although the thickened mandibular corpus of *C. crocuta* certainly offers a biomechanical advantage for bone cracking (see Biknevicius and Ruff, 1992a), the question of whether this condition represents an adaptation for osteophagy rather than a phylogenetic signal has yet to be investigated. The facts that early hyaenids were civet-like insectivores or omnivores and that craniodental features indicative of bone-cracking abilities did not evolve until later (e.g. Werdelin and Solounias, 1996; Turner et al., 2008) suggest that thickened mandibular corpora may be an adaptation for durophagy in that clade. Nevertheless, the fact that both *N. nebulosa* and the sabretooth *Smilodon* possess thicker mandibular corpora indicates that this condition also occurs in non-osteophagous taxa. As such, the presence of a thickened mandibular corpus may not be exclusively an adaptation for osteophagy but rather an adaptation to sustain greater stresses associated with powerful bites, be it for durophagy or for subduing large prey. Interestingly, a thickened mandibular corpus evolved independently in some aquatic vertebrates as an adaptation for buoyancy or bottom feeding (Domning and Debuffrenil, 1991; Houssaye, 2009; Jones et al., 2013) and not for delivering powerful bites.

Accuracy of bite force estimates derived from mandibular force profiles

The hollow mandible model should theoretically provide more accurate bite force estimates than the solid ellipse model because it

takes into consideration cortical bone distribution and thickness in the mandibular cross-section. Comparison of the two models, however, reveals that relative bite force estimates are usually close (within 4% of each other), with the greatest divergence (10–14%) observed in *C. crocuta*. This divergence is due to the significantly greater thickness of cortical bone in hyaenid mandibles (CA/TA ~90%) relative to other carnivorans (CA/TA ~60–85%). Thus the solid mandible models produce bite force estimates that are nearly identical to the hollow mandible models, except in taxa with a thick cortical bone layer in the mandibular corpus.

Large differences exist between bite force estimates derived from the hollow mandible model and those obtained from the dimension of the jaw adductor musculature (Fig. 7, Table 2). The least extreme differences are observed in *N. nebulosa*, where the bite force estimates derived from hollow mandible models are generally within 17% (depending on the landmark being considered) of those based on jaw musculature dimension. In canids, the hollow mandible model provides bite force estimates that are 7–27% higher than those based on jaw adductor musculature. The greatest differences are observed in *C. crocuta*, where the hollow mandible model provides estimates that are 42–70% higher than those based on jaw adductor musculature.

Ultimately, true assessment of the accuracy of bite force estimates produced by mandibular force profiles requires comparison with experimentally determined bite force values (i.e. recorded in live subjects). Despite a plethora of bite force values presented in documentaries and blogs, experimentally determined bite force values have been published for few mammal species (Thomason et al., 1990; Dessem and Druzinsky, 1992; Ström and Holm, 1992; Binder and Van Valkenburgh, 2000; Ellis et al., 2008). Of relevance to our study, the highest recorded bite force for *C. crocuta* approaches 4500 N (Binder and Van Valkenburgh, 2000; Fig. 3A) and preliminary attempts to empirically determine the bite force of *C. lupus* (Thomas et al., 2005) reveal a bite force of approximately 2000 N (N. L. Denton, Purdue University, personal communication). Comparison reveals that mandibular force profiles consistently produce bite force estimates that are far closer to the empirically measured bite force (accuracy to within 4–15% for the hollow model and 10–25% for the solid model) than those produced by the jaw musculature method (11–16% lower in *C. lupus* and 57–66% lower in *C. crocuta*) (Fig. 7, Table 2). Even after application of the correction factor for the disparity between dry skull and *in vivo* bite force (Thomason, 1991; Sakamoto et al., 2010), absolute bite force estimates produced by the jaw musculature method are still 23–52% lower than empirical bite forces for *C. crocuta* (also noted by Tseng and Binder, 2010), but are slightly closer for *C. lupus* (ranging from 15% lower to 39% higher than empirical values) (Fig. 7, Table 2).

These results support the long-held suspicion that Thomason's (1991) jaw musculature method greatly underestimates bite force (see Therrien, 2005a; Ellis et al., 2008; Davis et al., 2010). However, the congruence between empirically determined and hollow-model-derived bite force values expressed relative to *P. leo* suggests that the jaw musculature method might produce accurate bite force estimates for this felid (see Sakamoto et al., 2010). The poorer performance of the jaw musculature method has been ascribed to a variety of issues, such as the fact that the method: (1) does not account for interspecific variation in jaw muscle pennation, (2) assumes that muscle cross-sectional area and lever arm length correlate directly with bite force, and (3) considers the mandible as a two-dimensional object only, which overestimates the cross-sectional area of the masseter and pterygoid muscles and underestimates the cross-sectional area of the temporalis muscle

in many carnivorans (Wroe et al., 2005; Ellis et al., 2008; Davis et al., 2010; Tseng and Binder, 2010). Thus mandibular force profiles, particularly the hollow mandible model, are a more accurate and far simpler method to estimate bite force than Thomason's (1991) jaw musculature method.

