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# The effects of prey size on carnivore tooth mark morphologies on bone; the case study of *Canis lupus signatus*

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## ABSTRACT

Carnivore feeding behaviour is a valuable line of research of increasing value in taphonomic analyses. An interesting component of these studies lies in the differentiation of carnivore activity based on tooth marks left on bone. Among the methodological approaches available, a major protagonist in recent years has been the incorporation of hybrid geometric morphometric studies with artificially intelligent algorithms, reaching over 95% accuracy in some cases. In spite of this recent success, a number of methodological questions are still to be answered for wide-scale application of these techniques into other applied fields of science. One of these questions lies in the possible variability induced by prey size on tooth-mark morphologies. Here we compile data regarding these effects, using the Iberian wolf as a relevant case study in both contemporary and prehistoric European and North American ecology. The methodology employed opens new questions regarding carnivore tooth marks that should consider the effects of mastication biomechanics. While in most cases prey size is not a significant conditioning factor, caution is advised for future experimentation when considering small prey where some statistical noise may be present. Nevertheless, future experimentation into other carnivore case studies can be considered a valuable research goal.

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## Introduction

The study into carnivore interventions in archaeological site formation has been an ever-growing line of investigation going back at least two centuries. Since the 19<sup>th</sup> century and through the 20<sup>th</sup>, different authors such as Dawkins (1863, 1874, 1877) and Martin (1906, 1907, 1907-1910, 1909) hypothesised about the impact carnivores had on certain sites. These authors noted how sites such as Creswell Crags (Derbyshire, England) and La Quina (Charente, France) present evidence of bones possibly damaged by hyenas or wolves. In order to support these theories, some of the first archaeologically oriented experimental programmes with carnivore-modified bones were performed.

Upon developing this pioneering research, a large expansion of studies into carnivore behaviour and activities can be seen throughout the second half of the 20<sup>th</sup> century, integrating this line of research into the field of taphonomy and yielding many important publications (Schaller and Lowther 1969; Sutcliffe 1970; Houtson 1979; Haynes 1980, 1983; Brain 1981; Binford 1981). Carnivore taphonomy can then be considered a fundamental protagonist in the study of early human sustenance, playing a particularly important role in the hunter-scavenger debate (Blumenschine 1986, 1988; Tappen 1992).

The hunter-scavenger debate fuelled many studies into carnivore and early hominin palaeoecologies (Binford 1981, 1985; Bunn 1981, 1983; Blumenschine 1986, 1995), searching for taphonomic criteria that could be used to discern the carnivores involved in site

formation and modifications. From these studies, initial attempts at using quantitative methods for the metric analyses of these alterations to bones can be found towards the turn of the twenty-first century (Capaldo and Blumenschine 1994; Selvaggio and Wilder 2001). One of the most diagnostic features of carnivore modifications to bone are found in the marks left by their teeth (Haynes 1980, 1981, 1983; Binford 1981; Blumenschine 1995). The most frequent of these modifications can be divided into two different categories of tooth mark known as *pits* and *scores*. Pits are circular in nature, produced by the direct impact of the carnivore's tooth on bone. Scores are elongated, presenting an equally rounded base and is formed as the tooth is dragged across the surface.

Initial attempts at the quantification of these marks were limited in success to discerning between the agents intervening in the formation of osteological accumulations, noting tooth scores to be too variable among most carnivores (Domínguez-Rodrigo and Piqueras 2003). Through further studies into these two traces, taphonomists have been able to infer a number of different features, using simple metric variables such as the length and width of these marks to infer the size of the carnivore feeding (Delaney-Rivera et al. 2009; Andrés et al. 2012). While these simple metric variables have had some success in zooarchaeological analyses (Yravedra 2007, 2011; Domínguez-Rodrigo et al. 2007; Blasco et al. 2011; Sala et al. 2014; Saladié et al. 2014, 2019; Yravedra et al. 2016; Pineda and Saladié 2019), these variables present a high degree of overlap that are rarely sufficient in building stronger hypotheses.

In recent years, a number of efforts have been made to overcome these issues, using a new series of computational tools that provide a much higher degree of metric accuracy. The incorporation of tridimensional modelling and geometric morphometric studies in taphonomy have reached new limits in taphonomic trace classification. Adaptations of Bello and Soligo (2008), (2009), 2011, 2013) metric models for cut mark analyses were the first to overcome these issues, differentiating between carnivore agencies via tooth score cross-sections with the added inclusion of geometric morphometric analyses (Yravedra et al. 2017). Through extensive research efforts including tooth pits (Aramendi et al. 2017), analysts have reported up to 80% classification success when differentiating between carnivore agencies (Aramendi et al. 2017; Yravedra et al. 2018, 2019; Arriaza et al. 2017, 2019a, b). While the most recent inclusion of Machine Learning algorithms in processing this data has been able to achieve exceptional results (> 95% classification rates) (Courtenay et al. 2019; Yravedra et al. 2019), a number of investigation questions remain.

While success of this nature holds great potential for future research into site formation processes, a number of questions still remain regarding the efficiency of these methodological approaches. One example can be seen in how the aforementioned literature derives their models from tooth marks produced on horse bone (Aramendi et al. 2017; Yravedra et al. 2017, 2019; Courtenay et al. 2019). While Maté-González et al. (2019) were able to reject the size of the animal as a conditioning factor for cut mark formation, the biomechanics of mastication are very different and may cause variations in these results. The objectives of this study are thus to assess the effects of carcase size on tooth-mark formation. Studies of this nature can be considered a vital component for the orientation of future experimental programmes; providing a means of obtaining better analogies with the possible conditions under which tooth marks may be produced.

### A case study: *Canis lupus signatus*

In order to analyse the possible effect prey size has on carnivore tooth marks, this study presents a detailed analysis of the Iberian Wolf (*Canis lupus signatus*, Cabrera 1907).

The wolf can be considered an anomaly from other carnivores in the Northern Hemisphere. *Canis lupus* is the extant animal with the greatest bite force of all European and Northern American carnivores in proportion with its size (Van Valkenburgh and Ruff 1987; Thomason 1990; Meers 2002; Wroe et al. 2005). Using its posterior teeth, wolves have been estimated to have a total bite force of 1,412 N (Van Valkenburgh and Ruff 1987; Wroe et al. 2005), positioning its bite to be the third most powerful in the Northern Hemisphere (*ibid*). Moreover, the wolf separates itself in feeding behaviour from other European and North American carnivores by having the most diverse prey selection with regards to prey size (Thompson 1952; Mech 1970; Gittleman 1985; Vézina 1985). While most carnivores exhibit behavioural feeding attributes in hunting animals no larger than themselves (Gittleman 1985; Vézina 1985), the wolf (ca. 50 kg) is an example of a species that defies this correlation. This in turn can mostly, yet not exclusively, be attributed to the wolf being a social pack hunter.

