

1 **Scaling and**
2 **accommodation of jaw**
3 **adductor muscles in**
4 **Canidae.**

5
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1 **ABSTRACT**

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3 The masticatory apparatus amongst closely related Carnivoran species raises
4 intriguing questions about the interplay between allometry, function and
5 phylogeny in defining interspecific variations of cranial morphology. Here we
6 describe the gross structure of the jaw adductor muscles of several species of
7 canid, and then examine how the muscles are scaled across the range of
8 body sizes, phylogenies and trophic groups. We also consider how the
9 muscles are accommodated on the skull, and how this is influenced by
10 differences of endocranial size. Data were collected for a suite of
11 morphological metrics, including body mass, endocranial volume and muscle
12 masses and we used geometric morphometric shape analysis to reveal
13 associated form changes. We find that all jaw adductor muscles scale
14 isometrically against body mass, regardless of phylogeny or trophic group, but
15 that endocranial volume scales with negative allometry against body mass.
16 These findings suggest that head shape is partly influenced by the need to
17 house isometrically scaling muscles on a neurocranium scaling with negative
18 allometry. Principal component analysis suggests that skull shape changes,
19 such as the relatively wide zygomatic arches and large sagittal crests seen in
20 species with higher body masses, allow the skull to accommodate a relative
21 enlargement of the jaw adductors compared with the endocranium.

Keywords: canid, hypercarnivorous, jaw adductor, muscle, scaling,
accommodation

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1 **INTRODUCTION**

2 Interspecific differences of Carnivoran skull shape are dependent on
3 numerous factors, most notably phylogeny, dietary function and allometry with
4 the relative importance of each depending on the group of species under
5 investigation. Here, we attempt to resolve the relative importance of allometry
6 and diet in determining cranial morphology among one particularly
7 widespread and varied carnivoran family, the canids. We aim to account for
8 phylogeny and determine how labile the musculoskeletal morphology of the
9 wild canid head is by combining advances in imaging with conventional
10 dissection and more advanced computational methods such as geometric
11 morphometrics. In contrast to many previous studies (Christiansen and
12 Adolfssen 2005; Wroe and Milne 2007; Figueirido et al., 2011; Damasceno et
13 al., 2013) we directly quantify the masticatory muscles as well as the bony
14 morphology.

15 Radinsky (Radinsky 1981) was amongst the first to document that Carnivoran
16 skull shape is linked to negative allometric scaling of the brain among related
17 species but did not consider, in detail, questions concerning the potential
18 knock-on effects for the masticatory apparatus. In particular, are the areas for
19 muscle origin on the skull compromised with the relative reduction of brain
20 size and of the surrounding neurocranium, and does this influence the size of
21 the muscle mass that can be accommodated? In addition, is this further
22 compounded by the positive allometric scaling of the masticatory muscles
23 needed to maintain the same level of biomechanical function? Emerson and
24 Bramble (1993) state that large species can exert relatively less muscle force
25 than small species, and are required to move relatively and absolutely heavier
26 jaws. This implies that with increases of body size, species either lose
27 function or must have relatively larger muscles that in turn require a
28 commensurate increase in the bony areas for their attachments. Numerous
29 studies have also linked skull form with dietary function (Sacco and Van
30 Valkenburgh; Meachen-Samuels and Van Valkenburgh 2009; Tseng and
31 Wang 2010; Sicuro and Oliveira 2011; Tseng and Anton, 2011). Slater and
32 Van Valkenburgh (Slater and Van Valkenburgh 2008; Slater and Van
33 Valkenburgh 2009) have shown that big cats have lengthened their jaw to

1 facilitate a relatively wider gape than small cats. This suggests that big cats
2 are not simply 'scaled up' small cats, but make different functional demands of
3 their jaws. This morphological difference coincides with a difference in their
4 diet and hunting strategies; whereas small cats take prey smaller than
5 themselves, big cats require a relatively wider gape to subdue prey which may
6 be larger than them (Slater and Van Valkenburgh 2009).

7 Here we look collectively at the scaling of brain size and of masticatory
8 muscle size as well as at trophic niche as determinants of canid skull
9 morphology. Canids were selected for the present study because they are
10 diverse in body mass, geographical location and dietary group specialisation
11 and their phylogeny is relatively well documented (Gittleman 1985; Wayne et
12 al., 1989; MacDonald and Sillero-Zubiri 2004; Sillero-Zubiri et al., 2004;
13 Finarelli 2007; Macdonald 2009; Wang and Tedford 2010). All 36 species
14 (Nowak 2005) of extant canids, the canidae, belong to the subfamily caninae
15 and are thought to have evolved from a common ancestor that originated in
16 North America around 8-12million years ago (Wang and Tedford 2010).
17 Modern species are arranged in four main phylogenetic clades, the fox-like
18 vulpes clade, the wolf-like canis clade, the South American clade and the grey
19 fox-like Urocyon clade (Lindblad-Toh et al., 2005). Both convergent and
20 divergent patterns of morphological adaptation are found within and amongst
21 these clades. For instance, the South American foxes, although
22 phenotypically very similar to the fox-like vulpes are more closely genetically
23 related to the wolf-like canids (Wayne et al., 1997; Perini et al., 2010;
24 Nyakatura and Bininda-Emonds 2012). Conversely, morphologies amongst
25 closely related species such as the South American *Speothos venaticus* and
26 *Chrysocyon brachyurus* are very distinct and highlight a great potential for
27 phenotypic plasticity. Three trophic groups exist which allow us to correlate
28 head morphology with hunting behaviour and functional dietary requirements;
29 these are the small prey specialists, the generalists and the large prey
30 specialists. These dietary specialisms are not dictated by phylogenetic clade:
31 the fox-like group consists both of generalists and small prey specialists, the
32 South American group of generalists and small and large prey specialists and
33 the wolf-like group of generalists and large prey specialists. Both of the

