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RESEARCH ARTICLE

Functional Stabilization of Wolf Masticatory Muscle Architecture and Convergence of Attack and Defense Dog Breeds with Wolves

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Abstract
The masticatory system plays a key role in ecological adaptation. In grey wolves (*Canis lupus*), intraspecific variation in jaw muscle architecture and divergence from domestic dogs (*Canis familiaris*) remain poorly documented due to limited access to specimens. Here, we present the first large-scale quantitative analysis of jaw-closing muscles in wolves, based on dissections of 112 individuals from France (*C. l. italicus*, $n=98$) and North America (*C. l. nubilus*, $n=14$), compared with 86 domestic dogs. Muscle mass, fiber length, and pennation angle were measured to estimate physiological cross-sectional area (PCSA), a proxy for maximal muscle force. In French wolves, males exhibited greater absolute muscle mass and PCSA than females, but no differences in relative muscle proportions, indicating size-related scaling rather than shape dimorphism. No significant differences were detected between European and North American wolves, consistent with stabilizing selection maintaining a functionally 'optimal' masticatory design. In contrast, wolves displayed greater jaw-adductor mass and PCSA than dogs. Interestingly, large molossoid breeds overlapped with wolves, reflecting functional convergence under artificial selection for attack or defense. Together, these results show that wolf masticatory architecture is constrained by selection for large-prey predation, whereas domestication relaxes and can secondarily reimpose these functional demands.

Keywords Jaw muscle architecture · Physiological cross-sectional area · *Canis lupus* · Canids

Introduction

Understanding how morphology relates to function across ecological contexts is a central question in evolutionary biology. In vertebrates, the feeding apparatus plays a key role in mediating interactions between organisms and their environment, linking biomechanical performance to ecological specialization and evolutionary diversification (Anderson et al., 2008; Christiansen & Wroe, 2007). Among mammals, carnivorans provide a powerful model for exploring these relationships, as variation in cranio-mandibular morphology and muscle architecture is tightly associated with diet, prey capture strategies, and food processing (Hartstone-Rose et al., 2012, 2019, 2022). Grey wolves (*Canis lupus*) hold a pivotal position in this context. As apex predators and the wild ancestor of domestic dogs (*Canis familiaris*), they offer a unique opportunity to investigate how natural and artificial selection shape the functional architecture of the feeding apparatus.

The masticatory apparatus is central to social behavior, feeding performance and ecological specialization as it determines the ability to capture prey, process food and generate bite force *(e.g.* Christiansen & Wroe, 2007; Anderson et al., 2008; Damasceno et al., 2013). In wolves, cranio-dental morphology reflects specialization for large-prey predation, with robust skulls and jaws, adapted to the generation of high bite forces (Slater et al., 2009), enlarged carnassials for bone crushing (to access the lipid-rich marrow; Biknevicius & Van Valkenburgh, 1996; Ungar et al., 2010; Sala et al., 2014; Bosch et al., 2015), and elongated canines for gripping and tearing flesh (Severtsov et al., 2016). However, despite their functional importance, the architectural properties of the jaw-closing muscles, which include the temporalis, masseter, and pterygoid complexes, remain poorly

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quantified (Druzinsky et al., 2011). Physiological cross-sectional area (PCSA), calculated from muscle volume, fiber length, and the pennation angle (the angle between muscle fibers and the muscle's line of action), integrates muscle size and architecture and is widely regarded as the best anatomical predictor of a muscle's maximum force-generating capacity (Martin et al., 2020; Powell et al., 1984).

Comparative studies across Carnivora demonstrate strong links between muscle architecture and diet (Hartstone-Rose et al., 2012, 2019, 2022), yet intraspecific variation remains poorly documented, particularly in wolves. Existing data for this species are limited ($n=4$ according to Penrose et al., 2016, 2020; Hartstone-Rose et al., 2022) and incomplete (e.g. omission of pennation angles in PCSA estimates), preventing robust evaluation of functional variability within *C. lupus*.

Wolves are large generalist predators exhibiting substantial ecological flexibility, primarily feeding on large ungulates (Newsome et al., 2016) while adjusting their diet to local prey availability *(e.g.*, Szepanski et al., 1999; Lafferty et al., 2014; Zlatanova et al., 2014; Newsome et al., 2016; Watts & Newsome, 2017; Stanek et al., 2017). For instance, French wolves mainly consume cervids, such as red deer and roe deer, which together account for 55–80% of their diet (Fluhr, 2011; Poulle et al., 1997). North American populations exploit a broader range of prey, including elk (Burtt & DeSantis, 2022; Idaho Department of Fish and Game, 2023), moose and caribou, with coastal populations also supplementing their diet with salmon or other marine resources (Ballard et al., 1987; Lafferty et al., 2014; Szepanski et al., 1999; Watts & Newsome, 2017). This ecological variability provides a natural framework to examine how feeding structures respond to environmental constraints. In particular, geographic variation in prey composition and ecological context may influence muscle architecture. Differences in diet and competition have been shown to affect the jaw muscles in carnivorans (Hartstone-Rose et al., 2022; Penrose et al., 2016), including within species such as red foxes (Brassard et al., 2022) and experimental studies further demonstrate diet-induced changes in muscle architecture in mustelids (Hartstone-Rose et al., 2019) and mice (Hansen et al., 2025). Wolves in North America coexist with multiple large predators (brown bears, black bears, polar bears, cougars and wolverines), whereas French wolves experience reduced interspecific competition. Such ecological differences may impose distinct functional demands on the masticatory apparatus. In North American wolves, higher bite forces across gape angles might be favored, particularly through greater development of the masseter muscle. However, similar selective pressures could also arise in single-predator systems under conditions of prey scarcity or high wolf density, as observed in France, where diet composition varies with ungulate abundance and wolf pack structure (Fluhr, 2011). Sexual dimorphism may also influence feeding structures. In wolves, males are more involved in territorial defense and provisioning during the breeding season, and experience stronger male-male competition, which could favor increased bite performance (Gittleman & Valkenburgh, 1997; Morris & Brandt, 2014). However, whether such behavioral differences translate into differences in muscle architecture remains unclear.

Finally, domestication provides a complementary evolutionary context. Determining whether artificial selection has driven divergence in jaw muscle function among domestic dogs, or instead promoted functional convergence toward similar feeding performance across morphologically diverse lineages, is critical for understanding how evolutionary and selective forces have shaped canid feeding performance. Domestic dogs exhibit exceptional morphological diversity (Drake and Klingenberg 2010; Triquet 2013), resulting from intense artificial selection for morphology, behavior and working abilities. This diversity encompasses breeds selected for companionship, hunting, herding, guarding or fighting, and includes an exceptional range of skull morphologies, from brachycephalic to dolichocephalic forms. Yet the extent to which this diversification has affected masticatory muscle architecture remains poorly understood. The limited available evidence suggest broadly conserved patterns when comparing dog breeds with free-ranging dogs under minimal human selection (Brassard et al. 2025). However, marked variation exists among breeds in relative muscle development and bite force, with large brachycephalic dogs exhibiting enhanced force production relative to jaw length (Brassard, Merlin, Guintard, Brassard et al. 2020a, b; Kim et al. 2018). This pattern raises the possibility of functional convergence with wolves under targeted selection.

