Implications of predatory specialization for cranial form and function in canids

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Abstract

The shape of the cranium varies widely among members of the order Carnivora, but the factors that drive the evolution of differences in shape remain unclear. Selection for increased bite force, bite speed or skull strength may all affect cranial morphology. We investigated the relationship between cranial form and function in the trophically diverse dog family, Canidae, using linear morphometrics and finite element (FE) analyses that simulated the internal and external forces that act on the skull during the act of prey capture and killing. In contrast to previous FE-based studies, we compared models using a newly developed method that removes the effects of size and highlights the relationship between shape and performance. Cranial shape varies among canids based on diet, and different selective forces presumably drove evolution of these phenotypes. The long, narrow jaws of small prey specialists appear to reflect selection for fast jaw closure at the expense of bite force. Generalists have intermediate jaw dimensions and produce moderate bite forces, but their crania are comparable in strength to those of small prey specialists. Canids that take large prey have short, broad jaws, produce the largest bite forces and possess very strong crania. Our FE simulations suggest that the remarkable strength of skulls of large prey specialists reflect the additional ability to resist extrinsic loads that may be encountered while struggling with large prey items.

Introduction

Carnivorans exhibit a wide range of diversity in cranial shape (e.g. Van Valkenburgh & Koepfli, 1993; Wroe & Milne, 2007), but the factors driving the evolution of skull shape within this group remain unclear. Skulls are often studied in the context of feeding capabilities, in particular their ability to both produce and sustain loads. Skulls are expected to evolve to match these two functions; that is, they should not be greatly over- or underbuilt relative to the forces they must sustain. Studies that focus on force production tend to rely on estimates of muscle cross-sectional area and leverage (Wroe, McHenry & Thomason, 2005; Christiansen & Wroe, 2007), while those that focus on skull strength, or the ability to sustain loads, examine aspects of cranial and mandibular shape, as well as cortical thickness (Biknevicius & Ruff, 1992; Van Valkenburgh & Koepfli, 1993; Covey & Greaves, 1994; Biknevicius & Van Valkenburgh, 1996; Therrien, 2005). Until recently, quantitative explorations of skull strength relied largely on linear measurements and simple engineering models of crania and jaws as modified beams or cylinders (Thomason, 1991; Covey & Greaves, 1994). The advent of accessible 3-D modeling software and enhanced computer capacity has allowed the application of finite element (FE) analysis to studies of cranial form and function (Rayfield et al., 2001; Richmond et al., 2005; Ross, 2005). By combining CT scans and FE modeling, researchers can now produce anatomically detailed, 3-D models of skulls that can incorporate variations in skull thickness, muscle size and muscle fiber orientation (Dumont, Piccirillo & Grosse, 2005; Grosse et al., 2007; Wroe et al., 2007a,b).

In this paper we examine the relationship between cranial form, mechanical performance and diet within the dog family, Canidae. First, we investigate whether dietary differences are associated with variation in cranial shape among canids. We then use FE analysis to visualize and quantify the impact of cranial shape on strength during prey killing. Canids are ideally suited to this type of study because they exhibit a broad range of predatory strategies, from specialists on small vertebrate prey, to generalists, and specialists on large vertebrate prey (Van Valkenburgh & Koepfli, 1993). Furthermore, because of adaptations for cursoriality in their post-cranial skeletons (Van Valkenburgh, 1985; Janis & Wilhelm, 1993; Andersson, 2005), canids rely almost exclusively on their skulls and teeth for prey apprehension. Selection for adaptive, performance-enhancing phenotypes should therefore be evident when comparing cranial dimensions and mechanical performance among canids that have different hunting ecologies. By applying a newly developed

scaling method for FE models of biological structures (Dumont, Grosse & Slater, 2009), we provide the first analysis to focus exclusively on the impact of shape on mechanical performance of the cranium within a single clade.