1 urocyon clade members are generalists (Slater et al., 2009).

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3 **AIMS OF THE STUDY**

4 Scaling of masticatory muscle masses, as opposed to bony proxies, is not
5 widely described in many species of mammal but previous studies have
6 established that there is no common rule regarding the relative size of the jaw
7 adductors within clades. Primates demonstrate isometric scaling regardless
8 of diet or phylogeny (Cachel 1984; Perry and Wall 2008). Herrel describes the
9 mass of the temporalis muscles of a wide range of bats, including frugivorous,
10 insectivorous and sanguivorous species, scaling with negative allometry
11 (Herrel et al., 2008). Macropodoideal marsupials show a range of scaling
12 patterns in all jaw adductors, according to dietary preference (Warburton
13 2009). Similarly, the relative masseter muscle mass in ruminants has been
14 shown to differ amongst species with different feeding categories independent
15 of body mass or phylogeny (Clauss et al., 2008). Within the carnivoran order
16 Hartstone-Rose established that the masticatory muscle masses scale with
17 isometry that tends towards positive allometry (Hartstone-Rose et al., 2012).
18 Here we aim to describe the jaw adductor muscles of several species of canid
19 and establish whether they scale isometrically against body mass, or more
20 closely follow other patterns that reflect dietary function or phylogeny.
21 Specifically, we will consider how temporalis, masseter and the pterygoids
22 contribute to the entire jaw adductor mass, their gross architecture, their mass
23 compared to body mass and to endocranial volume, and their specific and
24 relative areas of attachment to the skull. We also evaluate the hypothesis that
25 species with a high bite force and large body mass, such as the
26 hypercarnivores (Wroe et al., 2005; Christiansen and Wroe 2007), have
27 absolutely and relatively larger muscles, and we speculate that the
28 morphology of the masticatory musculature of hypercarnivorous canid species
29 differs from those of generalists and small prey specialists and deviates
30 significantly from simple predictive patterns of size scaling. As the jaw
31 adductor muscles arise solely from the cranium and cover much of its external
32 surface, we also consider how they are accommodated on the skull and,
33 through shape analysis, explore whether the diversity of head shape among

1 canids is influenced by constraints and concomitant compensatory
2 adjustments for housing the masticatory muscles. Previous studies have
3 been able to categorise canids according to diet based on overall skull shape
4 (Radinsky 1981; Van Valkenburgh 2007) or upper jaw morphology (Slater et
5 al., 2009) with the hypercarnivorous species tending toward a broad stocky
6 skull and shortened snout, and the small prey specialists being more gracile
7 with a long rostrum and narrow jaws. Here we regard the bony skeleton of
8 the head to be made of three modules – the cranial part, the rostral part and
9 the mandible, and consider if all of the modules aid in determining diet or if
10 some are instead allied with muscle accommodation.

11

12 **MATERIALS AND METHODS**

13 **Specimens**

14 Specimens from 8 of the 13 genera that make up the canidae family were
15 obtained from either euthanased zoo stock or vermin control (Table 1). For
16 this study we follow Wozencraft and define the arctic fox as a member of the
17 *Vulpes* genus (Wozencraft 1993). There were 19 individuals from 12 species
18 with representatives from the three major clades and the three trophic groups.
19 The data set is not inclusive of all canid species, however, it covers a broad
20 range of head shapes, body sizes and phylogenetic groups, and it includes all
21 four of the hypercarnivorous species (Van Valkenburgh 2007). Although
22 numbers of specimens are low for all species in this study, diversity of scale
23 covers two orders of magnitude in the canidae and interspecific differences
24 are greater than intraspecific ones. For the purposes of this study species
25 were identified as being from one of the three trophic groups as described by
26 Slater et al (Slater et al., 2009) (Table 1). All specimens were adults and
27 exact ages as recorded by donor organizations were recorded in 6
28 specimens, and maturity established for the others with reference to dental
29 wear. In some cases only the heads were available and so mean body
30 masses as reported in the literature were used for all calculations (Table 1).
31 Sex was recorded in all individuals. Some degree of sexual dimorphism has
32 been documented in many canid species, but the literature concurs that it is
33 very modest and that overall body size is the greatest differential factor. Males
34 often have a slightly greater body mass and larger overall proportions than

1 females, however there appears to be a significant amount of overlap in body
2 mass data between the largest female and smallest males (MacDonald and
3 Sillero-Zubiri 2004; Sillero-Zubiri et al., 2004; Macdonald 2009; Wang and
4 Tedford 2010). Several species have also been shown to exhibit some sexual
5 dimorphism relating to dentition, although canids, along with hyaenids, are
6 noted to be the least dimorphic in this respect of all of the carnivores. Where
7 species have been shown to exhibit dental dimorphism, males typically have
8 8-15% longer canines but this is thought to relate to behavioral displays and is
9 not correlated to body mass or skull length (Gittleman and Van Valkenburgh
10 1997; Kim et al., 2012). Specimens were either chilled fresh or frozen and
11 then defrosted, but no fixative agent was used on any specimen. All
12 specimens were dissected at near occlusal bite, that is, with minimal gape
13 (Figure 2a).