While the current conservation status of most *Canis lupus* populations remains to be of the IUCN's least concern (IUCN 2007), in specific areas of Europe and Northern America human-wildlife conflict is beginning to endanger this carnivore species (*ibid*). This is especially relevant for the Iberian Wolf, whose current status is being threatened by poaching and hunting (Berger 1999; Berger et al. 2001; Treves et al. 2004; Blanco and Cortés 2009; Woodroffe and Redpath 2015). While numerous government

programmes are pushing towards the conservation of wolf populations, the increasing number of wolf attacks on livestock in the Iberian Peninsula and other areas of Europe is making this task difficult (Fritts et al. 2003; Treves et al. 2004; Skogen et al. 2008; Lagos-Abarzuza 2013; Miller et al. 2016; Pimenta et al. 2017, 2018).

In prehistoric research, the study of wolf populations is of great importance from numerous perspectives. Firstly, as with the case of any study in carnivore taphonomy, their cohabitation with human populations prior to domestication is of great importance. Wolves have occupied the same landscape alongside humans throughout the majority of the Pleistocene, with multiple sites presenting evidence of wolf and hominin populations occupying these areas at different times (Stiner 1994; Blasco-Sancho 1995; Díez et al. 1999). Even after domestication, documentation of conflict and competition for resources continue to persist (Treves et al. 2004; Campion-Vincent 2005; Pimenta et al. 2017, 2018). Moreover, the domestication of canid populations is a compelling line of research that reveals numerous details about the behavioural complexity and interactions between both human and carnivore species (Binford 1981; Germonpré et al. 2009; Guagnin et al. 2018; Grandal-d'Anglade et al. 2019; Yeomans et al. 2019).

From a taphonomic perspective, wolves are considered one of the animals to produce the highest degrees of modifications to osteological remains in the Euroasiatic Pleistocene (Martin 1907–10; Haynes 1980; Stiner 1994; Blasco-Sancho 1995; Díez et al. 1999; Yravedra 2001; Yravedra et al. 2011; Yravedra and Castanedo 2011). As for their tooth marks, the first approximations to wolf tooth-mark morphologies have noted wolves to produce a wide range of different shaped score and pits (Yravedra et al. 2011, 2017, 2019; Aramendi et al. 2017) usually creating a high degree of noise in statistical analyses (Aramendi et al. 2017; Yravedra et al. 2018; Courtenay et al. 2019). While wolves can be considered easily separable from other canids (Yravedra et al. 2019), their comparison with other carnivores that may occupy the same ecosystem can still be problematic.

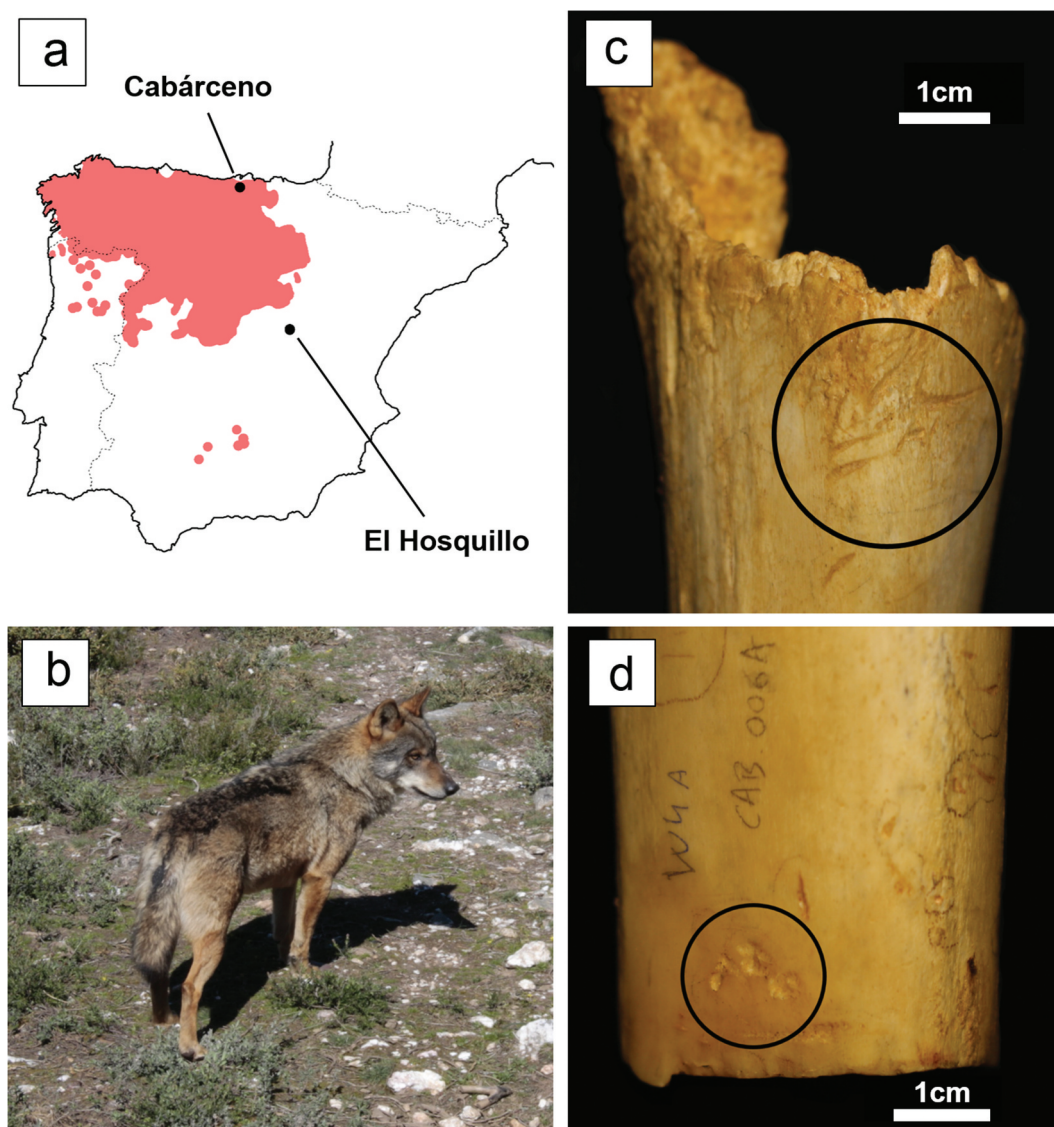
## Methods and sample

### Tooth-mark samples

Tooth marks produced by wolves were used for the purpose of this study. Wolves were chosen considering their wide variations in behavioural feeding patterns, thus fulfilling the analogy that it is more likely to find wolf tooth marks on animals of different sizes than most other types of carnivore.