Methods

Diet and upper jaw dimensions

We classified 32 extant species and one recently extinct species of canid to one of three dietary groups, based on literature review (Table 1, Fig. 1). Groups were defined as (1) small prey specialists, in which vertebrate prey smaller than 50% of predator body mass constitute 50% or more of the diet; (2) generalists/omnivores, in which invertebrates, plant matter or carrion constitute over 50% of the diet; (3) large prey specialists, in which vertebrate prey larger than 50% of predator body mass constitute more than 70% of the diet. Upper jaw dimensions were taken from adult skeletal museum specimens with digital calipers (Mitutuyo

Table 1 Sample sizes (n), prey type (s, small vertebrate specialist; g, generalist; l, large vertebrate specialist) and mean (standard deviation) l/w ratios for canids included in this study

| Species	n	Prey	l/w
Alopex lagopus	22	s	1.42 (0.05)
Atelocynus microtis	2	s	1.32 (0.01)
Canis adustus	12	s	1.53 (0.04)
Canis aureus	5	s	1.43 (0.04)
Canis latrans	20	s	1.5 (0.06)
Canis lupus	18	l	1.35 (0.05)
Canis mesomelas	7	s	1.38 (0.05)
Canis simensis	7	s	1.58 (0.04)
Cerdocyon thous	3	s	1.42 (0.05)
Chrysocyon brachyurus	8	s	1.57 (0.05)
Cuon alpinus	24	l	1.24 (0.05)
Dusicyon australis	5	s	1.41 (0.03)
Fennecus zerda	2	g	1.33 (0.04)
Lycaon pictus	18	l	1.18 (0.04)
Nyctereutes procyonoides	4	g	1.19 (0.04)
Otocyon megalotis	7	g	1.29 (0.05)
Pseudalopex culpaeus	10	s	1.5 (0.05)
Pseudalopex griseus	18	s	1.52 (0.05)
Pseudalopex gymnocercus	5	s	1.52 (0.05)
Pseudalopex sechurae	6	g	1.43 (0.04)
Pseudalopex vetulus	7	g	1.32 (0.05)
Speothos venaticus	7	l	1.19 (0.05)
Urocyon cinereoargenteus	20	g	1.44 (0.05)
Urocyon littoralis	20	g	1.41 (0.03)
Vulpes bengalensis	10	g	1.4 (0.03)
Vulpes cana	1	g	1.39
Vulpes chama	4	s	1.4 (0.03)
Vulpes corsac	2	s	1.45 (0.02)
Vulpes ferrilata	8	s	1.55 (0.06)
Vulpes pallida	10	g	1.39 (0.03)
Vulpes ruppeli	8	s	1.44 (0.03)
Vulpes macrotis	9	s	1.5 (0.05)
Vulpes vulpes	22	s	1.52 (0.05)
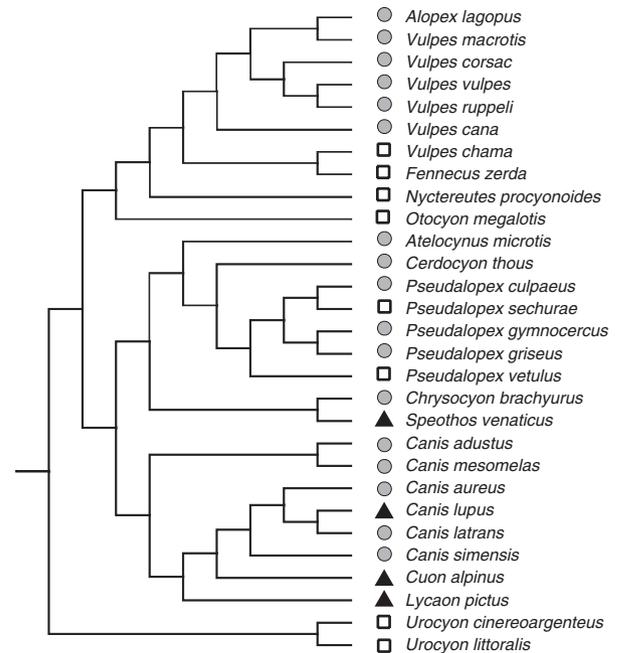
Figure 1 Phylogeny of Canidae used in phylogenetic ANOVA and the distribution of dietary groups. Gray circles, small vertebrate specialists; open squares, generalists; black triangles, vertebrate specialists.