14

15 **Dissection**

16 One side of the head, either left or right, was dissected for each specimen and
17 then photographed using a digital camera (Sony DSC-H200) that was
18 positioned perpendicular to the sagittal, axial and coronal planes of each
19 specimen. No individual was judged to have a preferential working side
20 judging from dental wear. For the present study we limit the definition of the
21 masticatory apparatus to the jaw adductor muscles (temporalis, masseter and
22 pterygoids) and associated skeletal components, although in reality other
23 structures such as the tongue and salivary glands also contribute towards
24 food prehension and mastication. The constituent bellies of the jaw adductor
25 muscles were photographed in situ alongside a graduated rule and removed
26 layer by layer to document architectural detail. After removal each layer was
27 wrapped in damp cloth along with the rest of the muscle division and stored in
28 plastic wrap to prevent dehydration. All muscle divisions were subsequently
29 weighed using digital scales (Redwag WPS600/C/2) to determine mass. Each
30 muscle sample was weighed three times and the average recorded. Muscle
31 classification and nomenclature of subdivisions within each muscle varies
32 between authors (Druzinsky et al., 2011). For this study we broadly follow the
33 plan of Turnbull (Turnbull 1970) who identifies the temporalis as subdivided
34 into suprazygomatic, superficial, and deep divisions and the masseteric

1 muscle mass subdivided into superficial, deep and zygomaticomandibularis
2 divisions. Some authors define zygomaticomandibularis as the deepest
3 division of the masseter complex (Evans and De Lahunta 2012). In
4 accordance with other authors (Davis 1955; Hartstone-Rose et al., 2012) we
5 recognise it as subdivision of the masseter as it also arises from the
6 zygomatic arch and inserts onto the lateral vertical ramus of the mandible.
7 The lateral pterygoid is very small in carnivores (Turnbull 1970; Herring 2007)
8 and in this study we have included it along with the much larger medial
9 pterygoid to be considered as one muscle mass, the pterygoids. In mammals
10 capable of rostro-caudal and lateral movement of the jaw the lateral pterygoid
11 is able to protract the jaw and aid in lateral translations. However, in carnivore
12 species rostro-caudal movement of the mandible is precluded by the
13 cylindrical form of the mandibular fossa of the temporal bone and the well-
14 developed retroglenoid process. Lateral movement is also greatly limited. As
15 a result the only movement at the temporomandibular joint in carnivores is
16 rotation around the mandibular condyle and, consequently, the lateral
17 pterygoid contributes to jaw closing (Getty 1975; Ström et al., 1988; Dyce et
18 al., 1996; Herring 2007; König and Liebich 2009; Evans and De Lahunta
19 2012).

20

21 **Imaging**

22 To capture the internal and external architecture of the skull in three-
23 dimensional detail, heads were scanned at the University of Liverpool using
24 computer tomography (CT) either at the Small Animal Teaching Hospital
25 using a Siemens Somatom Volume Zoom (Siemens AG, Munich) or a
26 Toshiba Prime Aquilion (Toshiba Medical Systems, Europe), or at the Philip
27 Leverhulme Equine Hospital using a GE Lightspeed Plus (GE Medical
28 Systems, Milwaukee). Pixel resolution ranged from 0.136 to 0.417mm and
29 slice thickness from 0.3 to 1.2mm. Current and voltages used were 120 kV
30 and 200 mA. Pre-processing of CT data was done with ImageJ v1.45s
31 (Schneider et al., 2012).

32

33 **Landmarking**

1 Scans for each specimen were reconstructed in virtual 3D by label mapping in
2 Avizo 8.1(FEI Systems, Oregon, USA). Reconstructions and oblique slices
3 were used to locate and place a series of 71 anatomical landmarks,
4 representing the whole skull and mandible. Three subsets of landmarks were
5 chosen to represent the three components, or modules (Klingenberg 2009), of
6 the bony skeleton – the neurocranium that is most closely associated with the
7 hypothesized constraint of muscle and brain size scaling, the rostral
8 component that is most closely associated with the nasal cavity and upper
9 dental arcade and the mandibular component associated with housing the
10 lower dental arcade (Appendix 1). Subsets were then used as variables in
11 further tests.

12

13 **Volume & Area Measurements**

14 Surface areas for the muscle attachment sites were calculated in Avizo 8.1 by
15 demarcating the bony boundaries of the muscle origins (Figure 7).