Here, we present the first large-scale quantitative analysis of jaw musculature in grey wolves and compare these data with domestic dogs. Our objectives are to (1) quantify intraspecific variation in wolves, including (i) sexual dimorphism and (ii) geographic differences by comparing French and North American populations, and (2) assess the impact of domestication and artificial selection on jaw muscle architecture. We hypothesize that (i) male wolves exhibit greater absolute muscle development than females, consistent with stronger selection for bite performance during prey handling and intrasexual competition; (ii) geographically separated wolf populations show differences in jaw muscle architecture reflecting ecological variation; and (iii) domestication has altered jaw muscle architecture relative to wolves, while artificial selection for attack or defense has promoted convergence toward the wolf condition in strong-biting breeds. By integrating intraspecific comparisons, this study aims to

clarify how natural and artificial selection have shaped the form–function relationship of the canid masticatory system and to provide a comprehensive framework for understanding the evolution of feeding biomechanics in wolves and their domestic descendants.

Materials and Methods

Specimens

Our sample comprised 112 adult wolves (*Canis lupus*) with fully erupted dentition. Only well-preserved carcasses without advanced decomposition were included. Most specimens originated from Southwestern France (*Canis lupus italicus*, $n=98$; Table 1; Fig. 1), whereas the remaining individuals were collected in North America (*C. l. nubilus*, $n=14$).

Table 1 Sample details

Species	Subspecies or breed	Sample size
Canis lupus	*italicus* from France	**98** (41 males, 47 females, 10 unknown
	nubilus from North America	**14** (unknown sex) (12 from Alaska, 2 from Idaho)
Canis familiaris		**86**
	Tunisian street dogs	29
	American Staffordshire terrier	1
	beagle	15
	Belgian shepherd	2
	border collie	2
	boxer	2
	bulldog	2
	Cane corso	1
	Chihuahua	1
	collie	1
	dachshund	1
	deerhound	1
	Dobermann	1
	fox terrier	1
	German shepherd	1
	golden retriever	2
	Siberian husky	1
	Jack Russel terrier	1
	Cavalier King Charles spaniel	1
	Leonberger	1
	mastiff	2
	papillon	1
	Parson Russel terrier	1
	pitbull	1
	Rottweiler	3
	Shetland sheepdog	1
	Yorkshire terrier	1
	unknown breed	9

French wolf specimens were collected between 2010 and 2021 as part of national monitoring programs coordinated by the French Biodiversity Office (OFB) and departmental veterinary laboratories (LVD). Individuals originated from road collisions or legally authorized culling operations. The collection, storage, and scientific use of these specimens complied with French regulations for protected species and were conducted under the ministerial decree of 20 December 2019 (Ministry for the Ecological Transition), in accordance with articles L.411-1 and L.411-2 of the French Environmental Code. All samples were obtained within the framework of the MORPHO-LOUP agreement (OFB-20–01331), and no animals were killed specifically for this study.

North American specimens originated from wildlife management programs or the fur and taxidermy industry. As these specimens were not collected for research purposes, their use was considered exempt from ethical review by the Institutional Animal Care and Use Committee (IACUC) of North Carolina State University.

All carcasses were stored frozen at −20 °C and thawed prior to dissection without chemical treatment.

To compare wolves with domestic dogs, we compiled data from 86 domestic dogs representing a wide diversity of breeds, including 29 free-ranging street dogs (Table 1). Most data were derived from previous studies using the same dissection protocol (Brassard et al., 2020b, 2025), supplemented with 12 additional specimens obtained from the veterinary schools of Sidi Thabet (Tunisia) and Nantes (France). Breed identity was assigned by the authors based on the external morphology of the intact head prior to dissection.

The sample encompassed a broad diversity of domestic dogs, including toy and giant breeds, brachycephalic, mesocephalic and dolichocephalic skull morphotypes, as well as breeds historically selected for companionship, hunting, herding, guarding and fighting. Although the life history of individual specimens was unknown, breed identity reflects the historical selective pressures under which these lineages were developed.

Exact age of the specimens was unavailable. Only individuals with fully erupted permanent dentition (thus 6 months old; Barone, 2010*)* were included to minimize ontogenetic variation in muscle architecture.

Dissections of the Jaw Muscles

Dissections followed established protocols (Brassard et al., 2020a; Penrose et al., 2016). The different steps are illustrated in Fig. 2. Only the jaw closing muscles (more commonly referred as jaw adductors) were analyzed: the temporal complex (including the *m. temporalis pars superficialis* TS, *pars profunda* TP, and *suprazygomatica* SZ),

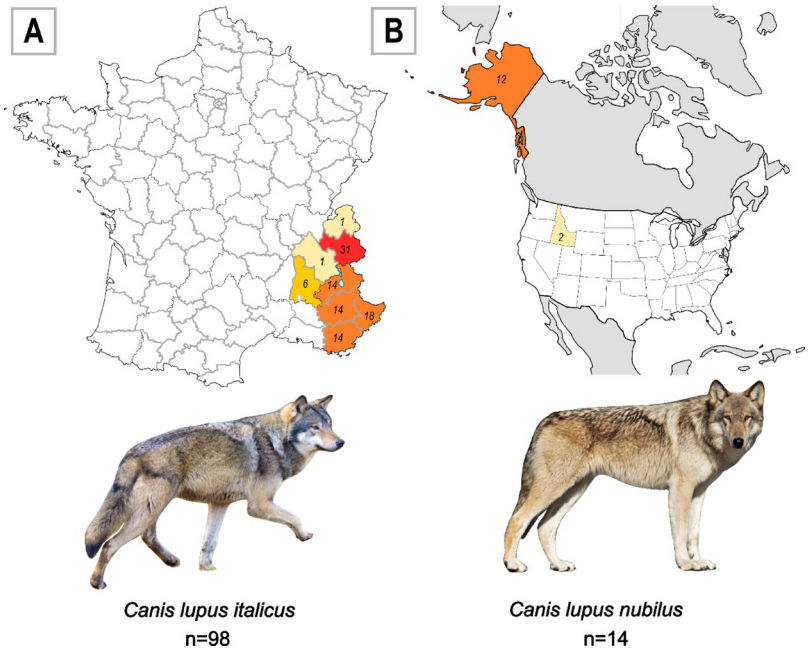

Fig. 1 Geographic origin of wolf specimens included in this study. **A**: The French wolf sample; **B**: The North American wolf sample. Darker shades indicate regions with a higher number of samples

the masseter complex (*m. masseter pars superficialis* MS, *pars profunda* MP, *zygomaticomandibularis anterior* ZMA and *posterior* ZMP), and the pterygoid complex (*m. pterygoideus medialis* PM). The digastric muscle (DIG) and the lateral pterygoid muscle (*m. pterygoideus lateralis* PL) were excluded from subsequent analyses, as they do not contribute to bite force: the digastric acts to open the mouth (i.e., is a mandibular abductor), whereas the lateral pterygoid functions primarily as a jaw stabilizer rather than a jaw adductor, owing to its insertion close to the temporomandibular joint.

Measuring Muscle Architecture

All muscle divisions were isolated and we measured the muscle mass for each using a digital scale, and fiber length and pennation angle (Fig. 2) with a ruler and protractor after sectioning the muscles along their line of action. We considered the mean of several measurements taken at different locations along the muscle. For all of the North American wolves, muscle density was collected directly using a density kit on a precision balance (Mettler Toledo MS-DNY-54), providing the first muscle density estimates for carnivorans. Averages of these muscle-specific densities were used across the rest of the sample.