Two samples produced by adult *Canis lupus signatus* individuals were consequently used in this study (Figure 1). The first sample originates from the Cabárceno Natural Park (Obregón, Cantabria; Figure 1(a)), a > 750 ha facility 17 km away from the city of Santander. The second sample originates from the Hosquillo game reserve in the upper mountain ranges of Cuenca (Spain, Figure 1(a)), with a similarly large extension of ca. 910 ha. Both parks are dedicated to the conservation and investigation of endangered species, keeping animals in 'semi-captivity' while also being open to the public for education purposes.

Both samples were produced by a group of adult *Canis lupus signatus* individuals (Cabárceno = 7, Hosquillo = 5, Figure 1(b)). Animals in semi-captivity were chosen to provide some control over the agents interacting with the samples collected, ensuring that no additional animals or different age groups were creating noise in the tooth marks recovered (Binder and Van Valkenburgh 2000). Animals were mostly fed disarticulated limb elements with meat attached; however, in some cases distal epiphyses of humerii and femora were articulated to the zygopodials. The exposure of



**Figure 1.** Details regarding the (a) distribution (in red) of (b) *Canis lupus signatus* populations in mainland Iberian Peninsula. To the right are examples of wolf tooth (c) scores and (d) pits from the Cabárceno sample. Figure A by L.A.C. compiled from numerous sources (IUCN, 2007; JCyL, 2009, 2015, 2016; Pimenta et al., 2018). Photos B, C and D by J.M.V.R. Final figure by L.A.C.

bones to carnivores varied according to the feeding protocol established by each of the parks (Cabárceno = 1 week, Hosquillo = 3 months).

The Hosquillo sample consists mainly of remains belonging to medium and small-sized animals. From these samples tooth marks on small-sized animals (ca. 10–100 kg) were collected from a mixture of mouflon (*Ovis orientalis*), Iberian ibex (*Capra pyrenaica*), roe deer (*Capreolus capreolus*) and boar (*Sus scrofa*) remains. These include the diaphyses of humerii (Number of Identified Specimens (NISP) = 42), radii (NISP = 47), femora (NISP = 62) and tibiae (NISP = 50). The medium-sized animal sample (ca. 100–350 kg) was obtained from *Cervus elaphus* long bone diaphyses also including humerii (NISP = 59), radii (NISP = 31), femora (NISP = 22) and tibiae (NISP = 45). In the case of the Cabárceno sample, remains consist mostly of large-sized animals (ca. 350–800 kg), namely equid and some bovid remains. A total of 33 equid bones were subsequently collected and used for this sample, including humerii (NISP = 6), radii (NISP = 3), femora (NISP = 3) and tibiae (NISP = 8).

From each of these samples, a total of 325 carnivore tooth marks on long bone shafts were studied. Of the different types of tooth

marks, only scores (n = 169, Figure 1(c)) and pits (n = 156, Figure 1(d)) were considered. Selection of marks found on diaphyses followed the taphonomic considerations that these elements have higher survival rates in archaeo-palaeontological sites; bone epiphyses are more likely to be destroyed during feeding or by other taphonomic agents. Secondly, diaphyses are denser than other elements, therefore punctures are less likely to occur, i.e. providing a clear morphology that can be quantified. Additional criteria for mark selection were based on the preservation and conditions of the marks and the bone. Inconspicuous marks or those where no clear morphology could be defined (overlapping or superficial traces) had to be excluded from the study.

The final sample consisted in 54 pits and 56 scores on *Large* sized animals, 52 pits and 60 scores on *Medium* sized animals, and 50 pits and 53 scores on *Small* sized animals.

### 3D modelling

Tooth marks were digitalised using the DAVID SLS-1 Structured-Light surface scanner located at the TIDOP Research Group of the Polytechnic School of Ávila (University of Salamanca, Spain). This equipment consists, namely, of a DAVID USB CMOS Monochrome

2-megapixel camera and an ACER K11 LED projector. Both the camera and the projector were connected to a portable ASUS X550VX personal laptop (8 GB RAM, Intel Core i5 6300HQ CPU (2.3 GHz), NVIDIA GTX 950 GPU) via USB and HDMI, respectively. The DAVID's Laser scanner Professional Edition software is stored in a portable USB Flash Drive, requiring no additional software and only the additional installation of the USB camera (ca. 1 min) in order to run.

Calibration is performed using a calibration marker board set at a scale in accordance with the object that is to be digitalised, in this case 15 mm (Maté-González et al. 2017). To obtain optimal resolution at such a small scale (ca. 0.016 mm), both the projector and the camera can be equipped with additional macro lenses. The size and type of lens varies according to the analyst's needs; for example, in this study a single 52 mm lens on the camera was sufficient in obtaining optimum resolution. Both the camera and the projector are then mounted on a tripod, oriented towards the calibration marker board at an angle between 15° and 25°. Once positioned the equipment are calibrated employing a V3 triangulation pattern which is projected across the marker board. After calibration is complete, neither the camera nor the projector can be moved; the marker board can now be replaced by the object to be digitalised.

The process of digitalising bone surface modifications consists in a projected structured-light pattern over the object's surface, using a Delaunay triangulation algorithm to calculate the external topography of the object under study. The scanning process takes ca. 1 min to create a final 3D model, producing a point cloud density of up to 1.2 million points. Once the point cloud is created, this is exported into external software for processing.

### Metric and geometric morphometric data collection

The process of extracting landmark data and measurements for geometric morphometric analyses were performed in multiple software. Firstly, 2D data derived from the 3D models of each tooth score's cross section were performed in the Global Mapper v.18 software. Cross-sections were obtained at mid-length, always between 30% and 70% of the mark (Maté-González et al. 2015;

Yravedra et al. 2017). 2D coordinate data and metric analyses extracted from these profiles were performed using the tpsDig2 (v.2.1.7) software (Rohlf 2017). Amira 5.0 was used in the case of 3D landmark data.

Two primary geometric morphometric landmark models were used for the purpose of this study (Figure 2). The first consists in a 2D 7-landmark model proposed by Yravedra et al. (2017) for analysis of carnivore tooth scores. This model was slightly adjusted to avoid noise produced by subjectivity or the analyst's experience. Adjustments included the conversion of landmarks 1, 4 and 7 into fixed landmarks while landmarks 2, 3, 5 and 6 were digitised using sliding semi-landmarks. The use of computational semi-landmarks is the most efficient and objective means of digitising curves, computing the position of each of the points so as to ensure they are equidistant from one another (Gunz et al. 2004). From these 7 landmarks, their coordinates can be used to extrapolate an additional 6 measurements of the profiles' dimensions, inspired by the methods originally described by Bello and Soligo (2008).