16 Endocranial volume (EV) is used as a proxy for brain volume and was
17 calculated from CT images using the automatic segmentation 3D Active
18 Contours function built into ITKsnap v2.4 (Yushkevich et al., 2006) (Figure 1).

19 In addition to endocranial volume, the endocranial volume surface area
20 (EVSA) was calculated from the endocranial volume models using the Model
21 module in 3D Slicer v4.3 (Fedorov et al., 2012). The EVSA values were then
22 used as a proxy for the internal surface area of the cranium. This then allowed
23 us to consider the internal surface area of the cranium and external
24 attachment surface areas of the neurocranium as two separate variables.

25

26 **Statistics**

27 Differences between the dietary groups regarding the percentage contribution
28 of each muscle to the overall jaw adductor mass, and percentage contribution
29 of each muscle division to the total muscle mass, were tested using analysis
30 of variation (ANOVA). To evaluate body size scaling trends log transformed
31 values of muscle mass, muscle attachment surface area, endocranial volume,
32 endocranial volume surface area, geometric mean and zygomatic arch width
33 were regressed against body mass using the non-parametric Reduced Major
34 Axes (RMA). RMA regression was used as there is measurement error in both

1 variables. However, it is worth noting that whilst the non-parametric RMA is
2 the most appropriate method for these particular bivariate comparisons, the
3 findings do not differ significantly from those calculated with ordinary least
4 squares regression. Evaluations of isometry were made on the basis of the
5 RMA slope 95% confidence intervals and *t*-tests against predicted slope
6 values. As temporalis is the largest of the jaw adductors, with the largest
7 surface area attachment, we chose it to be the main focus of the
8 accommodation part of this study.

9

10 Because the species in our samples may not be statistically independent due
11 to a shared phylogeny, we repeated regressions with a phylogenetic
12 independent contrast analyses based on an open access phylogenetic tree
13 published by Nyakatura (Nyakatura and Bininda-Emonds 2012). The tree
14 was pruned to include only our sample species (Appendix 2). Diagnostic tests
15 were performed using the PDAP:Pdtree module v 1.16 in Mesquite v. 3.01
16 (Maddison and Maddison 2010) (Midford et al., 2005). Eleven variables
17 representing species means were analysed (Table 2). We determined the
18 absolute values of the standardized phylogenetic independent contrasts (PIC)
19 for each character versus their standard deviations. A *P*-value of ≤ 0.05
20 would be regarded as significant and would indicate phylogenetic influence
21 (with values greater than 0.05 indicating no phylogenetic signal). The
22 reduced major axes regressions were also repeated using the PICs and the
23 slopes compared against those for the standard data.

24

25 Geometric morphometric analysis was used to identify and quantify patterns
26 of morphological variation across species and between dietary niche groups.
27 To ensure that all species had equal weighting in the analysis, one
28 representative individual was chosen for each species. These individuals
29 were identified from a preliminary morphometric analysis as the specimen
30 closest to the mean shape for that species. The three-dimensional co-
31 ordinates for all sets of landmarks were imported into MorphoJ 1.45s and
32 paired across the midline (Klingenberg 2010). Generalised least squares full
33 Procrustes fit was performed on all sets of data, which were then aligned by
34 their principal axes. The asymmetric component of the shape change was

1 briefly reviewed as it can highlight errors as well as asymmetries and the
2 symmetric component was then further explored with a covariance matrix and
3 principal components analyses to ascertain interspecific shape changes
4 (Klingenberg 2010). Scatterplots of the principal component (PC) scores
5 were produced to visualize the distribution of datum points within the shape
6 space, and wireframe models were created using key landmarks to visualize
7 the range of shape deformation between the extremes. ANOVAs were used
8 to test for significant differences between skull shapes (PC scores) and
9 dietary groups. The pruned phylogenetic tree (Nyakatura and Bininda-
10 Emonds 2012) was then mapped against the principal component datum
11 points to indicate the overall influence of phylogeny on shape variation and
12 permutation tests were performed on the null hypothesis of no phylogenetic
13 signal (Klingenberg and Gidaszewski 2010). Multivariate regression of the
14 Procrustes coordinates against the body mass, where the shape landmark
15 datasets were the dependent variables, tested for allometric signal, that is, the
16 percentage of shape change that could be predicted by the change in body
17 mass. Similarly, multivariate regression of the Procrustes co-ordinates of the
18 shape landmark datasets on both temporalis mass and endocranial volume
19 identified the percentage of shape change that was related to the change in
20 temporalis mass and endocranial volume. The statistical significance of the
21 regression analyses was tested with permutation tests against the null
22 hypothesis of independence, and *P*-values reported.
23 Reduced major axes regressions, analyses of variation (ANOVAs), post-hoc
24 Tukey analyses and *t*-tests were computed in PAST (Hammer et al., 2001).
25 Mapping the phylogeny onto shape, and the multivariate regression of shape
26 on body mass, temporalis mass and endocranial volume were computed in
27 MorphoJ (Klingenberg 2010). A significance level of 0.05 was used in all
28 statistical tests.