We used these data to calculate the corrected physiological cross-sectional area (PCSA), a proxy for the maximal intrinsic strength of the muscles (Haxton, 1944), using the average muscle-specific densities and accounting for pennation according to the following formula:

$$PCSA\ [cm^2] = \frac{mass\ [g] * \cos(angle\ of\ pennation\ [rad])}{muscle\ density\ d\ [g.cm^3] * fiber\ length\ [cm]}$$

We considered the following muscle density values: d_{MS} = 1.071 g.cm^{-3}; d_{MP} = 1.069 g.cm^{-3}; d_{ZMA} = 1.061 g.cm^{-3}; d_{ZMP} = 1.067 g.cm^{-3}; d_{SZ} = 1.064 g.cm^{-3}; d_{TS} = 1.071 g.cm^{-3}; d_{TP} = 1.069 g.cm^{-3}; and d_{PM} = 1.068 g.cm^{-3}(as noted above, although the mandibular abductors were excluded from analyses, their measured average densities were d_{Dig} = 1.065 g.cm^{-3} and d_{PL} = 1.059 g.cm^{-3}, provided here for completeness of information only).

Analyses

Analyses were performed using R (version 4.4.2).

To reduce noise and strengthen statistical robustness, muscles were grouped into three complexes (temporal, masseteric, and pterygoid) rather than analyzed separately. For each complex, we summed the mass or PCSA of its constituent bundles. The masseter complex included the *pars superficialis*, *pars profunda*, and the *pars zygomaticomandibularis anterior* and *posterior*. The temporal complex comprised the *pars suprazygomatica*, *pars superficialis*, and *pars profunda*. The pterygoid 'complex' was restricted to the *pterygoideus medialis.*

Analyses focused on (i) the total jaw-adductor mass and PCSA (univariate analyses); (ii) absolute (i.e., non-scaled) mass and PCSA of each muscle complex (multivariate and univariate analyses); and (iii) relative proportions (i.e., relative contributions of each muscle complex to the total jaw-adductor mass or PCSA) of the jaw muscles (multivariate and univariate analyses).

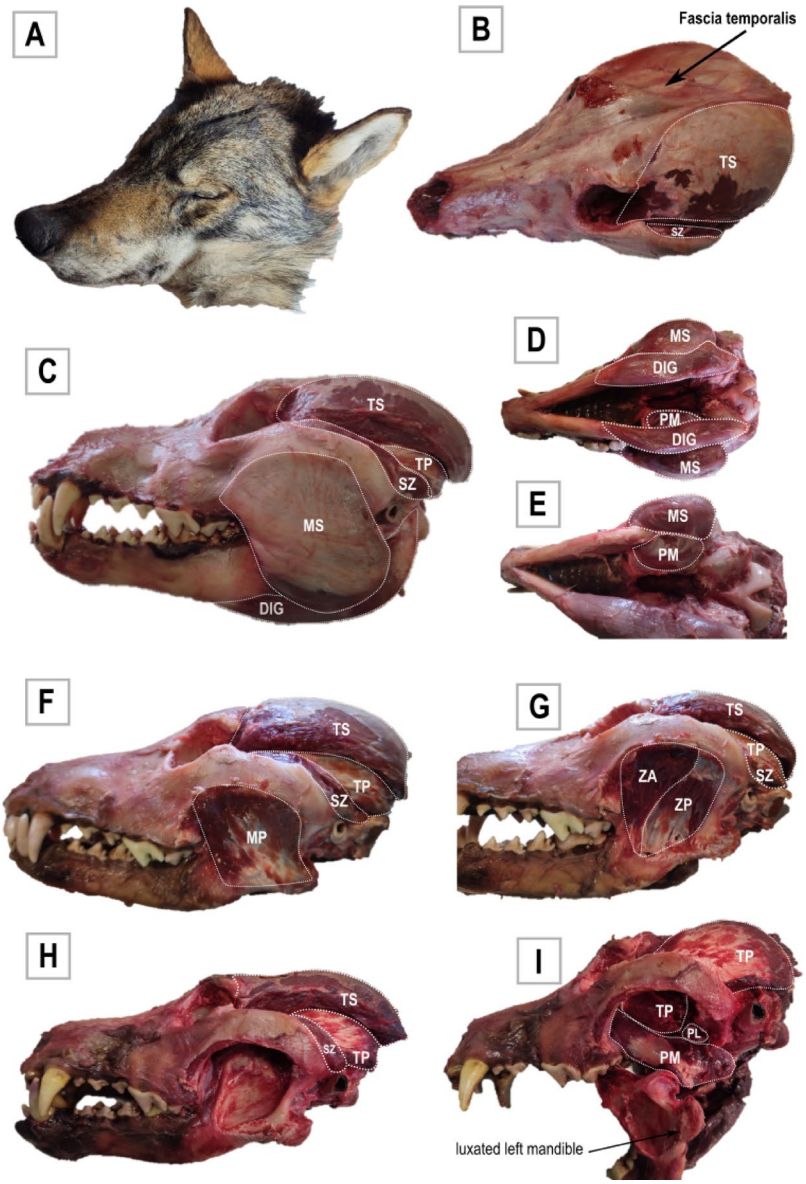

Fig. 2 Sequential steps of the dissection illustrating all masticatory muscle bundles examined in this study. **A** Head prior to skinning. **B** Removal of the deep fascia covering the temporalis muscle to separate its different bundles. **C** Lateral view showing all superficial masticatory muscles. **D** Ventral view with the digastric muscle (not considered in this study; DIG) covering the superficial masseter (lateral to the mandible; MS) and the pterygoid (medial; PM) muscles. **E** Same view after removal of the digastric muscle. **F** Removal of the superficial masseter revealing the deep masseter (MP). **G** Removal of the deep masseter exposing the zygomaticomandibularis (anterior part: ZA, and posterior part: ZP). **H** After removal of the entire masseter, the three parts of the temporalis muscle are visible. **I** After removal of the superficial (TS) and suprazygomatic (SZ) portions of the temporalis, the remaining muscles were detached at their mandibular attachments, and the temporomandibular joint was disarticulated to luxate the mandible, thereby exposing the deep temporalis (TP) and the two pterygoid muscles (PM and PL)

Sexual Dimorphism in Wolves

Sexual dimorphism was assessed in French wolves by comparing males ($n=48$) and females ($n=41$). Means and standard deviations (SD) were calculated for each sex, and the same analyses as above were performed to compare (i) the total mass and PCSA of the jaw adductors; (ii) absolute mass and PCSA values (considering all three muscle complexes simultaneously, followed by separate analyses for each muscle complex); and (iii) the relative proportions of each muscle complex using the same analytical framework. MANOVAs (function "manova"), ANOVAs ("aov") with post-hoc test ("TukeyHSD") with Bonferroni correction) and two-sample t-tests ("t.test") were performed on log-10 transformed data to reduce right-skewness, improve homogeneity of variances and satisfy the assumptions of parametric analyses.

To examine scaling relationships and potential sex differences in muscle architecture, we performed MANCOVAs on log-transformed absolute muscle mass and PCSA values, using isometric size (derived from the log-shape ratios method; Mosimann, 1970*)* as a proxy for body size, since body mass data were not available, and sex as cofactors, including their interaction. This analysis tested for overall scaling effects (dependence of muscle variables on isometric size) and for possible differences in scaling slopes between males and females. In addition, to explore allometric shape effects (i.e., whether relative muscle proportions vary with size) we conducted complementary MANOVAs on log-shape residuals from regressions on isometric size (Mosimann, 1970). Similar analyses were performed on the

relative proportions of muscle masses and PCSAs. All analyses were restricted to the French wolf sample, for which sex was known.

Comparison Between French Wolves, North American Wolves, and Dogs

(i) Comparison of Total Mass and PCSA Between Wolves and Dogs The total mass and PCSA of the jaw adductors were obtained by summing these variables for all muscles. Variation within each group (French wolves, North American wolves, domestic dogs) was quantified by calculating means and SDs by group. Distributions were visualized with jittered points overlaid on boxplots to illustrate among-breed variation in dogs and allow direct comparison with wolves.