CD-8″CX, Mitutuyo Corps., Aurora, IL, USA) or from digital images with a scale bar using ImageJ v.1.37 (Rasband, 2006). Following Covey & Greaves (1994), we measured upper jaw width (distance across the lateral borders of the glenoid fossae) and upper jaw length (distance from posterior glenoid process to the upper canine tooth) to obtain upper jaw l/w ratio. The number of individuals measured for each species ranged from one to 24 (mean = 10). We assessed differences in jaw dimensions among groups by using ANOVA. We used phylogenetic ANOVA (Garland Jr *et al.*, 1993; Garland Jr, Midford & Ives, 1999; Garland Jr & Ives, 2000) to determine whether the distribution of jaw dimensions among dietary groups differs from that of a randomly evolving trait across a phylogeny (see supporting information for details).

FE analyses

Model construction

We constructed FE models of crania from three taxa that represent the range of skull shapes observed in wild canids. To limit phylogenetic effects, we focused on three African canids from the monophyletic wolf-like canid clade (Bardeleben, Moore & Wayne, 2005): Ethiopian wolf *Canis simensis*, black-backed jackal *Canis mesomelas* and African wild dog *Lycaon pictus*. Upper jaw dimensions of these canids differ significantly (one-way ANOVA, $F_{2,29} = 239.8$, $P < 0.001$), as does diet. *Canis simensis* has a long, narrow snout and specializes on small rodents, *C. mesomelas* has a

Table 2 Information for the three finite element models used in this study

Taxon	Specimen	CT slice thickness (mm)	Model size (tet4)	Volume (mm^3)
Canis simensis	AMNH 81001	0.25	931 998	93 797.15
Canis mesomelas	UCLA 3000	0.1981	1 039 276	89 286.13
Lycaon pictus	USNM 368443	0.25	1 002 902	106 544.1

Model size and volume applies to scaled models.

snout of intermediate length and has a more generalized diet, while *L. pictus* has a short, broad snout and specializes on large ungulates (Sillero-Zubiri, Hoffmann & MacDonald, 2004). Although *C. mesomelas* was classified as a small prey specialist in our dietary classifications, it also scavenges extensively. Furthermore, the shape of its cranium is more similar to generalized taxa, making it suitable for comparison to the other two, more extreme morphologies.

We constructed models of the three crania from CT scans (Table 2), following methods of Dumont *et al.* (2005). We applied muscle forces over the origins of the temporalis, masseter and pterygoideus muscles using the tangential-plus-normal traction model in the program BoneLoad (Grosse *et al.*, 2007). This method incorporates the effects of muscle wrapping around curved bone surfaces and eliminates artifacts caused by point loads in areas of muscle insertion. In the absence of species-specific data, muscle forces were distributed in each model according to the percentage contribution of temporalis (64%), masseter (26%) and pterygoideus (10%) to total jaw muscle mass in the domestic dog (Davis, 1955). Available data suggest that these values are fairly consistent across Carnivora (Davis, 1955; Turnbull, 1970).

We assigned homogeneous material properties to the models based on values for domestic dog cortical bone ($E = 13.7$ GPa, $v = 0.3$; Cook, Weinstein & Klawitter, 1982; Verrue, Dermaut & Verheghge, 2001). Including heterogeneous values for bone can impact the results of FE analyses (Strait *et al.*, 2005; McHenry *et al.*, 2007; Wroe *et al.*, 2007*b*). However, this study focuses on the performance of FE models that differ markedly in form. We therefore made the modeling assumption that material properties of the three species do not vary. This allowed us to interpret differences in performance as a result of differences in model geometry only.

We scaled our models using a new method that allowed us to remove the effects of size and focus solely on how shape affects mechanical performance for a given loading condition (Dumont *et al.*, 2009). Previous comparative FE analyses have typically not considered the effects of scaling on performance (but see McHenry *et al.*, 2007). Dumont *et al.* (2009) have recently shown that if the objective of an analysis is to compare the relative performance of two or more structures then models and their loads must be appropriately scaled. Specifically, if performance is to be assessed in terms of model stress, the ratio of applied muscle force to the model's surface area must be held constant. Similarly, if performance is assessed in terms of total strain energy, a measure of energy lost to deformation, the ratio of applied

muscle force to the model's volume$^{1/6}$ must be held constant. Scaling in these ways generates null hypotheses of no differences in stress distributions, stress magnitudes or total strain energy among the models for a given loading condition. Furthermore, because muscle forces should scale to mass$^{2/3}$ (e.g. Emerson & Bramble, 1993), bite forces should be identical in analyses with muscle forces scaled to surface area. Any differences in stress, strain energy or bite force production among the models are thus a result of shape differences.