29
30

31 **RESULTS**

32

33 **Muscle morphology**

34 The masses (g) of the individual jaw adductor muscles and their subdivisions

1 are presented in Table 1. Temporalis contributed between 57.4 and 69.3% to
2 the total muscle mass (mean 62.1%), masseter contributed between 23.6%
3 and 35.1% (mean 29.8%), and the pterygoids contributed between 6.7 and
4 10.5% (mean 8.2%). Next, individual muscles were considered. Temporalis
5 was made up of three distinct divisions; suprazygomatic, superficial and deep
6 temporalis. All species exhibited a well-defined suprazygomatic portion of
7 temporalis (Figure 2b). This was consistently the smallest subdivision of
8 temporalis, contributing 3.5 – 9.2 % (mean 6.5%) of the overall temporal
9 mass. Origin was by way of a short wide tendon arising from the temporal
10 bone just dorsal to the external auditory meatus, and insertion was on the
11 rostral aspect of the vertical ramus of the mandible. The remaining bulk of
12 temporalis arises from the calvarium and divides into discrete superficial and
13 deep parts. In the smallest species, *Vulpes zerda*, *Vulpes corsac* and
14 *Otocyon megalotis*, the origin of temporalis was lateral to midline. In all other
15 species left and right temporalis met at midline, and in the larger species were
16 associated with a pronounced sagittal crest (Figure 7). Both the superficial
17 and deep parts of temporalis insert onto the coronoid process and medial
18 vertical ramus of the mandible (Figures 2c and 2d). The superficial part of
19 temporalis contributes between 39.7 and 59.5% (mean 46.5%) of the overall
20 temporalis mass and the deep between 33.2 and 54.8% (mean 47.0%). The
21 masseter is highly complex with more than the previously noted superficial,
22 deep, and zygomaticomandibularis layers. The superficial division was well
23 defined and contributes between 38.3 and 56.8% (mean 47.6%) to the overall
24 masseteric mass. The origin is chiefly from the most ventral part of the
25 zygomatic arch, but there is also a strong tendinous component originating
26 dorsal to the upper molars (Figures 2e and 2f). The caudal part of the
27 superficial masseter extends beyond the caudal angle of the mandible to
28 insert partly on the medial aspect of the mandible, and partly on the superficial
29 aspect of the medial pterygoid (Figure 2j). The deep masseter (Figure 2g)
30 originates from the medioventral aspect of the zygomatic arch. It is less
31 clearly defined than the superficial division with many fibres arising or
32 inserting onto aponeuroses within the muscle rather than directly to the bone
33 of the mandible or zygomatic arch. It contributes between 12.2 and 36.4%
34 (mean 24.1%) of the masseteric mass. Zygomaticomandibularis (Figure 2h)

1 originates from the caudal medial zygomatic arch and contributes between
2 16.7 and 44.0% (mean 28.3%) of the overall masseteric mass. Both of the
3 pterygoid muscles were considered together as one muscle, the pterygoids,
4 as the medial pterygoid was considerably more extensive than the lateral
5 pterygoid (Figure 2i). The (combined) pterygoids contributed between 7.0 and
6 10.5 % of the total jaw adductor mass (mean 8.2%). The fascicles originate
7 from the pterygoid plate of the skull and insert on the medial mandible.
8 Temporalis arises from an extensive area of the lateral calvarium, in particular
9 from the parietal, temporal, frontal and occipital bones (Figure 7). The
10 masseter arises from the ventral and medial borders of the zygomatic arch,
11 which itself is made up from the zygomatic and temporal bones, and the
12 pterygoids arises from the sphenoid, pterygoid and palatine bones.
13 Temporalis originates from a mean of 69.0% of the total jaw adductor
14 attachment surface area, the masseter 18.6% and the pterygoids 12.0%.

15

16 **Metric analysis**

17 Results for the dietary group ANOVA tests revealed that there were no
18 statistically significant differences between the dietary groups both for
19 percentage contribution of each muscle to the overall jaw adductor mass, and
20 percentage contribution of each muscle division to the total muscle mass
21 (Table 4). Probability *P*-values for the phylogenetic independent contrasts,
22 comparing absolute values of the standardized phylogenetic independent
23 contrasts versus their standard deviations ranged from 0.054 to 0.39. This
24 suggests that phylogeny has a negligible effect. The RMA regressions on the
25 pairs of variables that were generated with PICs showed no significant
26 differences to those generated from the standard data, with similar slope and
27 confidence intervals in all cases (Table 2). Phylogenetic influence on these
28 variables and regressions is therefore considered minimal and subsequent
29 allometric analyses focused on the raw metric data.

30

31 Reduced major axis regressions of variables scaling against body mass are
32 reported in Table 2. Scaling of total muscle mass was not significantly
33 different to isometry and no trophic group appeared to deviate from this
34 general scaling trend (Figure 3). All three individual jaw adductor muscles

1 scale close to isometry. Therefore species with a greater body mass have, in
2 general, the same proportion of masticatory muscles to body mass as smaller
3 species. Some regressions for muscle attachment surface area
4 measurements may appear to be indicative of deviations from isometry (e.g.
5 pterygoids and total muscle mass) but the confidence intervals encompass
6 isometry in all cases and were not significantly different from isometry.
7 Scaling of endocranial volume to body mass shows significant negative
8 allometry (Figure 4) with our results showing a slope of 0.68 from an expected
9 isometric slope of 1 and a *t*-test *P*-value of 0.0007. That is, as species size
10 increases the brain size increases to a lesser degree, and the brain takes up
11 a lower proportion of overall body mass in large species of canids than in
12 small ones. This was also reflected in the scaling of EVSA to body mass,
13 which has a slope of 0.43 from an expected slope of 0.66 (*t*-test *P*-value
14 0.0001). The zygomatic arch width scales isometrically to body mass.