These measurements take into consideration multiple components of the cross-sections biometric morphology, including the width of the mark at varying intervals as well as its depth, opening angles and the slope of the edges. In accordance with the slight modification to the landmark model from which these measurements are derived, it is important to point out that original definition of variables Width of Incision at Mean (WIM: Yravedra et al. 2017) and Width of Incision at Base (WIB: Yravedra et al. 2017) have been modified. These variables have been updated under the names; Width of Incision Midway, and Width of Incision in proximity with the Base (preserving their original acronyms WIM & WIB). These modifications take into account how computed landmarks 2 and 6 no longer mark the precise middle of the wall. Likewise landmarks 3 and 5 no longer mark the lowermost 10% of the total depth, yet mark a computed mid-way point along each groove's wall in proximity with the base. Nevertheless, measurements Width of Incision at Surface (WIS), Depth (D), Left and Right Depth of incision at the Convergent (LDC & RDC) remain the same.

Considering previous observations on the weight of the variables originally suggested by Bello and Soligo (2008) (see Maté-González

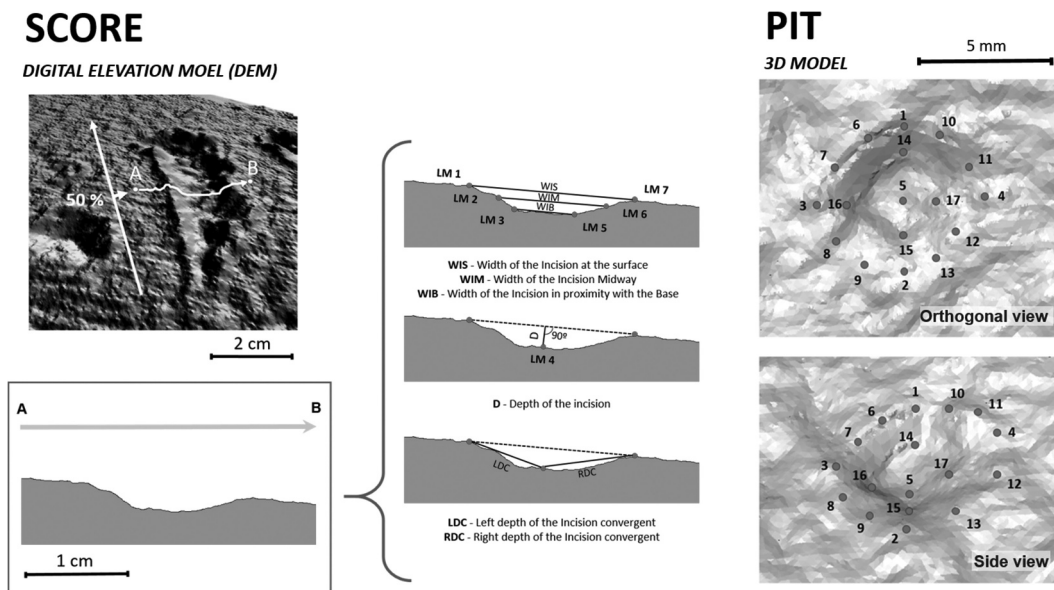


Figure 2. Location of measurements and landmarks used for both metric and geometric morphometric analyses, as proposed by Aramendi et al. (2017) and adapted from Yravedra et al. (2017). Figure by M.Á.M.G.

et al. 2017; Courtenay et al. 2018), it was decided that the variable Opening Angle (OA) would be excluded for this study.

Finally for the case of tooth pits, a 3D 17-landmark model was used as described by Aramendi et al. (2017, Figure 2).

Both measurements and geometric morphometric landmark data were then formatted and imported into the free software R (www.rproject.org) for further statistical analysis.

### Statistical and geometric morphometric analyses

Biometric data obtained from each tooth score profile were initially processed by Principal Component Analyses (PCA), assessing the differences in variation according to the weight of each variable through the use of bi-plots. Measurements were then subjected to univariate and multivariate statistical analyses to assess the significance in differences and similarities among sample distributions. Before this could be performed, Shapiro tests of normality were performed. Depending on these results, either an Analysis of Variance (ANOVA) or Fligner–Killeen test was performed for homogenous and inhomogenous distributions, respectively (Conover et al. 1981). Finally, a ‘two one-sided’ equivalence test (TOST) was carried out to assess the magnitude of differences according to Cohen’s *d* (Cohen 1988; Lakens 2017; Maté-González et al. 2019). TOST was preferred over more typical analyses of variance as a means of detecting the presence or absence of ‘meaningful effects’ among variables. Results from TOST are interpreted using  $p < 0.05$  as an indicator of significant similarities between samples.

In the case of geometric morphometric analyses, the first steps included an orthogonal tangent projection and full Procrustes fit of landmark data (Dryden and Mardia 1998). This is a common technique in morphological analyses for data preparation and standardisation. The procedure, commonly known as Generalised Procrustes Analysis (GPA), performs a series of superimposition procedures including translation, rotation and scaling. This can either be performed in shape space or form space (Oxnard 1986; Goodall 1991; Jungers et al. 1995), including or excluding the scaling part of the procedure, respectively. These superimposition techniques then allow for the exposure of morphological differences through patterns of variation and covariation that can be assessed statistically (Rohlf 1999; Slice 2001). To explore the influence scaling procedures have on shape and form, additional allometric regressions were performed to test for significance in shape-size relationships (Klingenberg 1996). For each of these tests, the logarithmic function of Centroid Size was used.

From the superimposed landmark data, PCAs can also be performed. In this case, PC scores can additionally be accompanied by visualisations of morphological variations that are calculated via transformation grids and Thin-Plate Splines (TPS) (Bookstein 1989). Finally, PC scores are extracted and processed with further statistical analyses. For the purpose of this study, the TOST test was used to assess the degree of overlapping among samples.

## Results

### 2D measurements

Distributions of different measurement values obtained from tooth score profiles show mostly inhomogeneous distributions with high degrees of variation on most accounts (Figure 3). univariate testing (Table 1) presents significant differences in distributions between groups *Large* vs *Small* as well as *Medium* vs *Small*. *Medium* and *Large* are mostly indistinguishable presenting the highest degree of variation in tooth-mark dimensions. In most cases, the *Small* group

can be seen to present the lowest degree of variation, usually presenting the smallest tooth score dimensions in general.

Further evaluation of univariate test results presents a tendency for the width of the marks (WIS, WIM, WIB) to be the most distinguishing factor between *Small* and *Large/Medium* samples (Table 1: chi-square and *p* Values), while the depth of the mark (D) appears to present the lowest degree of variation.