We scaled models to common surface area (72 067.26 mm^2) and applied identical muscle forces (2682 N). These values were derived from those for the intermediate-sized Ethiopian wolf, with the muscle forces based on a dry-skull estimate of bite force (Thomason, 1991). Note however that any constant applied force/surface area ratio could be used, and the results would be identical, because we employed linear FE analyses (Dumont *et al.*, 2009). Bone is an elastic material and fails under a ductile mode of fracture (Nalla, Kinney & Ritchie, 2003). We therefore assessed cranial strength using von Mises stress, a scalar function of the principle stresses at each element and a good predictor of failure due to ductile fracture (Dumont *et al.*, 2005). Strain energy values for the jackal and wild dog were scaled to produce values at comparable force/volume$^{1/6}$ ratios to that of the Ethiopian wolf using equation (5) from Dumont *et al.* (2009).

Intrinsic loads

We simulated two intrinsic loading conditions that canids experience during prey apprehension, bilateral and unilateral canine biting (supporting information). We did not model posterior (carnassial or molar) bites as canids rely almost exclusively on canine biting during prey capture and killing (Ewer, 1973).

Extrinsic loads

We simulated four extrinsic loading conditions that canids may experience during hunting; a 'pull back,' a 'lateral shake,' bilateral canine loading (bending) and unilateral canine loading (torsion). Boundary conditions are described in the supporting information. We modeled all extrinsic load cases twice; first with only extrinsic loads applied and then with extrinsic and intrinsic loads applied simultaneously (supporting information). In previous studies, extrinsic loads have been modeled alone, without intrinsic jaw muscle forces (McHenry *et al.*, 2007; Wroe *et al.*, 2007*a*,*b*; Wroe,

2008). However, canids are likely to be biting and recruiting jaw musculature at the same time that they experience extrinsic loads from struggling prey, and addition of muscle forces may profoundly affect the stress and strain regimes resulting from biting (e.g. Buckland-Wright, 1978). For each extrinsic load case, 298 N of total force was applied to the models, based on Wroe *et al.*'s (2007*a*) value for the similarly sized dingo *Canis familiaris dingo*. Force/surface area ratios were held constant among models within each set of extrinsic load cases, allowing comparison of relative performance among the three taxa. Linear static FE analyses for intrinsic and extrinsic load cases were completed using Strand7 (Strand7 Pty Ltd, G + D Computing, Sydney, Australia).

Results

Diet and upper jaw dimensions

Jaw dimensions differed significantly among canids that specialize on different sized prey, based on both regular
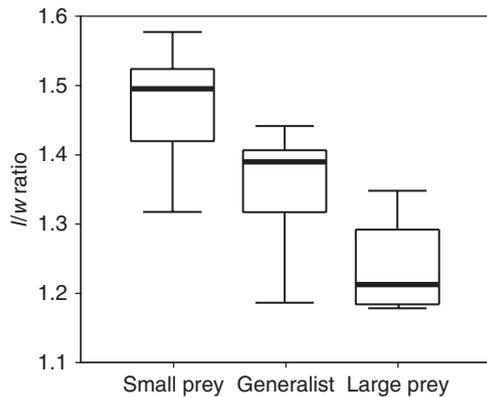

Figure 2 Box plots for jaw dimensions among the three prey groups. Groups are significantly different from each other.

and phylogenetic ANOVAs (Fig. 2; $F_{2,30} = 20.15$, $P < 0.001$; phylogenetically-informed critical $F_{\alpha = 0.05} = 5.29$, $P < 0.001$). Pair-wise Bonferroni *post hoc* tests confirm that significant differences exist among the groups (small prey specialists vs. generalists, $P < 0.001$; small prey specialists vs. large prey specialists, $P < 0.001$; generalists vs. large prey specialists, $P = 0.027$). Predators of large prey have short, stout upper jaws (mean $= 1.2463 \pm 0.081$), generalists are intermediate (mean $= 1.3801 \pm 0.76$), and predators of small prey have long, narrow upper jaws (mean $= 1.4877 \pm 0.74$).