Given the greater accuracy of bite force estimates derived from mandibular force profiles, this method can be used to infer the bite force of the extinct *C. dirus* and of the elusive *N. nebulosa*. Previous studies have shown that *C. dirus* was similar to *C. lupus* in terms of feeding behavior but, because of its overall larger size and robustness, could deliver a stronger bite (see Therrien, 2005a; Anyonge and Baker, 2006; Meloro et al., 2015). Supporting this view, the hollow mandible model indicates that *C. dirus* had a bite force that was 66–70% that of *P. leo*, which is 11–59% stronger than that of *C. lupus* (8%–25% when expressed relative to *P. leo*). The hollow mandible model thus confirms that *C. dirus* was capable of a very powerful bite, presumably an adaptation to kill large Pleistocene prey. In comparison, the estimated bite force of *N. nebulosa* is approximately 20% that of *P. leo*, values that are generally lower than estimates produced by the jaw adductor musculature method, except for one study (Fig. 7, Table 2). It is unclear why bite force estimates based on the jaw musculature method are generally higher in this instance, but it does not seem to be related to the study of larger individuals as both methods employed individuals of similar size (compare table 1 in Therrien, 2005a with table 1 in Wroe et al., 2005).

Implications for the calibration of finite-element analysis (FEA) models

Over the past two decades, FEA has been used extensively to investigate the relationship between form and function in extant and extinct animals (for reviews, see Fastnacht et al., 2002; Rayfield, 2007; Cunningham et al., 2014). Although this non-destructive approach has gained in popularity, it remains anchored in numerous assumptions, including some about cranial and muscle architecture and the amount of force generated by the jaw musculature (Fastnacht et al., 2002; Bright, 2014). While muscle architecture can be inferred from muscle scars and dissection of extant relatives, the amount of force muscles can generate is often based, in the absence of empirically determined values, on bite force estimates derived from jaw musculature reconstructions (e.g. Wroe et al., 2007; McHenry et al., 2007; Wroe, 2008; Slater et al., 2009). As noted above, bite force estimates derived from such methods tend to dramatically underestimate true bite force in mammalian predators. As such, although FEA can be used to document and compare stress and load distributions in skulls of different morphology, use of this method to infer the bite force generated by a predator or to infer stress distribution during 'typical bite' ought to be done with caution (Bright, 2014). While other approaches have been developed to produce more accurate bite force estimates in carnivorans (e.g. Wroe et al., 2008; Tseng and Wang, 2010; Tseng and Binder, 2010; Slater et al., 2010), mandibular force profiles may represent a simpler alternative method to obtain accurate bite force values (after converting relative bite force estimates to absolute values) with which FEA models can be calibrated.

Conclusions

The mandibular force profile approach provides a simple and widely applicable method to investigate the feeding behaviors and bite force of extant and extinct predators. Although the method is theoretically sensitive to the distribution of cortical bone within the mandibular corpus, comparison of results derived from the precise quantification of bone distribution via CT (i.e. the hollow mandible

model) with those derived from external mandibular dimensions assuming a solid mandible (i.e. the solid mandible model) reveals that the two models are highly congruent. The solid mandible model generally overestimates biomechanical properties relative to the hollow mandible model, but the overall pattern of change along the jaw is accurately represented. Furthermore, bite force estimates produced by the two models are highly similar to each other and to empirically determined bite force, except for the spotted hyena *C. crocuta* owing to the greater cortical bone thickness in the mandibular corpus of this osteophagous taxon. Consequently, reconstruction of the feeding behavior and bite force for most carnivorans can be achieved with the solid mandible model without the need for time-consuming, often limited access and costly CT. Only when dealing with a taxon that possesses thicker cortical bone within its mandibular corpus (e.g. hyaenids, sabertooths) will the solid model slightly underestimate the bite force of the animal. Thus, CT may help provide more accurate bite force estimates for these taxa by permitting documentation of the internal distribution of cortical bone in the mandibular corpus.

Finally, mandibular force profiles, based on either the solid or the hollow models, are shown to produce more accurate bite force estimates than those derived from jaw muscle architecture measurements on dry skulls. This discrepancy has important implications for the use of FEA, as this method often uses bite force estimates inferred from muscle architecture measurements to calibrate virtual models of extant and extinct taxa. Use of incorrect bite force values may affect the validity of FEA models, especially as it relates to predicting the bite force of extinct taxa and documenting stress distribution during bite. Mandibular force profiles may thus provide an alternative method to obtain more accurate bite force estimates for FEA in the absence of empirically determined bite force values. Furthermore, given that the feeding behaviors reconstructed from mandibular force profiles are generally consistent with those obtained from the FEA studies (e.g. Tseng and Binder, 2010), mandibular force profile analysis has great potential for elucidating the ecology of extinct predators known from limited fossilized remains.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

F.T. conceived the study. F.T. and A.Q. conducted the analyses. All authors assessed the results and wrote the manuscript.

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Data availability

CT images are freely available on ResearchGate at https://www.researchgate.net/publication/309702204_CT_scans.

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