Multivariate approximations through PCA (Figure 4) confirm a greater within-group variation for both *Large* and *Medium* samples with *Small* occupying a more restricted portion of feature space (PC1 & PC2 cumulative proportion of variance = 99.93% from a total of 6 PC scores). Detailed analysis of variable weights additionally highlights the tendency for tooth marks on *Smaller* animals to be narrower and more superficial than those found on *Medium* and *Large* sized animals. Results considering effect size according to Cohen’s *d* (Table 2) additionally underline these significant differences.

### 2D geometric morphometrics

When analysing the distribution of samples in pure morphological shape space, analysis of tooth score shapes begin to present greater overlap among samples (Figure 5; PC1 & PC2 = 91.3% out of 14 PC scores). PCAs and transformation grids additionally display tendencies for all groups to occupy a portion of shape space represented by both superficial as well as deep grooves. The exclusion of scaling in GPA reveals similar patterns in form space (Figure 6; PC1 & PC2 = 98.9% out of 15 PC scores), with both shape and form presenting significant overlapping of samples. This is confirmed through TOST results displayed in Table 3. The only exception to this rule is seen in comparisons of groups *Large* and *Small* in shape space, with a deviation in effect size *p* values of 0.0047 from the null-hypothesis threshold (0.05) (Table 3). This is also confirmed through the graphical consultation of 95% confidence intervals with regards to upper ( $\Delta U$ ) and lower ( $\Delta L$ ) equivalence bounds during equivalence testing (Figure 7). Shape-size relationships studied through allometry prove significant when considering general morphological changes ( $F = 11.2$ ,  $p = 0.002$ ). Nevertheless, no significant shape-size relationship was detected conditioned by animal size ( $F = 2.6$ ,  $p = 0.06$ ).

### 3D geometric morphometrics

3D geometric morphometric data obtained from tooth pits generate PCA graphs that present a much higher degree of overlap in both shape (Figure 8) and form space (Figure 9). Transformation grids across PC1 and PC2 in both shape (Figure 8; cumulative proportion of variance = 32.4%) and form (Figure 9; 90.6%) mark a noticeable shift in the location of landmark 5 while the width of tooth pits is additionally greatly represented across multiple PC scores. Neither of these features, however, seem to be more representative of one particular group. Combined with the high number of dimensions produced by PCA results (total PC scores for Shape = 51; Form = 51), wolf tooth pits appear to present a very high degree of morphological variation and complexity.

Patterns presented through both PCA and TPS results reveal the *Large* sample to display a more contained distribution across shape and form space while *Medium* and *Small* present the greatest similarities. Overall patterns in PCA each feature space for all three groups are similar, with effect size *p* values showing no significant differences in any of the tests (Table 4, Figure 7). Nevertheless, greater similarities are observable in shape space than in form space, with *Large* vs *Medium* and *Medium* vs *Small* presenting almost significant deviances from the null-hypothesis in equivalency testing (Figure 7).

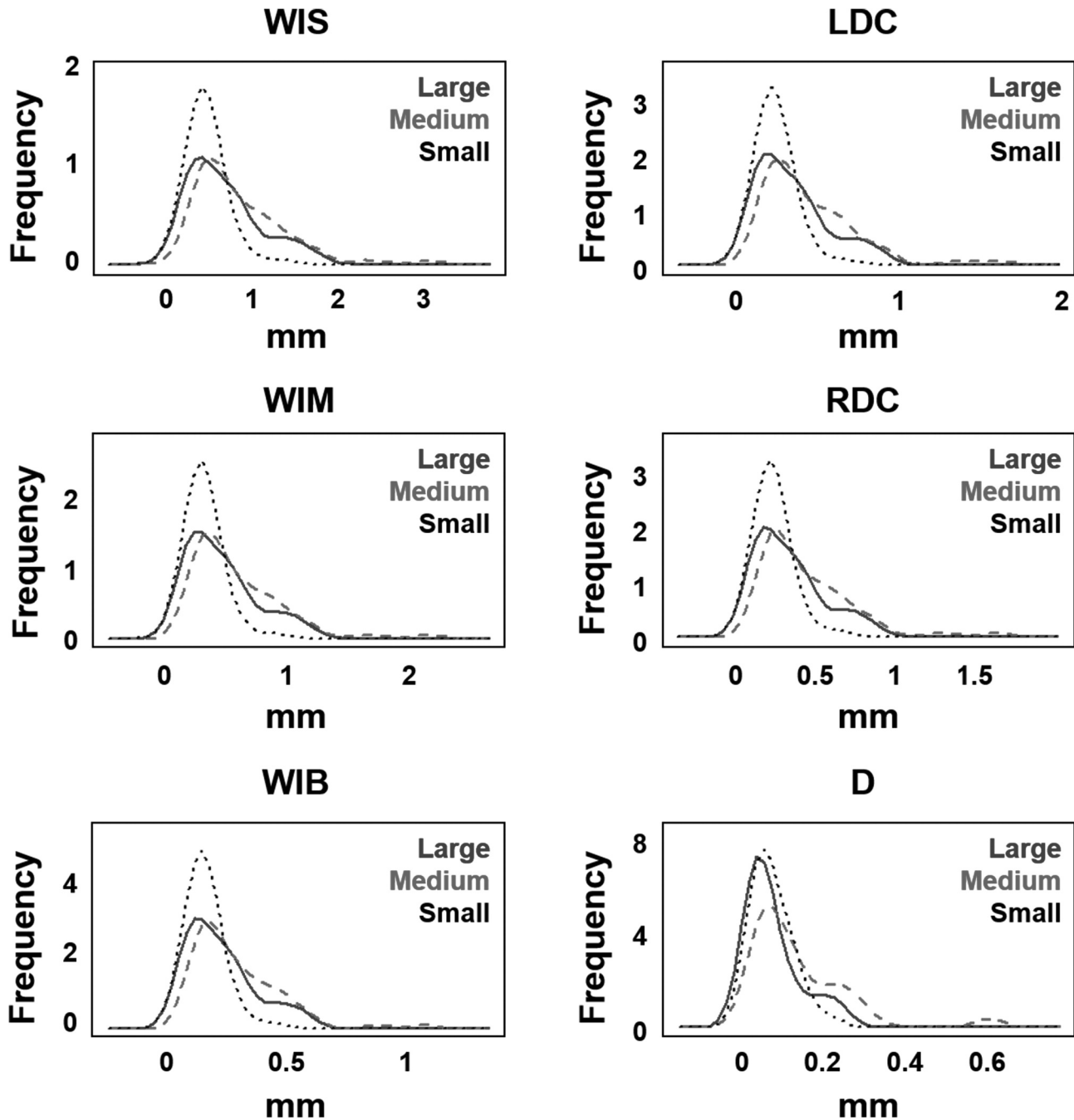


Figure 3. Distributions of tooth score profile measurements. Consult Figure 1 for definitions of measurement acronyms.