FE analyses

Intrinsic loads

Stress distributions in FE analyses of intrinsic loads are broadly similar among taxa (Fig. 3). Stress accumulates in the snout and peak stresses are higher during unilateral canine biting than bilateral biting. During unilateral biting, the jaw joint on the balancing-side undergoes higher stress than the joint on the working-side, while the working-side of the snout undergoes higher stress than the balancing-side.

Intrinsic loads demonstrate that bite force at the canine is inversely related to jaw length (Table 3). The long-jawed Ethiopian wolf produces the lowest bite force per unit muscle force, while the short-jawed wild dog produces the largest bite force. Contour plots of von Mises stresses show that the Ethiopian wolf and jackal exhibit similar levels of stress in the rostrum during both bilateral and unilateral biting (Fig. 3). Plots of stress taken from 10 morphological landmarks along the mid-sagittal plane (Fig. 3g and h) show that the stress magnitudes and distributions are similar for the two taxa. Values of strain energy within these two models are comparable during bilateral and unilateral biting (Table 3).

In contrast, the wild dog exhibits relatively low and evenly dissipated stress during bilateral and unilateral canine biting (Fig. 3). Although a small stress peak is present on the working-side of the rostrum during unilateral biting, mid-sagittal stress plots are remarkably even (Fig. 3g and h).
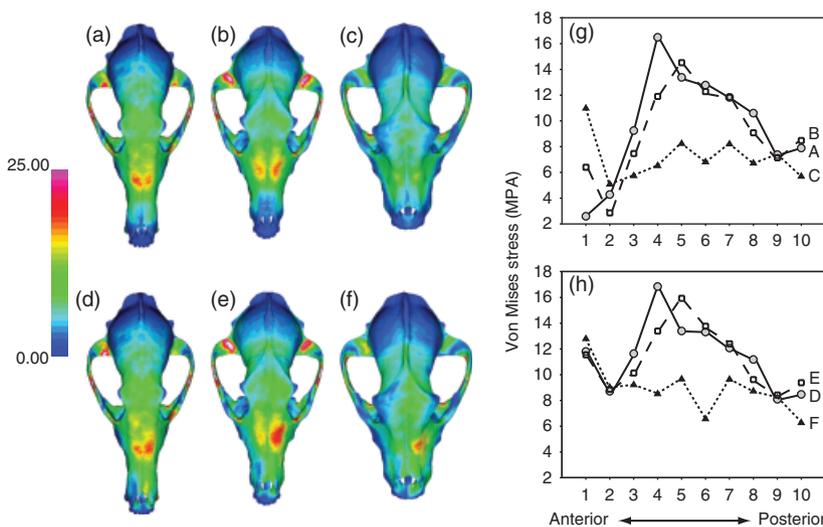

Figure 3 Contour plots of von Mises stress from the analysis of intrinsic loads during bilateral (a–c) and unilateral (d–f) biting. Models are *Canis simensis* (a, d) *Canis mesomelas* (b, e) and *Lycaon pictus* (c, f). Plots show stress in megapascals (MPa) for each model at comparable positions from anterior (1) to posterior (10) along the mid-sagittal line during bilateral (g) and unilateral (h) biting. *Canis simensis*, gray circles, solid line; *C. mesomelas*, open squares, broken line; *L. pictus*, black triangles, dotted line. Scale bar indicates von Mises stress. Cool colors indicate low stress and warm colors indicate high stress.

Table 3 Bite forces (N) for intrinsic loads and strain energy values (J) for intrinsic, extrinsic only, and extrinsic+intrinsic loading of the three FE models

	Taxon		
	Canis simensis	*Canis mesomelas*	*Lycaon pictus*
Bite Force			
bilateral	189	233.6	255.3
unilateral	374.4	459.2	499.8
Intrinsic loads			
bilateral	0.156	0.153	0.14
unilateral	0.178	0.18	0.179
Extrinsic only loads			
pull-back	0.018	0.018	0.016
lateral shake	0.542	0.809	0.497
bilateral canine	0.061	0.032	0.025
unilateral canine	0.083	0.049	0.049
Extrinsic + Intrinsic loads			
pull-back	0.223	0.260	0.212
lateral shake	0.675	0.965	0.586
bilateral canine	0.123	0.138	0.087
unilateral canine	0.143	0.154	0.109

Strain energy values are also lower in the wild dog than in the other two taxa (Table 3), demonstrating that it performs most efficiently (i.e. loses less energy through deformation, or is stiffer) under both biting conditions.