15

16 **Form analyses**

17 In the whole skull landmark data set, the first 4 PCs make up 78.5% of the
18 variance. PCs 1 and 2 are described in detail and shown in Figure 5. PC1
19 constituted 32.3% of shape variance. At the negative extreme of the axis (-
20 0.11, represented by wireframe S3) the rostral landmarks move
21 caudolaterally, resulting in an overall shape change of a shorter broader snout
22 and mandible. The landmarks associated with the zygomatic arches and
23 caudal mandible move laterally, representing a relative broadening of the
24 skull, and the dorsal landmarks of the inion and dorsal skull move dorsally - a
25 shape change associated with a larger sagittal crest. Landmarks relating to
26 the ventral aspect of the skull move ventrally resulting in an overall deepening
27 of the cranium. At the other extent of the axis (0.07, represented by
28 wireframe S4), the snout and mandible become longer and more gracile and
29 the cranium appears dorsoventrally flattened. The PC1 axis clearly
30 differentiated the data into dietary groups. The species occupying the lower
31 end of the range (-0.12 to - 0.01) were exclusively hypercarnivorous, the
32 generalists occupied the middle zone and (0 to 0.03) and the small prey

1 specialists the higher end of the range (0.015 to 0.07) with some overlap of
2 the generalist species at their lower values. The ANOVA for the whole skull
3 PC1 scores shows significant difference between the dietary groups, $F = (2,9)$
4 $= 12.29$; $p = 0.003$. Tukey's pairwise post hoc tests showed that the
5 hypercarnivores were significantly different to both small prey (P -value 0.004)
6 and generalists (P -value 0.013). Of particular note are *Speothos venaticus*, a
7 small hypercarnivorous canid that lies with the other three hypercarnivores at
8 the low value extreme of this axis despite weighing only 6.5 kg, and its close
9 relative, *Chrysocyon brachyurus*, a 22.5kg specimen, that lies with the *Vulpes*
10 group at the other extreme of the axis. PC2 makes up 25.5% of variance. At
11 one extreme (-0.06, represented by wireframe S2) the cranium appears
12 relatively shorter and more domed and the dorsal border of the mandible is
13 straighter. At the other extreme, (0.11, represented by wireframe S1) the
14 cranial component appears dorsally flattened and elongated and the dorsal
15 border of the mandible is curved. The ANOVA for the whole skull PC2
16 scores shows significant difference between the dietary groups, $F = (2,9) =$
17 11.24 ; $p = 0.004$). Tukey's pairwise post hoc tests showed that the
18 hypercarnivores were significantly different to the generalists (P -value 0.008)
19 and that the generalists were significantly different to the small prey
20 specialists (P -value 0.003).

21 In the cranial subset (32 landmarks) the first 4 PCs make up 76.8% of the
22 variation: PCs 1 and 2 are described in detail and shown in Figure 6. PC1
23 constituted 33.1% of the shape variance. At the negative extreme of the axis
24 (-0.11, represented by wireframe C3), caudal landmarks move rostrally and
25 dorsal landmarks move dorsally resulting in a relatively shorter deeper skull.
26 Lateral landmarks moving laterally achieve relative widening of the zygomatic
27 arch. At the positive extreme of the axis (0.09, represented by wireframe
28 C4), the cranium lengthened whilst the zygomatic arches became relatively
29 narrower. All dorsal landmarks shifted ventrally, resulting in a flatter skull.
30 The relatively ventral position of the inion indicates a small or absent sagittal
31 crest. The PC1 axis showed some differentiation of the data into dietary
32 groups. At the negative end of the axis were 3 of the hypercarnivores and at
33 the other, the generalists. The small prey specialists occupied the middle

1 space with some overlap with the hypercarnivores. *Speothos venaticus*, the
2 fourth hypercarnivore appeared between the small prey specialists and
3 generalists. The ANOVA for the cranial PC1 scores shows significant
4 difference between the dietary groups $F = (2,9) = 7.38$; $p = 0.01$). Tukey's
5 pairwise post hoc tests showed that the hypercarnivores were significantly
6 different to the generalists (P -value 0.008). PC2 made up 19.6% of the shape
7 variance. At the negative extreme of the axis (-0.06, represented by
8 wireframe C2), the zygomatic landmarks move dorsally and the dorsal
9 landmarks move ventrally. At the positive end of the axis (0.11 represented
10 by wireframe C1) the zygomatic landmarks move ventrally and the dorsal
11 landmarks move dorsally. However, only one specimen, *Speothos venaticus*,
12 lay towards the extreme end of the positive axis, all other specimens were
13 closely grouped between -0.06 and 0.03. PC2 showed no appreciable
14 grouping of species into dietary specialisms and ANOVA tests showed no
15 significant differences between the dietary groups.