Table 1. Univariate Fligner-Killeen chi-squared and  $p$  values comparing tooth marks on different sized animals. Consult Figure 1 for definitions of measurement acronyms.

|     | Large vs Small |          | Large vs Medium |          | Medium vs Small |          |
|-----|----------------|----------|-----------------|----------|-----------------|----------|
|     | Chi            | $p$      | Chi             | $p$      | Chi             | $p$      |
| WIS | 21.53          | 3.48E-06 | 0.40            | 0.53     | 23.93           | 9.99E-07 |
| WIM | 22.66          | 1.93E-06 | 0.35            | 0.55     | 23.69           | 1.13E-06 |
| WIB | 20.76          | 5.21E-06 | 0.62            | 0.43     | 23.85           | 1.04E-06 |
| D   | 1.18           | 0.28     | 8.76            | 3.08E-03 | 15.84           | 6.90E-05 |
| RDC | 21.46          | 3.61E-06 | 0.82            | 0.36     | 24.70           | 6.71E-07 |
| LDC | 20.78          | 5.15E-06 | 0.92            | 0.34     | 24.42           | 7.75E-07 |

Finally, shape-size relationships prove insignificant on all accounts (General morphology:  $F = 1.6$ ,  $p = 0.084$ ; Influence by sample;  $F = 1.2$ ,  $p = 0.25$ ).

## Discussion

In a recent study, Maté-González et al. (2019) analysed the effects carcass size may have on the formation of anthropic butchery traces in archaeological sites. Said authors consequently attributed the lack of variation in cut mark morphology to variables such as cortical hardness (Öhman et al. 2012; Walden et al. 2017), arguing the tool used for butchery to be a greater conditioning factor than the type of bone being processed (Maté-González et al. 2019: see discussion). Considering the physical properties behind the formation of incisions of this type, such conclusions are logical (Potter 2005). The mechanics behind mastication, however, are much more complicated.

Bite force and the physical act of chewing are conditioned by cranial architecture (Smith and Savage 1959; Moore 1965; Radinsky

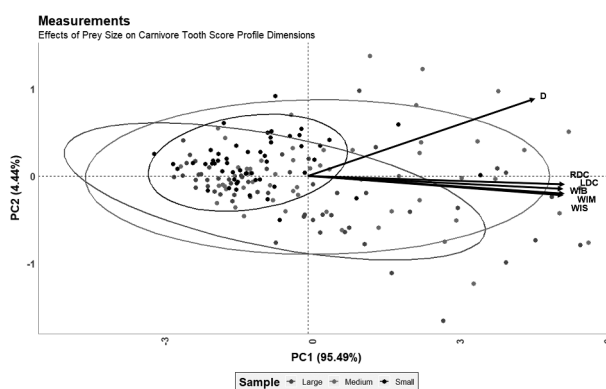


Figure 4. PCA scatter bi-plots with 95% confidence intervals analysing degree of variance in tooth score dimensions.

Table 2. Multivariate TOST effect size  $p$  and  $t$ -values for 2D biometric measurements of tooth score profiles.

|                 | $t$ value | $p$ value |
|-----------------|-----------|-----------|
| Large vs Small  | 1.497     | 0.069     |
| Large vs Medium | -2.266    | 0.0127    |
| Medium vs Small | 1.075     | 0.143     |

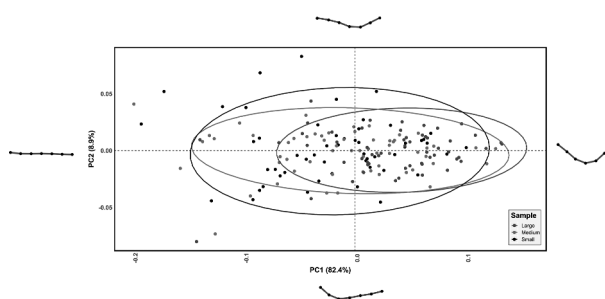


Figure 5. PCA scatter plots with 95% confidence intervals presenting variance in tooth score morphology in shape space. Morphological variance calculated through grid wrappings are presented at the extremity of each PC score.

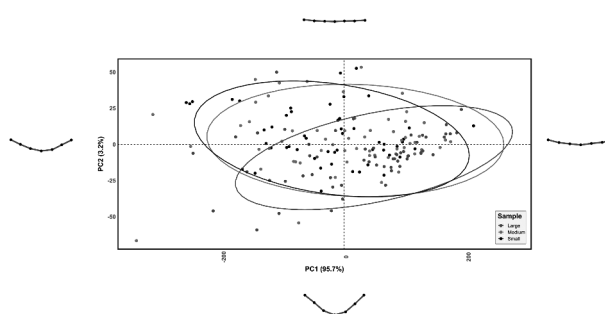


Figure 6. PCA scatter plots with 95% confidence intervals presenting variance in tooth score morphology in form space. Morphological variance calculated through grid wrappings are presented at the extremity of each PC score.