Extrinsic loads

There were three marked differences among models that simulated extrinsic loads with and without muscle forces (Figs 4 and 5, Table 3). First, stresses were lower in analyses that only included extrinsic loads. Second, the patterns of stress distribution varied remarkably under 'lateral shake' loads. When only extrinsic loads are applied, the inter-orbital region is stressed symmetrically (Fig. 4d–f). However, when muscle forces are added, stresses are concentrated along the right orbit and rostrum (Fig. 5d–f). This is particularly evident in the Ethiopian wolf and jackal models. Similarly, stress accumulates in the basicranium during extrinsic-only loading, while stresses were distributed more evenly over the entire cranium during extrinsic plus intrinsic loading (not shown). Third, relative values of strain energy differ in bilateral and unilateral canine loading. When only extrinsic forces are considered, the jackal and wild dog models have similar strain energy values. In contrast, when both intrinsic and extrinsic loads are considered, strain energy values are most similar in the jackal and Ethiopian wolf.

Because of the more realistic nature of simultaneous extrinsic and intrinsic loading, we focus our discussion on results from analyses incorporating both loads. All models performed more poorly during 'lateral shake' and 'pull back' loads (Fig. 5a–f). Strain energy values (Table 3) illustrate that the jackal loses more energy to deformation than the Ethiopian wolf in all load cases, although this result
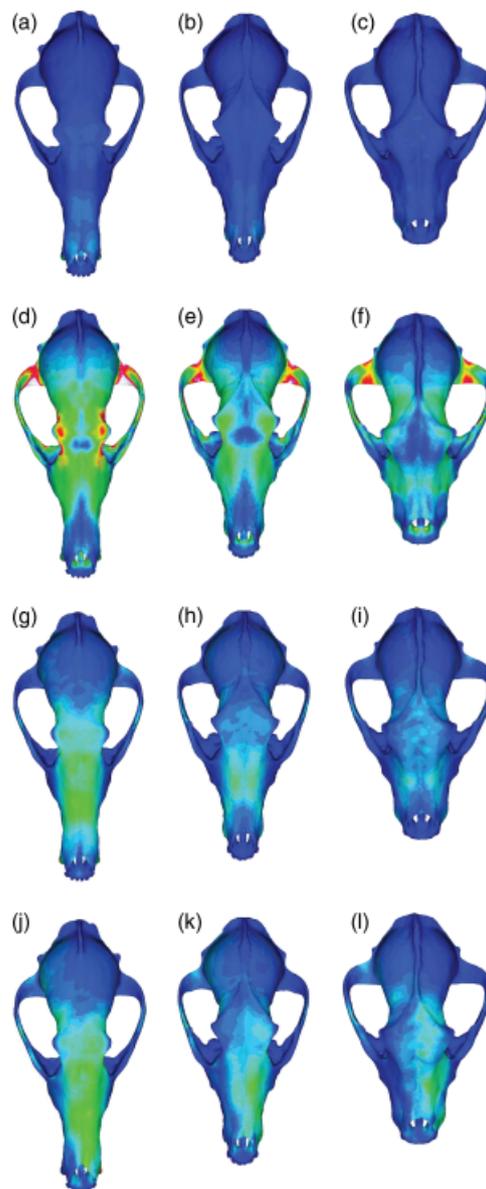

Figure 4 Contour plots of von Mises stress for the extrinsic only load cases. Pull-back (a–c), lateral shake (d–f), dorsal (g–i) and torsion (j–l). Models are: *Canis simensis* (left), *Canis mesomelas* (center) and *Lycaon pictus* (right). As in Fig. 3, cool colors indicate low stress and warm colors indicate high stress.

is reversed in analyses incorporating extrinsic loads only. The wild dog performs very well under all extrinsic loading conditions, with low, uniform stresses throughout the cranium (Fig. 5) and better work efficiency (lower strain energy) than the other two taxa (Table 3).