Group differences were tested with non-parametric ANOVAs (Kruskal-Wallis rank-sum test, "kruskal.test"), followed by pairwise comparisons ("pairwise.wilcox.test") with Holm corrections for multiple testing. Because the North American wolf sample was small ($n=14$), non-parametric tests were preferred to minimize sensitivity to deviations from normality and unequal variances.

(ii) Comparison of Absolute Masses and PCSAs of the Temporal, Masseter, and Pterygoid Complexes Means and SDs were calculated for each muscle complex and group. To visualize overall data structure, we performed Principal Component Analyses (PCA) on log10-transformed raw masses and PCSAs. Multivariate differences were assessed using PERMANOVAs on log10-transformed data ("adonis2", package "vegan"), followed by post-hoc tests ("pairwiseAdonis") with Holm correction. Before interpreting PERMANOVA results, we tested for homogeneity of group dispersions with "betadisper" and "permutest".

Each muscle complex was also analyzed separately using non-parametric ANOVAs and pairwise comparisons as described above. Distributions were visualized with jittered points overlaid on boxplots.

(iii) Comparisons of Jaw-Muscle Proportions Between Wolves and Dogs The relative proportion of each complex (temporal, masseter, pterygoid) to the total jaw-adductor mass and PCSA were calculated, with means and SDs reported. Because proportions are interdependent, an isometric log-ratio transformation was applied to obtain Euclidean data ("ilr", package "compositions"; Aitchison et al., 2002; Egozcue et al., 2003). PERMANOVAs and post-hoc tests were then performed on transformed data, with homogeneity of dispersions tested as described above. Each muscle complex was further analyzed and visualized separately using the same protocol.

Results

Sexual Dimorphism in French Wolves

French male wolves have significantly larger jaw adductor muscles and greater PCSA than females ($P<0.001$; Tables 2 and 3). This sexual dimorphism is consistent across all three muscle complexes, with males displaying significantly greater temporal, masseter, and pterygoid muscle masses and PCSAs (Fig. 3; Tables 2 and 3). In contrast, no significant differences are observed between sexes for muscle proportions (Table 3).

Absolute muscle masses and PCSAs were strongly correlated with isometric size ($P<0.001$), with no significant effect of sex (mass: $P=0.7$; PCSA: $P=0.3$). A significant size-sex interaction is however detected ($P<0.01$). Analyses of log-shape data show that scaled muscle masses and PCSAs remain significantly correlated with size in all cases ($P<0.001$) except male PCSA ($P=0.6$). In females, residual masseter mass and PCSA increase with size (slopes of 0.16 and 0.23), whereas temporal PCSA (−0.18) and pterygoid mass (−0.13) decrease with size. In males, residual temporal mass increases with size (0.12), masseter mass shows a weaker positive relationship with size (0.08), and pterygoid mass decreases (−0.20). Proportional muscle data also remain significantly correlated with isometric size ($P<0.001$) but show no significant effect of sex or size–sex interaction ($P=0.3$).

Comparison Between French and North American Wolves and Dogs

Total Mass and PCSA of the Jaw Adductors

The total mass and PCSA of the jaw adductors are significantly greater in both French and North American wolves than in domestic dogs ($P<0.001$; Table 4), whereas no significant difference are detected between the two wolf populations ($P>0.2$; Table 4). Several dog breeds overlap with the wolf range and display the highest values, including the Rottweiler, Cane Corso, Pitbull, Leonberger, and American Staffordshire terrier (Amstaff; Fig. 4A).

Absolute Jaw Adductor Muscle Masses and PCSAs

Multivariate analyses reveal highly significant differences in jaw-adductor muscle masses and PCSAs between wolves

Table 2 Mean and standard deviations of absolute muscle masses and PCSAs of French wolves, North American wolves, and domestic dogs, with relative muscle group proportions shown in brackets

	MASS (g)				PCSA (cm^2)			
Species	Temporal	Masseter	Pterygoids	Total	Temporal	Masseter	Pterygoids	Total
Domestic dogs (n=86)	89.9±52.3[64.3±3.0%]	37.4±22.2[26.6±2.3%]	12.7±7.2[9.1±1.4%]	140.1±81.1	21.3±8.8[50.6±5.0]	15.7±7.3[36.4±4.3]	5.5±2.6[13.0±3.0]	42.5±17.9
Street dogs (n=22)	93.0 ± 23.8(64.3 ± 2.0%)	38.1 ± 11.4 (26.2 ± 1.8%)	13.6 ± 3.2 (9.5 ± 0.8%)	144.7 ± 37.8	24.4 ± 6.7 (50.9 ± 4.5%)	17.5 ± 5.3 (36.3 ± 4.0%)	6.1 ± 2.0 (12.7 ± 2.3%)	47.9 ± 12.9
French wolves (n=98)	161.1±40.8[61.5±1.9%]	77.1±19.3[29.4±1.7%]	23.4±5.1[9.1±1.0%]	261.6±63.8	31.2±7.1[45.7±3.4]	28.6±6.7[41.7±3.9]	8.5±2.2[12.6±2.5]	68.3±14.3
Females(n=41)	134.9±25.9[61.3±1.7%]	65.1±14.2[29.4±1.9%]	20.3±4.0[9.3±1.0%]	220.4±43.0	27.3±4.6[45.4±3.2]	25.7±6.3[41.9±3.7]	7.6±1.7[12.7±1.9]	60.6±11.7
Males(n= 47)	179.4±40.6[61.5±2.1%]	86.0±18.4[29.6±1.7%]	25.5±4.8[8.9±1.1%]	290.9±62.0	33.7±7.2[45.9±3.6]	30.4±6.3[41.6±4.0]	9.0±2.3[12.4±3.1]	73.2±13.5
North American wolves (n=14)	183.9±49.8[63.6±1.4%]	79.4±19.8[27.5±1.2%]	25.3±5.2[8.9±0.9%]	288.5±74.0	34.1±6.9[45.6±3.4]	31.1±8.6[41.0±4.1]	10.0±2.8[13.4±2.6]	75.2±16.4

Table 3 Comparison of muscle masses and PCSAs between female and male French wolves

Analyses		Test	Mass (g)	PCSA (cm^2)
Total mass and PCSA		Student t-test	P<<0.001 – t=-5.1 – df=86.0	P<<0.001 – t=-4.0 – df=81.4
Multivariate analyses on absolute mass and PCSA data		MANOVA	P<0.001 – F = 8.9 – df= 1	P=0.001 – F = 5.7 – df= 1
Homogeneity of group dispersions		betadisper	P=0.8 – F=0.05	P=0.8 – F=0.06
Absolute mass and PCSA data	Temporal	Student t-test	P<<0.001 – t= -5.1 – df=85.6	P<0.001 – t=-4.2– df=85.7
	Masseter	Student t-test	P<<0.001 – t= -4.8 – df=84.0	P=0.002 – t=-3.3 – df=74.9
	Pterygoid	Student t-test	P<<0.001 – t= -5.1– df=83.9	P=0.006 – t=-2.8 – df=85.8
Multivariate analyses on proportions		MANOVA	P=0.2– F=1.6 – df=1	P=0.5 – F=0.61– df=1
Homogeneity of group dispersions		betadisper	P=0.4 – F=0.7	P=0.056 – F=3.7
Proportions	Temporal	Student t-test	P=0.7 – t=-0.4 – df=84.9	P=0.5 – t=-0.7 – df=86
	Masseter	Student t-test	P=0.5 – t= -0.6 – df=80.9	P=0.7 – t= -0.38 – df=85.6
	Pterygoid	Student t-test	P=0.07 – t= 1.8 – df=86.0	P=0.4 – t=0.9 – df=79.5

and dogs ($P<0.001$), whereas no significant differences are detected between French and North American wolves, although North American wolves tend to exhibit slightly larger PCSAs ($P=0.09$; Table 4; Fig. 4B). The principal component analysis separates wolves and dogs mainly along PC1, with wolves loading positively and dogs predominantly negatively (Fig. 5A). Dogs occupy a broader region of the morphospace than wolves (Fig. 5A), consistent with the significant differences in group dispersion (Table 4).