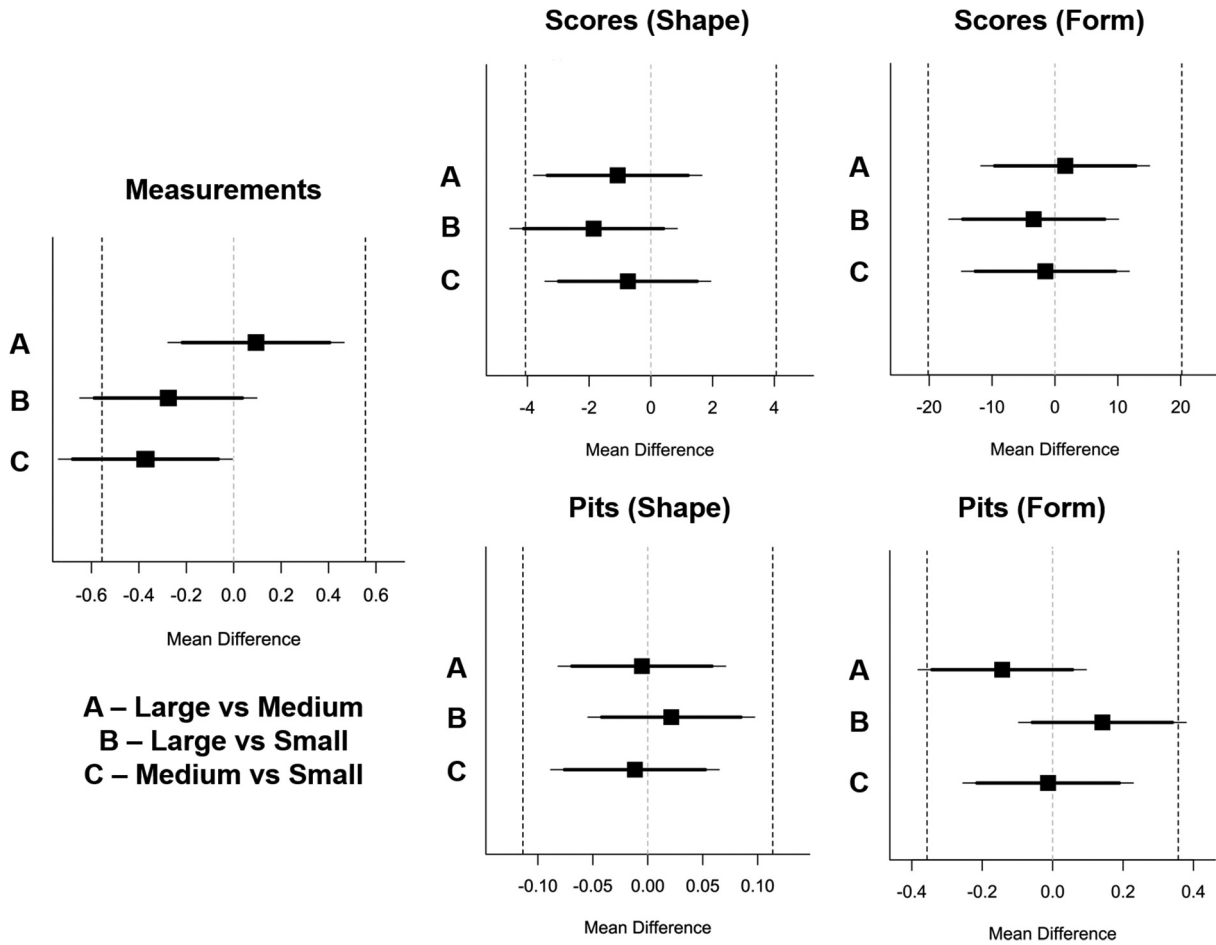
1981a, 1981b, 1982; Ferretti 2007), tooth morphology (Koenigswald and Clemens 1991, 1992; Hilson 2005; Ferretti 2007) and the functional demands of the muscles involved (Hoh 2002). Each of these factors in turn are largely dependent on lifestyle, diet, eating habits as well as genetic variables that condition carnivore evolution (Thompson 1952; Mech 1970; Gittleman 1985; Vézina 1985; Hoh 2002). While it is important to consider the effects of bite force and body mass on the determination of prey choice (Meers 2002),

inferring feeding patterns is different for pack hunters and scavengers. For these cases, conditioning factors are more likely to be dependent on the size of food rather than the force necessary to inflict mortal damage. For consumption of large prey, wolves have the distinct advantage of a pronounced muzzle allowing for a wider gape. Further consideration of the wolf's preference for using molars while chewing indicates a larger capacity for exerting greater forces (Greaves 1983, 1985, 1988, 2000; Van Valkenburgh and Ruff

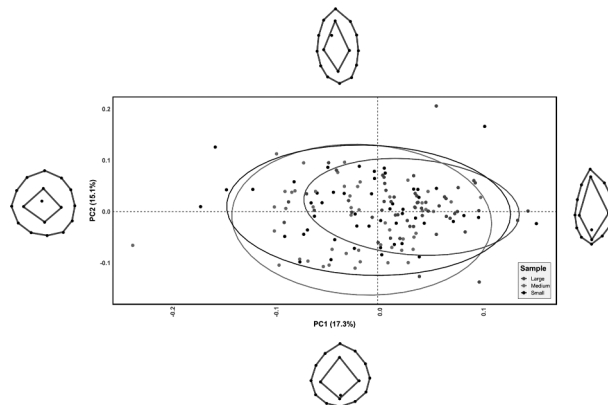


**Table 3.** Multivariate TOST effect size  $p$  and  $t$ -values for geometric morphometric analysis of tooth score morphology in both shape and form space.

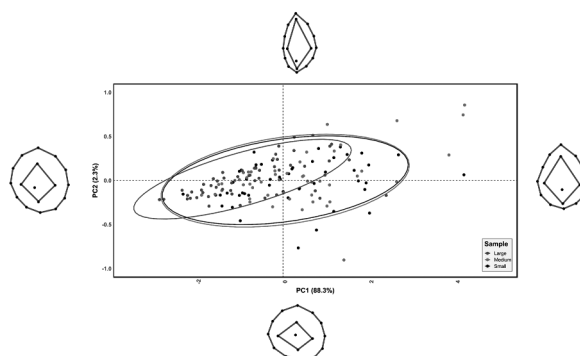
|       |                 | t value | $p$ value |
|-------|-----------------|---------|-----------|
| Shape | Large vs Small  | 1.614   | 0.0547    |
|       | Large vs Medium | 2.213   | 0.0145    |
|       | Medium vs Small | 2.491   | 0.00713   |
| Form  | Large vs Small  | 2.466   | 0.00763   |
|       | Large vs Medium | -2.74   | 0.00357   |
|       | Medium vs Small | 2.774   | 0.00329   |



**Figure 7.** Two one-sided equivalence test results according to Cohen's  $d$ . Graphs include mean differences (black squares), 90% confidence intervals (thick horizontal line), 95% confidence intervals (thin horizontal lines) and equivalence bounds  $\delta_L$  and  $\delta_U$  (leftmost and rightmost vertical dotted lines respectively) for each of the samples studied (A, B and C) using standard biometric data and geometric morphometrics in both shape and form space.



**Figure 8.** PCA scatter plots with 95% confidence intervals presenting variance in tooth pit morphology in shape space. Morphological variance calculated through grid warplings are presented at the extremity of each PC score.



**Figure 9.** PCA scatter plots with 95% confidence intervals presenting variance in tooth pit morphology in form space. Morphological variance calculated through grid wrappings are presented at the extremity of each PC score.

**Table 4.** Multivariate TOST effect size  $p$  and  $t$ -values for geometric morphometric analysis of tooth pit morphology in both shape and form space.

|       |                 | t value | $p$ value |
|-------|-----------------|---------|-----------|
| Shape | Large vs Small  | -2.413  | 0.00881   |
|       | Large vs Medium | 2.817   | 0.00291   |
|       | Medium vs Small | 2.639   | 0.00483   |
| Form  | Large vs Small  | -1.796  | 0.0378    |
|       | Large vs Medium | 1.776   | 0.0397    |
|       | Medium vs Small | 2.828   | 0.00296   |

1987; Thomason 1990; Clausen et al. 2008; Diedrich 2013). This possibly explains the wide variation in tooth-mark depth and overall morphologies that has been observed by multiple authors (Yravedra et al. 2011, 2017, 2018, 2019; Aramendi et al. 2017; Courtenay et al. 2019).