16 When the pruned phylogenetic tree was mapped onto the PC scores it
17 showed that the whole skull, rostral and mandibular component analyses
18 contained phylogenetic signal, with P -values from 0.009 to 0.014, whereas the
19 cranial subset demonstrated no statistically significant phylogenetic signal
20 (Table 3). This indicates that the rostral and mandibular components of the
21 skull are strongly linked to phylogeny, whereas the form of the cranial
22 component changes in response to other constraints. The overall
23 phylogenetic maps (Figures 5 and 6) show some long terminal branches,
24 compared to shorter internal branches, indicating that some closely related
25 species have diverged considerably within the shape space demonstrating
26 substantial differences in related morphologies. In tests for allometric signal,
27 regression of the cranial component shape on body mass showed the
28 greatest percentage (16.5%) of shape variance of any of the landmark sets,
29 and was the only landmark dataset with a statistically significant permutation
30 P -value (Table 3). The cranial component thus demonstrates evidence
31 against the null hypothesis of complete independence, suggesting that shape
32 change is related to size change. The multivariate regression analyses of
33 shape on temporalis mass shows that the highest percentage change relates

1 to the cranial shape dataset and was statistically significant. Similarly the
2 highest percentage shape change linked to endocranial volume was also the
3 cranial dataset, and was also statistically significant. This demonstrates that
4 change in temporalis mass and endocranial volume are linked with change to
5 cranial shape (Table 3). Figure 9 compares the cranial wireframe shapes of
6 two distantly related species with the cranial wireframe shape representative
7 of the low PC1 score. The low PC1 score wireframe indicates a short deep
8 skull with increased space medial to the zygomatic arches for housing the
9 temporalis muscles. Although *Canis lupus* and *Chrysocyon brachyurus* are
10 from different clades and exhibit distinct dietary preferences and hunting
11 strategies both have large body masses and relatively small endocranial
12 volumes. The wireframes indicate that in both species cranial shape is very
13 similar, both to each other and to the PC1 wireframe. The remaining three
14 shape datasets shapes showed lower percentage changes and had no
15 statistical significance, indicating that overall head shape, rostral shape and
16 mandibular shape changes are independent of temporalis mass or
17 endocranial volume change.

18

19 **DISCUSSION**

20 Our results show that the morphology of the jaw adductor muscles is
21 remarkably conserved across canid species. The form of each muscle and its
22 subdivisions were surprisingly similar in all cases given the diverse dietary
23 niches, different body sizes and phylogeny. We also found that the jaw
24 adductor mass as a whole, and all three of the jaw adductor muscles
25 individually, scale isometrically. Although we reported a couple of differences
26 of muscle subdivision scaling between the different dietary groups, non were
27 statistically significant and morphological variance was minimal and much less
28 than we expected – that is, hypercarnivorous species, which might be
29 expected to have a have relatively larger muscles to generate greater bite
30 force, have the same ratio of muscle masses to body mass as those with
31 assumed weaker bites, the generalists and small prey hunters. All individuals
32 were consistent with the scaling pattern and there were no correlations

1 relating to phylogeny or dietary groups (Figure 3). Skull shape variation is
2 therefore not attributable to housing differently scaled muscle masses for
3 specialist dietary or different phylogenetic groupings. Whilst our sample sizes
4 per species were relatively modest and were not sex matched, there were
5 large scale interspecific differences and evidence from previous studies (see
6 methods) suggests that there is minimal sexual dimorphism.

7 Our endocranial volume scaling results are in accordance with previous
8 studies (Jerison 1955; Gould 1966; Bauchot 1978) that describe interspecific
9 scaling at a rate of two thirds relative to body mass. This presents the
10 problem of accommodating isometrically scaling muscle masses onto
11 negatively scaling neurocrania. We considered the cranium to have two
12 discrete surface areas: an internal one which reflects the accommodation
13 needs of the brain and which was calculated as the surface area of the
14 endocast (EVSA), and an external one, which was calculated as the area of
15 origin for temporalis (we acknowledged that this only accounts for part of the
16 external surface of the cranium). The EVSA scales to body mass with marked
17 negative allometry, whilst the scaling of temporalis surface area to body mass
18 is not significantly different to isometry. The disparity between the demands
19 of the internal and external surfaces of the neurocrania was further evidenced
20 by the very small canids displaying a sagittal gap at dorsal midline where
21 there is no muscle attachment, demonstrating that in these species the
22 external surface of the cranium more closely reflects its internal surface area
23 which is driven by brain accommodation. The sagittal gap was only seen in
24 species below 5kg, that is, *Vulpes zerda*, *Vulpes corsac* and *Otocyon*
25 *megalotis*. From 5-10 kg the contralateral temporalis muscles met at midline
26 as temporalis utilised all of the available external surface area, with little or no
27 sagittal crest present. Above 10 kg a pronounced sagittal crest was seen
28 which increased the surface area available for temporalis (Figure 7). The
29 exception to this was the 6.5kg *Nyctereutes procyonoides* that also had a
30 well-developed sagittal crest. However, this was also the species with the
31 smallest endocranial volume relative to body mass, as evidenced by the
32 greatest negative distance from the regression line for endocranial volume
33 against body mass (Figure 4). By contrast, the *Nyctereutes* temporalis surface