Discussion

Our morphometric analysis confirms that upper jaw dimensions vary among canids based on diet. Specialization on
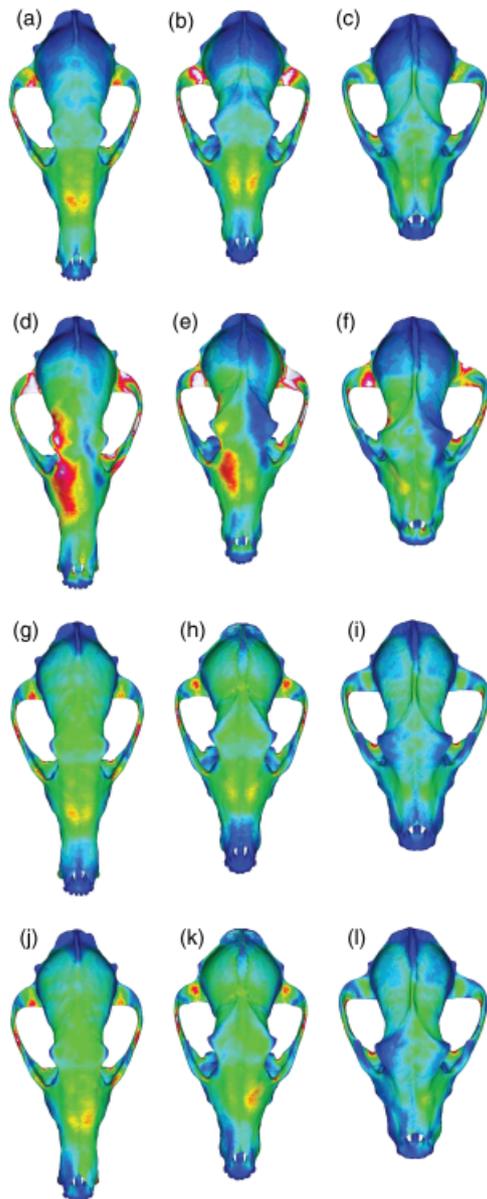
Figure 5 Contour plots of von Mises stress for the extrinsic plus intrinsic load cases. Pull-back (a–c), lateral shake (d–f), dorsal (g–i) and torsion (j–l). Models are: *Canis simensis* (left), *Canis mesomelas* (center) and *Lycaon pictus* (right). As in Fig. 3, cool colors indicate low stress and warm colors indicate high stress.

small prey is associated with repeated evolution of long, narrow jaws, while specialization on large prey is associated with repeated evolution of short, broad jaws. Furthermore, based on the results from our FE analyses, there is a clear inverse relationship between upper jaw length and bite force. These results appear to reflect differences in the mechanics of prey capture. Selection should favor faster closing jaws in canids that specialize on small, fast moving prey. These canids achieve faster jaw closure by lengthening the jaw out-lever, albeit at the expense of bite force (Preuschoft &

Witzel, 2005). In contrast, large bite forces are probably required to subdue large vertebrate prey. Short, broad jaws allow large prey specialists to produce large bite forces efficiently by reducing the length of the jaw out-lever, thereby increasing the leverage of the jaw musculature (Biknevicius & Van Valkenburgh, 1996; Wroe *et al.*, 2005; Christiansen & Wroe, 2007). Generalists fall between the two specialized groups in jaw dimensions and bite force, perhaps reflecting their need to be efficient predators on a range of prey. These morphological and functional differences might also illuminate some macroevolutionary patterns. Canids show a tendency to increase in body size throughout their fossil history. This is associated with increased specialization on large prey, probably in response to the energetic requirements of large body size, and shorter species durations (Van Valkenburgh, Wang & Damuth, 2004). Selection for increased bite force, at the expense of bite speed, may limit the ability of these taxa to effectively utilize smaller prey during times of limited resource availability, contributing to their higher rates of turnover.