Univariate analyses show that both French and North American wolves have significantly greater temporal, masseter, and pterygoid muscle masses and PCSAs ($P<0.001$ for all comparisons), whereas no significant differences are detected between the two wolf populations ($P=0.2$–0.9; Table 4). Dog breeds displaying the highest values and overlapping with the wolf range include Rottweiler, pitbull, Leonberger, Cane corso, and Amstaff (Fig. 4B).

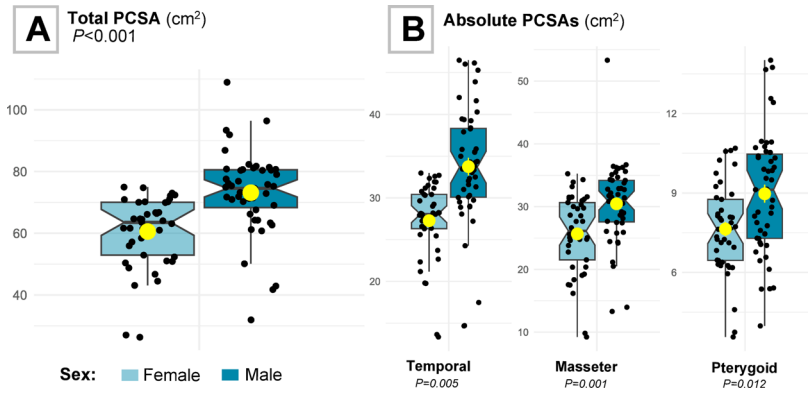

Fig. 3 Distribution of PCSA data of the jaw adductors in female and male French wolves: **A** Total summed PCSA; **B** Absolute PCSAs of the temporal, masseter, and pterygoid muscles. Females are shown in light blue and males in dark blue. Means and standard deviations are shown in yellow. P values of Student t tests are reported (see Table 3)

Proportions of the Jaw Muscles Relative to the Total Mass and PCSA

Multivariate analyses show significant differences in jaw-adductor muscle proportions between French wolves and dogs ($P<0.001$) and between North American wolves and dogs for PCSA proportions only ($P=0.044$; Table 4). Significant differences between the two wolf populations are detected for mass proportions but not for PCSA proportions (Table 4). PCA shows that dogs occupy a broader morphospace than wolves, extending further along the negative side of PC1, which is mainly driven by temporal and masseter proportions (Fig. 5B). This pattern is consistent with the analyses of group dispersion (Table 4). Univariate analyses show that dogs have higher temporal proportions, whereas wolves have higher masseter proportions ($P<0.001$; Table 4; Fig. 4C). No significant differences are detected for pterygoid proportions (Table 4).

Dog breeds with relatively high masseter proportions and/or low temporal proportions that overlap with the average wolf range include mastiff, Rottweiler, Belgian shepherd, pitbull, boxer, and Doberman (Fig. 4C). In contrast, Yorkshire terrier, dachshund, deerhound, Jack Russell terrier, beagle, and Chihuahua display relatively low masseter proportions and high temporal proportions and fall outside the wolf range (Fig. 4C; Supplementary Material S1). These differences are also visible during dissection. For example, the mastiff shows a particularly large masseter muscle reminiscent of French wolves, whereas the Yorkshire terrier displays a comparatively larger temporal muscle (Fig. 4D).

For mass proportions, significant differences are observed between French wolves and dogs, but not between North American wolves and dogs. No significant differences are detected for pterygoid proportions (Table 4). North American wolves also show higher temporal and lower masseter mass proportions than French wolves, whereas no significant differences are detected for PCSA proportions (Tables 2 and 4).

Discussion

By combining extensive, standardized measurements of muscle architecture, this study provides the first large-scale comparison of jaw musculature within *Canis lupus* and between wild grey wolves and domestic dogs. The results reveal three major findings. First, male wolves possess significantly larger jaw adductor muscles than do females, indicating sexual dimorphism in functional performance, despite similar relative muscle contributions to the overall mass and PCSA of the jaw adductors. Second, no significant difference was detected between French (*C. l. italicus*) and North American (*C. l. nubilus*) wolves, suggesting broad functional conservation of the masticatory system across subspecies despite ecological divergence. This pattern, however, should be further tested using larger samples of North American wolves ($n=14$ in the present study) of known sex, and for additional subspecies (e.g., those from Southwest Asia). Finally, grey wolves overall display greater total muscle mass and PCSA, as well as relatively larger masseter and pterygoid complexes than do domestic dogs. However, wolves overlap with large, strong-biting breeds such as mastiffs, Rottweilers, and pitbulls. These findings shed new light on how both natural and artificial selection have shaped the form–function relationships of the canid feeding apparatus.

Intraspecific Diversity in Grey Wolves

Sexual Dimorphism and Selective Context

Within the French wolves, males possess larger masticatory muscles than females, but this dimorphism is largely driven by body-size differences. Muscle masses and PCSAs were strongly correlated with isometric size, and no main effect of sex was detected on size-corrected data, indicating that sexual dimorphism in the wolf masticatory system primarily reflects differences in overall body-size rather than intrinsic sex-specific investment in muscle mass or force capacity.

Table 4 Comparison of muscle mass and PCSA between dogs and wolves

Analyses	Test andpairwise comparisons	Mass (g)		PCSA (cm^2)	
Total mass and PCSA	Kruskall-Wallis	Chi^2= 90.9	P<0.001***	Chi^2= 84.1	P<0.001***
	D vs FW		P<0.001***		P<0.001***
	D vs AW		P<0.001***		P<0.001***
	AW vs FW		P=0.4		P=0.25
Multivariate analyses on absolute data	PERMANOVA	R^2 = 0.43	P<0.001***	R^2 = 0.37	P<0.001***
	D vs FW	R^2 = 0.41	P<0.001***	R^2 = 0.35	P<0.001**
	D vs AW	R^2 = 0.21	P<0.001***	R^2 = 0.21	P<0.001**
	AW vs FW	R^2 = 0.01	P=0.2	R^2 = 0.023	P=0.09
Homogeneity of group dispersions	Betadisper	F= 18.1	P<0.001***	F= 12.8	P<0.001***
	D vs FW		P<0.001***		P=0.01**
	D vs AW		P=0.02**		P=0.03*
	AW vs FW		P=0.6		P=0.8
Absolute data of the temporal	Kruskall-Wallis	Chi^2=86.3	P<0.001***	Chi^2=67.7	P<0.001***
	D vs FW		P<0.001***		P<0.001***
	D vs AW		P<0.001***		P<0.001***
	AW vs FW		P=0.18		P=0.23
Absolute data of the masseter	Kruskall-Wallis	Chi^2=96.1	P<0.001***	Chi^2=93.0	P<0.001***
	D vs FW		P<0.001***		P<0.001***
	D vs AW		P<0.001***		P<0.001***
	AW vs FW		P=0.9		P=0.44
Absolute data of the pterygoid	Kruskall-Wallis	Chi^2=93.9	P<0.001***	Chi^2=65.3	P<0.001***
	D vs FW		P<0.001***		P<0.001***
	D vs AW		P<0.001***		P<0.001***
	AW vs FW		P=0.28		P=0.063*
Multivariate analyses on proportions	PERMANOVA	R^2 = 0.12	P<0.001***	R^2 = 0.11	P<0.001***
	D vs FW	R^2 = 0.12	P<0.001***	R^2 = 0.11	P<0.001**
	D vs AW	R^2 = 0.008	P=0.4	R^2 = 0.02	P=0.044*
	AW vs FW	R^2 = 0.01	P=0.02**	R^2 = 0.008	P=0.4
Homogeneity of group dispersions	Betadisper	F= 6.5	P=0.002**	F= 2.44	P=0.09
	D vs FW		P=0.01*		
	D vs AW		P=0.03*		
	AW vs FW		P=0.22		
Proportions of the temporal	Kruskall-Wallis	Chi^2=53.0	P<0.001***	Chi^2=47.5	P<0.001***
	D vs FW		P<0.001***		P<0.001***
	D vs AW		P=0.24		P<0.001***
	AW vs FW		P<0.001***		P=0.8
Proportions of the masseter	Kruskall-Wallis	Chi^2=68.0	P<0.001***	Chi^2=56.7	P<0.001***
	D vs FW		P<0.001***		P<0.001***
	D vs AW		P=0.08		P=0.0021
	AW vs FW		P<0.001***		P=0.48
Proportions of the pterygoid	Kruskall-Wallis	Chi^2=0.82	P=0.7	Chi^2=1.8	P=0.4