1 area scales at a similar rate to other species and so the sagittal crest
2 demonstrably increases the external surface area commensurate with
3 temporalis requirements. These findings suggest that the exterior surface
4 area of the calvarium does not simply reflect the interior, but is driven by the
5 necessity to accommodate the temporalis and probably the other muscles too.
6 The other major morphological adaptation to increase the space on the skull
7 for housing the temporalis is the isometrically scaling zygomatic arches
8 (Figure 8). Other authors (Radinsky 1981; Emerson and Bramble 1993) have
9 speculated that if the arch width remains relatively constant but the
10 endocranial volume decreases relatively, the space medial to the arches
11 increases and could be used to accommodate a larger temporalis. Our
12 studies have shown that this 'increased accommodation' principle is correct
13 but that in canids, the space is utilised to house an isometrically, rather than
14 positively, scaling temporalis. Interestingly, primates have also been shown to
15 have isometrically scaling masticatory muscles (Cachel 1984) as well as
16 negatively scaling endocrania (Rilling 2006) and large species of primate
17 exhibit similar morphological features as large species of canid, such as
18 sagittal crests (Ankel-Simons 2007) and relatively wide zygomatic arches
19 (Frost et al., 2003). This might suggest that the problem of muscle
20 accommodation is more universal than indicated here, although it is important
21 not to extrapolate our findings too far as the two groups have, for instance,
22 distinct dietary behaviours.

23 Principal component analysis of the whole skull form differentiated the species
24 into the three broad dietary groups and in the multivariate regression analyses
25 demonstrated phylogenetic signal but no allometric signal. Total skull shape
26 aligned broad stocky head shapes with hypercarnivorous hunters, and
27 narrow slender head shapes with the small prey specialist. The generalists
28 lay in the middle ground. This is in agreement with previous studies (Wroe
29 and Milne 2007; Goswami et al., 2011). However, when we removed all of
30 the rostral and mandibular components and focused only on the cranial
31 component, there was no significant phylogenetic signal, dietary specialism
32 grouping was less marked and a significant allometric signal indicated that
33 shape change was related to size change. More specifically, cranial shape

1 changes correlate with body mass and temporalis mass and endocranial
2 changes indicating that shape changes of shorter, dorsoventrally enlarged
3 calvaria, increased sagittal crests and widened temporal spaces correspond
4 with the decreasing endocranial volume to temporalis ratio that is seen as
5 body mass increases. This directly links shape change in the cranium with
6 accommodation of temporalis, and suggests that the rostral and mandibular
7 components are chiefly concerned with dietary specialism, whilst the cranial
8 component is more strongly associated with muscle accommodation. In the
9 whole skull analysis (figure 5), *Chrysocyon brachyurus*, for example, is closely
10 aligned with the *Vulpes* group at the furthest distance from the hypercarnivore
11 species. All species at the positive end of the axis exhibit the long narrow
12 jaws of the small prey hunter, and in the case of *Chrysocyon brachyurus*, the
13 crossing tree branches also demonstrate convergent evolution (Gidaszewski
14 et al., 2009). However, when we focus on the cranial component (Figure 6)
15 *Chrysocyon* shape is more closely aligned with the hypercarnivores, due to
16 the large sagittal crest and wide medial zygomatic space that accommodates
17 the temporalis. It is presumed that some elements of cranial shape change
18 will not directly associate themselves with muscle accommodation, but may
19 be linked with considerations other than scaling. Such factors may include
20 generating biomechanical advantage to facilitate certain bite behaviors such
21 as fast jaw snapping, or increasing bite force. Similarly, other biomechanical
22 functions of the skull such as withstanding stress or dissipating bite forces
23 have not been considered in this study. These factors warrant further
24 consideration in order to understand how canids have applied similar muscle
25 proportions in the generation of different bite forces and speeds to occupy
26 remarkably distinct dietary niches.

27

28 **Summary**

29 There are two main factors that influence shape change in the canid skull:
30 features that are scaled relative to body mass (whether isometrically or
31 allometrically), and features that change independently of body mass. Our
32 findings show that the jaw adductor muscles scale isometrically to body mass,
33 even though they are functionally aligned to independently changing features

1 such as jaw length or bite force, both of which are allied to dietary specialisms
2 (Christiansen and Wroe 2007; Van Valkenburgh 2007; Figueirido et al., 2011;
3 Damasceno et al., 2013). Our results suggest that much of the cranial shape
4 change is related to accommodating temporalis. These findings may help
5 inform work on interpreting the feeding habits of extinct species (e.g. Wroe et
6 al., 2005; Meloro et al., 2015). It should be noted, however, that our findings
7 do not preclude the cranial shape changes also being biomechanically
8 advantageous to the different trophic groups. In future work we hope to
9 consider how the architectural details of the jaw adductor muscles such as
10 fascicle orientation, fascicle length and angles of pennation, may affect
11 muscle force capability, and how the spatial relationships between muscle
12 centroid size and key skull features such as the temporomandibular joint and
13 carnassial or canine teeth, influence bite force.

14

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23

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