By appropriately scaling FE models, we can draw conclusions about the relative strength of crania of different shapes under similar loading conditions, and hypothesize about what may drive the evolution of these shapes in canids. Performance of the jackal and Ethiopian wolf models is similar under intrinsic loading conditions, based on both stress and strain energy values. These crania appear well matched to their loads, even though the jackal produces a somewhat higher bite force than the Ethiopian wolf for the same amount of muscle force. The larger bite force in the jackal model, combined with similar stress values to those in the Ethiopian wolf model, might lead one to speculate that the jackal's cranium is stronger. However, because the models are properly scaled, the similarity in stress and strain energy indicates that we cannot reject the null hypothesis of comparable strength for these loading conditions (Dumont *et al.*, 2009).

During extrinsic loading, both the Ethiopian wolf and the jackal perform relatively poorly. The Ethiopian wolf incurs higher stresses, particularly during lateral shaking, indicating it is the weaker of the two shapes under these loading conditions. However, the jackal incurs higher strain energy than the Ethiopian wolf for all extrinsic loads. This result is not found when extrinsic loads are modeled alone, suggesting that not accounting for all loads can lead to misleading results.

The short, broad cranium of the wild dog, experiences low stress, shallow stress gradients, stores less strain energy during both bilateral and unilateral canine biting, and produces the largest bite force per unit of muscle force. The existence of steep stress and strain gradients in skulls has been invoked as evidence that skull shape is not optimized for routine mechanical loads (Thomason, 1991; Ross & Metzger, 2004). In this sense, the presence of relatively even stress suggests that the cranium of *L. pictus* is more optimized for load bearing than are the crania of the Ethiopian wolf or the jackal. If that is true, then selection for a cranial shape resistant to both bending and torsional loading has

occurred in this lineage. These results add to previous work, which showed wild dogs and other canids that take large prey possess stronger canine and incisor teeth and deeper jaws than small prey specialists or generalists (Van Valkenburgh & Koepfli, 1993).

The results of our intrinsic load cases suggest that the cranium of the wild dog is overbuilt with respect to loads encountered during biting alone. Although large bite forces are undoubtedly important for canids that hunt large prey, bite force does not fully explain the degree of cranial strength observed in the wild dog. Our models were scaled so as to remove the effects of size and focus solely on the effects of shape on model performance (Dumont et al., 2009). Therefore, the null hypothesis in all of our loading experiments was that stress and strain energy would be identical among models (i.e. shape differences have no effect on model performance). In our intrinsic loading experiment, the Ethiopian wolf and the jackal exhibited similar strength as evidenced by similar levels of stress, despite the fact that bite forces are higher in the jackal. The wild dog, on the other hand, exhibits much lower stresses in combination with the highest bite forces. Therefore, either the skull of the wild dog is simply 'overbuilt' relative to the Ethiopian wolf and the jackal, or some factor in addition to biting is associated with increased cranial strength in this taxon.

We suggest that cranial form in canids that take large prey may be reflective of selection for increased skull strength and work efficiency under extrinsic loading, in addition to that for intrinsic (bite force) loading alone. Large forces are likely to be generated by even moderately sized prey during prey apprehension (Preuschoft & Witzel, 2005). Our extrinsic load cases show that the cranium of the wild dog is stronger and more work efficient than the other two canids under all extrinsic loading conditions. Wild dogs probably routinely subject their skulls to large and unpredictable loads when killing large mammals. These loads are probably not often experienced by canids that have generalized diets, such as jackals, or those that specialize on small prey, such as Ethiopian wolves. Large prey specialists tend to be highly cursorial, relying on a combination of speed and pack-hunting to capture and kill prey (Ewer, 1973; Biknevicius & Van Valkenburgh, 1996). As a result, selection for cranial shapes that minimize mass while imparting maximum strength under a range of loading conditions should be strong in such forms. FE analyses of scaled models of additional canid crania, spanning a range of body sizes and dietary specializations, will help further test this hypothesis.

For most FE analyses of cranial form, in vivo data on bite force and physiological cross-sectional areas of jaw musculature are not available, particularly for rare species such as those studied here. In such cases, it is not possible to accurately predict the actual performance of the structures under study. However, when models and their loads are properly scaled, as we did here, it is possible to assess the relative performance of the models under a set of specified loading conditions. This in turn should illuminate the functional factors that drive the evolution of form in biological structures.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Phylogenetic ANOVA.

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