D Dogs, *FW* French wolves; AW: North American wolves. Level of significances: P<0.001***; P<0.01**; P<0.05*

This pattern aligns with previous analyses of cranial morphology, which showed that males have slightly broader zygomatic arches and more robust skulls, yet largely overlap with females in overall cranial shape once size effects are accounted for (MacLeod & Kolska Horwitz, 2020). Together, these findings suggest that the wolf masticatory apparatus is largely conserved between sexes, with dimorphism expressed mainly through allometric scaling of a shared structural design.

Beyond this general pattern, our analyses revealed a significant interaction between isometric size and sex for raw muscle masses and PCSAs, highlighting sex-specific allometric trajectories in the architecture of the jaw adductor system. In females, increasing size was associated with an increase in size of the masseter for both relative mass and PCSA, while relative temporal PCSA and pterygoid mass scaled negatively with size. This pattern suggests a disproportionate reinforcement of the masseter's force-generating capacity in larger females, suggesting selection for force

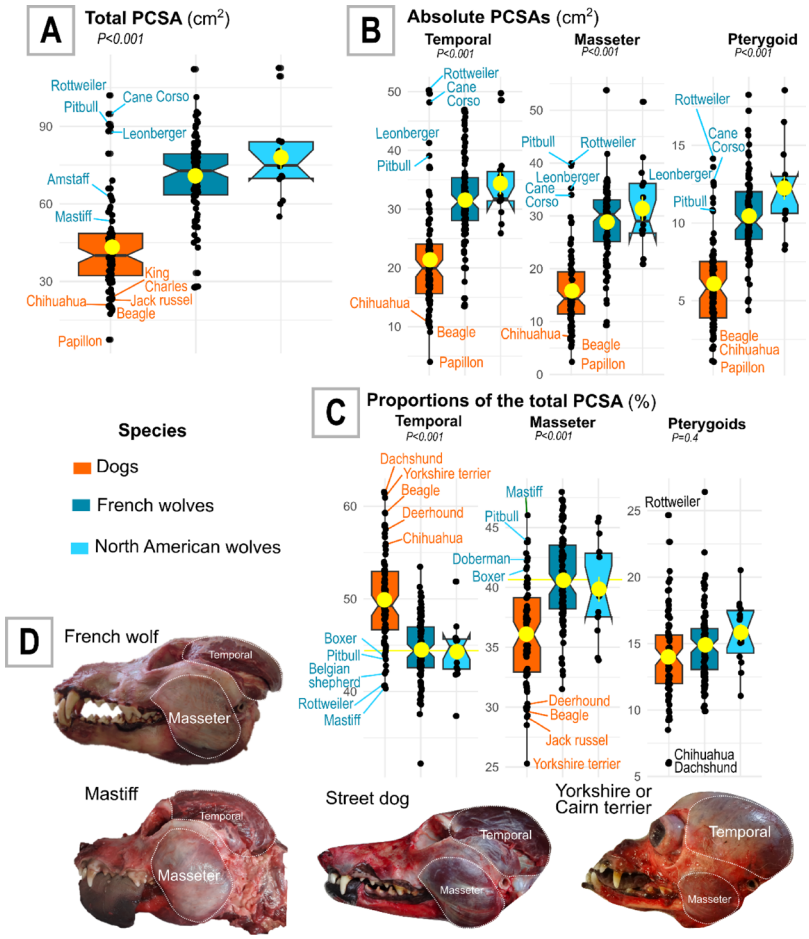

Fig. 4 Distribution of PCSA data of the jaw adductors. **A** Total summed PCSA; **B** Absolute PCSAs of the temporal, masseter, and pterygoid muscles; **C** proportions relative to the total PCSA; **D** lateral views of dissections from a French wolf, a mastiff, a Tunisian street dog and a Yorkshire terrier, with the temporal and masseter muscles circled. Dogs are shown in orange and wolves in blue. Dog breeds falling within the wolf range are labeled in blue, whereas those outside the wolf range are labeled in orange. Means and standard deviations are shown in yellow

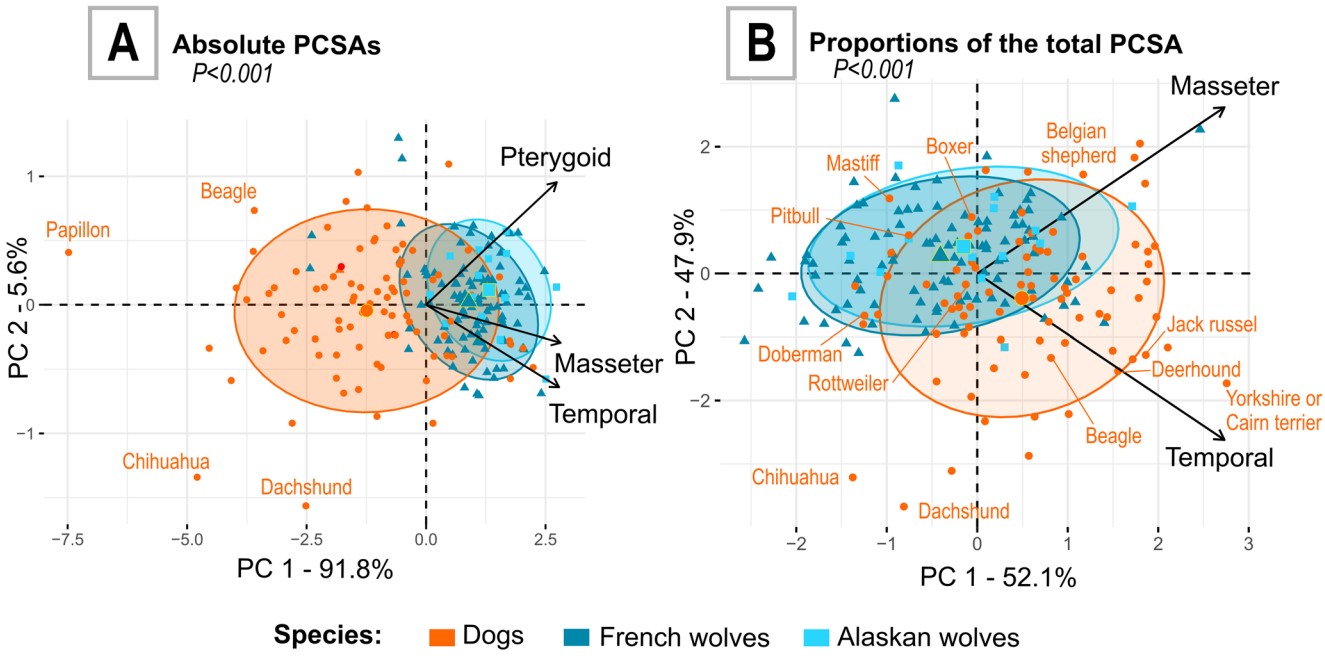

Fig. 5 Principal Component Analyses based on (**A**) Absolute PCSAs of the temporal, masseter, and pterygoid muscles, and (**B**) their proportions relative to the total jaw-adductor PCSA. Dogs are shown in red, wolves in blue (dark blue for French wolves and light blue for North American wolves)

transmission at low gape angles. In contrast, males exhibited more heterogeneous scaling trajectories with weak positive allometry for masseter mass, while relative PCSA values were not size-dependent, indicating no clear increase in force increase with size. Instead, relative temporal muscle mass increased, whereas relative pterygoid mass decreased with size. Together, these results suggest that increasing size in males is primarily associated with greater relative investment in temporalis muscle mass rather than the masseter. These differences are highlighting divergent functional strategies between sexes in how jaw adductor architecture scales with body size.

These different size-dependent relationships between males and females indicate alternative biomechanical strategies rather than simple differences in overall bite force and may reflect differences in behavioral demands between sexes. In males, the increasing dominance of the temporal muscle with size suggests functional requirements associated with forceful jaw closure or biting at a wider gape angle. Such demands could be linked to behaviors such as mate competition, territorial defense, and provisioning prey for mates and pups (Mech et al., 1999; Morris & Brandt, 2014), which, although secondary to cooperative hunting, may impose additional energetic and mechanical constraints on males and favor greater force production under specific functional contexts. In contrast, the opposite scaling pattern observed in females may favor efficiency and control during repeated biting or food processing. Importantly, the magnitude of these differences remains modest, suggesting subtle architectural reorganization rather than a pronounced functional divergence.

The limited degree of sexual dimorphism observed in wolves is consistent with their cooperative social structure and supports Gittleman and Van Valkenburgh's (1997) hypothesis that pronounced sexual dimorphism in feeding structures evolves primarily in species with intense male–male competition and limited cooperative feeding. Male and female wolves hunt together and share prey, reducing the likelihood of divergent selection on feeding structures. In contrast, stronger cranial and muscular dimorphism is particularly observed in solitary or sexually segregated carnivores where males and females exploit different prey sizes or habitats (Gálvez-López et al., 2022; Law, 2020). In wolves, overlapping ecological roles likely homogenize selective pressures on feeding structures, such that sexual dimorphism is expressed mainly through allometric scaling and subtle architectural adjustments rather than through pronounced functional specialization.

Subspecies Variation and Ecological Stability

The contrasting ecological constraints experienced by French vs. North American populations led us to expect differences in jaw musculature reflecting adaptive divergence. Given that French wolves are more specialized on large ungulates, in contrast to North American wolves which face stronger interspecific competition and consume a more diverse prey spectrum (Ballard et al., 1987; Burtt & DeSantis, 2022; Idaho Department of Fish and Game, 2023; Lafferty et al., 2014; Newsome et al., 2016; Poulle et al., 1997; Stanek et al., 2017; Szepanski et al., 1999; Watts & Newsome, 2017), one could predict muscle adaptations favoring higher bite forces at large gape angles (mediated by a relative stronger temporalis) in French wolves, and higher bite forces at low gape angle (mediated by the masseter) in North American wolves.

However, our results revealed that the two populations exhibited nearly identical absolute and proportional jaw muscle masses and PCSAs. This may be explained by the mechanical demands imposed by processing large prey (which constitute the primary food source for most wolf populations, regardless of their geographic origin) imposing strong functional constraints that maintain powerful jaw muscles even when smaller or softer food items are occasionally consumed. This apparent similarity should, however, be interpreted with caution due to the limited representation of North American specimens ($n = 14$), most originating from Alaska ($n = 12$), and only two from Idaho. Future studies incorporating larger and more balanced samples from North American wolves and other subspecies living under contrasting ecological conditions will be essential to refine these interpretations and test the extent of functional stability across *C. lupus* populations.

The apparent conservation of muscle architecture may indicate that the wolf's jaw musculature represents a functionally optimized compromise, enabling efficient processing of a wide range of prey types, from large ungulates to smaller mammals or carrion, without requiring marked morphological specialization. As hypercarnivores, wolves are likely subject to strong stabilizing selection maintaining high bite forces and robust cranio-mandibular mechanics (Wroe et al., 2005). Consequently, minor dietary or ecological shifts may be accommodated primarily through behavioral flexibility (e.g., cooperative hunting, bone-cracking) rather than anatomical change.

The overlap in jaw muscle architecture between *C. l. italicus* and *C. l. nubilus* may also reflect phylogenetic constraint and functional integration of the cranio-mandibular system. Because muscle forces shape cranial growth (Ito & Endo, 2016) and cranial shape constrains muscle orientation, evolutionary changes in one component likely require

coordinated changes in the other. Overall, the wolf's cranial and muscular system appears to represent a stable adaptive configuration that balances force generation, gape amplitude, and mechanical efficiency, traits essential to both predation and social food sharing.

Natural Versus Artificial Selection in Canids

Obviously, the most pronounced differences observed in this study occur between wolves and dogs, as a consequence of domestication and artificial selection. Domestication results from both the relaxation of ecological constraints (e.g., those imposed by hunting and carcass processing) and the selective breeding for behavioral traits such as tameness and reduced aggression, as well as morphological traits associated with aesthetic or functional purposes (Björnerfeldt et al., 2006; Larson & Fuller, 2014; Lord et al., 2020; Trut, 1999; Zeder, 2012). This artificial selection likely involved correlated effects on the jaw musculature.

Overall Functional Divergence in Absolute Bite Capacity

Wolves display significantly greater absolute total jaw-adductor mass and physiological cross-sectional area (PCSA) than domestic dogs on average, suggesting a greater absolute bite force capacity despite the large morphological diversity among dog breeds. As many modern pet dogs consume dry commercial food or soft prepared diets, the mechanical properties of these foods (high or low brittleness, respectively, and low toughness) require limited bite force compared with the processing of whole prey tissues and the need to crush bones to get the marrow. Moreover, in wolves, jaw-adductors are likely shaped not only by food consumption but also by prey capture, restraint, killing, and carcass dismemberment. The relaxation of these functional demands in domestic dogs, associated with changes in feeding behavior and reliance on humans, likely contributes to the reduced absolute jaw muscle volume and force observed in dogs. Nonetheless, the largest breeds overlap with the upper range of wolves (Fig. 4). Because body mass data were unavailable for the specimens under study, we could not assess whether domestication led to a reduction in size-independent bite capacity. Nevertheless, this overlap suggests that human selection for specific morphologies or behaviors (e.g., livestock guardians or attack dogs) has secondarily favored jaw-muscle architectures approaching those of wolves, and thus associated with strong bites. If confirmed, such a reduction would align with previous reports on decreased cranial size and robusticity (Evin et al. 2016; Morey 1992), tooth size (Pionnier-Capitan 2010; Wayne 1986) and relative brain size (Balcarcel et al. 2021, 2022; Garamszegi et al. 2023) following domestication. Finally, the present study only considered intrinsic architectural parameters of the jaw muscles. Because muscle orientation and position relative to the jaw joint also influence the mechanical advantage and moment arms of the adductors (Herrel et al. 2008), these factors should be integrated in future studies estimating bite force in wolves using comparable methods as those already used for dogs or foxes (Brassard et al. 2021; Brassard, Merlin, Guintard, Brassard et al. 2020a, b).

Specialization of the Jaw Musculature to Ecological Constraints in Wolves

Interestingly, we found significant differences in jaw muscle proportions between wolves and dogs. Wolves possess relatively stronger masseter (and medial pterygoid) muscles, whereas dogs show a relatively stronger temporalis, on average. Given that the temporalis is crucial for producing high bite force at large gape angles (consistent with predatory strikes and vertical clamping; Turnbull, 1970; Herrel et al., 2008; Santana et al., 2010), we might have expected wolves, which typically hunt large prey (Lafferty et al., 2014; Newsome et al., 2016; Stanek et al., 2017; Szepanski et al., 1999; Watts & Newsome, 2017; Zlatanova et al., 2014) to have exhibited an enlarged temporalis (Herrel et al., 2008; Santana et al., 2010; Turnbull, 1970). The opposite pattern suggests that the masseter (and medial pterygoid) act as complementary force generators, enhancing bite strength at low gape angles. In absolute terms, wolves still possess powerful temporalis muscles for wide-gape bites, but the relatively greater masseter and pterygoids may enhance force production during low-gape clenching or bone crushing. Electromyographic data indeed indicate that the masseter contributes more linearly and consistently to bite force generation than the temporalis during strong clenching (Bogdanov, 2023), reinforcing its role in producing high forces at small gape angles.

Such capability is particularly relevant for bone processing and accessing lipid-rich marrow (Bosch et al., 2015). Although taphonomic evidence suggests bone fracturing consistent with marrow consumption (Sala et al., 2014), direct behavioral observation of bone-cracking by grey wolves are scarce (Van Valkenburgh et al., 2019; Willey & Snyder, 1989). Feeding experiments with captive Arctic wolves and spotted hyenas revealed that wolves rarely fracture the long bones of large ungulates to access marrow, unlike hyenas, and only gnaw intensively when the marrow cavity is already exposed (Nascou & Morin, 2014). However, the authors did not include small prey species, for which marrow would be more easily accessible. Thus, marrow consumption by wolves appears mostly opportunistic, facilitated by pre-fractured bones (or maybe small

prey) rather than systematic bone-crushing as seen in hyenas (Tanner et al., 2008). This behavioral difference likely reflects energetic trade-offs, as breaking thick cortical shafts is costly and yields limited energetic benefit. Although bone crushing likely contributes to the preferential development of the masseter in wolves, it is unlikely to provide a complete explanation. Several non-exclusive mechanisms may underlie this pattern.

A second, non-exclusive hypothesis is that a larger masseter optimizes the slicing function of the carnassials, the specialized shearing blades formed by the upper fourth premolars and lower first molars. A more developed masseter would help maintain precise occlusion between the upper and lower carnassial blades, improving slicing efficiency. Ito and Endo (2016) reported that felids exhibit relatively stronger masseters than canids, which they interpreted as an adaptation for killing and consuming prey via a slicing mechanism rather than crushing. Accordingly, the larger relative proportion of the masseter in wolves may serve a dual role: enabling powerful low-gape bites for both flesh slicing and marrow extraction from already fractured bones or from small prey. In other words, it may represent a functional compromise between slicing and limited bone-crushing performance, as observed to a lesser extend in felids (Hartstone-Rose et al., 2012).

Variability Within Dogs: Impact of Selection and Developmental Constraints

The relatively smaller masseter in most dogs can be explained by the relaxation of natural selective pressures associated with carcass processing, as they rarely require prolonged occlusal contact and lateral stabilization of the mandible while feeding on soft or pre-processed food. Nevertheless, the range of jaw-muscle configurations among dog breeds is extraordinarily broad. Some breeds (e.g., mastiffs, pitbulls, Rottweilers, Dobermans) exhibit masseter proportions and absolute PCSAs comparable to those of wolves, whereas others (e.g., beagles, Chihuahuas, papillons, Yorkshire terrier) show reduced masseters and proportionally larger temporalis muscles.

The overlap between dog breeds and wolves suggests that, although most dogs have weaker jaws, targeted artificial selection can recreate the functional attributes of their wild ancestor. Breeds selected for defense or restraint behaviors converge on the wolf phenotype, an example of functional re-evolution under domestication. This aligns with previous studies showing that large brachycephalic breeds (Rottweiler, pitbull, Cane corso, Leonberger, Amstaff) optimize bite-force production relative to other dogs (Brassard, Merlin, Guintard, et al. 2020a). The convergence of strong-biting dog breeds with wolves demonstrates that artificial selection can produce jaw-muscle configurations approaching those of wolves despite extensive cranial diversification. These findings highlight the evolutionary flexibility of the canid masticatory system under artificial selection.

At the opposite end of the spectrum, the highest temporal muscle proportions occur in small breeds dedicated to companionship (papillon, Chihuahua, Yorkshire terrier) or to small-game hunting (beagle, deerhound, dachshund). For hunting breeds, producing high size-relative bite forces at wide gape angles may favor temporalis recruitment. However, for toy breeds, extreme cranial shortening likely constraints muscle space. These geometric constraints may shift muscle balance toward temporalis dominance, compensating for reduced jaw length but at the expense of overall force capacity.

Yet, the persistence of similar proportions in jaw muscles despite profound cranial diversification suggests that muscle architecture remains functionally integrated with skeletal morphology. This integration reflects enduring biomechanical trade-offs: high bite force requires both short lever arms and large muscle cross-sections, but muzzle shortening compromises olfactory and respiratory efficiency. Natural selection in wolves likely optimized this balance, whereas artificial selection in dogs has decoupled it according to human preference, occasionally restoring performance in specific functional breeds.

Conclusions

Our comparative analysis reveals that (1) male wolves possess larger, but not proportionally different, jaw adductors than do females, reflecting size-based rather than shape-based dimorphism; (2) French and North American wolves share nearly identical muscle architecture despite ecological divergence, demonstrating functional stability across subspecies; (3) grey wolves exhibit greater absolute jaw-muscle size and strength and relative masseter development than do dogs, yet overlap with strong-biting breeds shaped by artificial selection.

Together, these results suggest that both natural and artificial selection act on a shared, tightly integrated musculoskeletal template. The wolf masticatory system appears to represent a robust functional design maintained by strong ecological constraints, whereas domestication relaxed some of these constraints while preserving the potential for renewed functional specialization under targeted artificial selection. More broadly, these results illustrate how domestication can reshape the functional organization of the feeding apparatus while retaining the capacity for convergence toward the ancestral condition under specific selective pressures.

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Author Contributions C.B. and A.H. conceived the study. C.B. analyzed the data and wrote the first draft of the manuscript. Data were acquired by C.B., A.H (dissections of dogs and French wolves), J.J., S.L. and S.S. (dissections of French wolves), R.A.B. (calculation of North American wolf muscle densities), and L.O. (measurements on street dogs). Material access was provided by C.D., A.D., A.L., A.H.-R., and C.G. A.H. contributed to writing and critical revision of the manuscript. All authors reviewed, approved the final version of the manuscript, and agree to be accountable for all aspects of the work.

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Data Availability All data generated or analyzed during this study are included in this article and its supplementary information files. Detailed information on the sample and aquired data is provided in Supplementary Information 1. The R code used for the analyses is available from the corresponding author upon reasonable request.

Code Availability The R code is available from C.B. on request.

Supplementary material

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Ethical Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

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