The complexity of the general mechanics behind mastication increase when considering the type of feeding activity occurring. The masticatory function behind production of furrowing marks is likely to be completely different to those involved behind the production of pits and scores. Erickson et al. (1996) calculate a significant positive correlation between peak penetration force and cortical thickness, however their study mostly considers elements of the axial skeleton and cannot be extrapolated to those marks frequently found on diaphyses shafts. While the thickness of bone cortical is a significant variable when considering the consumption of ovicaprids as opposed to equids, a stronger correlation between the overall size of the bone and the stress behind occlusion is likely present. Additional non-biomechanical variables such as the absorption of biting energy produced by flesh help underline the difficulties in fully modelling variations that could be produced in tooth-mark morphology during feeding. Finally, the general mechanics, strength and toughness of osteological materials are of great importance as well (Currey 1984, 2012; Weiner and Wagner 1998; Ritchie et al. 2009; Wang and Gupta 2011).

The present results highlight a mixture of differences and similarities among the tooth mark samples studied. The majority of results indicate the size of the tooth mark to be the greatest conditioning factor, indicated through insignificant similarities in equivalency testing in most measurements. Nevertheless, when dealing with pure morphology the effect animal size has on shape is seen to reduce considerably. In multiple cases *Large* and *Medium* are seen to group together, with *Small* usually observed as an outlier. Nevertheless, in some of these cases,  $p$  values only pass the threshold of  $p = 0.05$  by a small percentage on either side. This puts into question the degree to which a result should be considered reliable based on the  $p$  value

alone (GreavesGoodman 2019; Rougier 2019). A useful example can be seen when comparing similarities/differences between *Large* and *Small* score shapes, considering that  $p = 0.0547$  equates to a Bayes factor that still leaves an important margin of error for the acceptance of either hypothesis (Benjamin and Berger 2019). Likewise, while  $t$ -values still support stronger similarities between these samples for geometric morphometric data ( $t = 1.614$ ), over those obtained in metric studies ( $t = 1.497$ ), these differences may still be minute. In either case, geometric morphometric data still seems to hold greater reliability for carnivore tooth-mark studies.

Conclusions withdrawn from these results thus advise caution for future analyses. This is especially evident when considering the weight form and shape data have been observed to hold over the development of classification models for carnivore agencies (Courtenay et al. 2019). Through a comparison of results with previous studies (Aramendi et al. 2017; Yravedra et al. 2017, 2018, 2019; Arriaza et al. 2017, 2019a, 2019b; Courtenay et al. 2019), the morphological variance of different carnivore cuspids on a taxonomic level seems to statistically overrule the effects produced by carcass size. While predator and prey size are important variables to consider, more experimentation is needed to truly understand the weight other variables might have during mastication and jaw occlusion processes. These could include components of dental attrition or the age of individuals chewing (Binder and Van Valkenburgh 2000).

Similarly, possible inter-carnivore variations according to populations may be a concept worth studying. While the inclusion of two separate population samples presented limited differences in this study (Hosquillo vs Cabárceno), the inclusion of more samples produced by different wolf groups may be able to answer questions regarding this research question. Likewise, some authors could argue that the types of teeth involved in chewing (e.g. molars, premolars) could possibly create variations in tooth-mark morphology. As pointed out by Andrés et al. (2012, p. 216–217), however, we agree that this is unlikely. On average, molar and premolar cuspids are similar in shape, while teeth such as the incisors and canines are not commonly used in defleshing activities, especially in the case of canids (Van Valkenburgh and Ruff 1987). This is also supported by a stronger correlation between carnivore size over dentition (Domínguez-Rodrigo and Piqueras 2003; Saladie et al. 2012). A detailed and broader study of inter-species variations, however, would likely confront this question and solve any of these existing doubts, provided that each of the wolf populations cluster in morphological feature space regardless of their origin. Needless to say, we do predict variations in tooth-mark patterns according to the carnivore being studied, considering more

durophagous animals such as Hyaenids are a likely exception to the patterns observed in this paper.

In other studies, Arriaza et al. (2019a) noted significant similarities in leopard tooth marks on bovid and baboon skeletal elements (Multivariate Analysis MANOVA  $p = 0.12$  and  $0.55$ ). The ungulates used in said study fall into African sizes 1 and 2 ( $< 120$  kg; Bunn 1987; Bunn and Pickering 2010), and do not vary as much in size with most living baboons (*Papio sp.* = 6.3–45 kg, Kingdon 2015, p. 117–121; *Aepyceros melampus* = 38.5–63 kg, Fritz and Bourgarel 2013, p. 487; *Raphicerus campstris* = 7–16 kg, Kingdon 2015, p. 549–550). This additional data supports the homogeneity of tooth mark morphologies according to the size of the animal rather than the species (or in this case taxonomic order). Through comparisons of this type it is important to highlight that prey weight can be considered a slightly more significant conditioning variable, even if the effect size of this variable is mostly insignificant (Figure 7). Likewise, data obtained by Aramendi et al. (2017) argue morphological changes to occur on the internal structure of crocodile tooth marks when comparing marks found on sheep and cow bones ( $p$ -values  $\approx 0.002$ ). Nevertheless, the present study shows through a significantly larger sample size with an increase of statistical power by 0.26 (according to Cohen's  $D$  with an effect size of 0.8), the magnitude of depth and structure variations are still insignificant.

The data presented within this study serves as a valuable addition to the present experimental reference samples available for carnivore tooth-mark studies. Through different analyses, it can be seen how the recent inclusion of geometric morphometrics in the characterisation of microscopic osteological anomalies has opened up numerous possibilities for archaeological and palaeontological research (some include the aforementioned studies by Aramendi et al. 2017; Arriaza et al. 2017, 2019a, 2019b; Maté-González et al. 2017, 2019; Yravedra et al. 2017, 2018; Courtenay et al. 2018, 2019). The combination of 3D modelling with these advanced statistical approaches are reaching new resolutions with high degrees of precision that aid in differentiating between carnivore agencies responsible for the tooth marks observed. While the possibilities presented by these techniques for disciplines outside of archaeology/palaeontology are only beginning to become apparent, research objectives should continue this line of investigation by looking into how interdisciplinary approaches can benefit different fields of science. The data provided in this paper thus provide an interesting starting point for future experimental designs that can help ecological sciences of both a prehistoric, historic and contemporary nature.

## Conclusions

This paper presents an effort to expand the available experimental samples and current knowledge on the morphology of wolf tooth marks on small (ca. 10–100 kg), medium (ca. 100–350 kg) and large (ca. 350–800 kg) sized animals. The present data provides a valuable basis for compiling future experimental samples. Future considerations should thus include:

- Tooth marks on medium and large-sized animals present high degrees of equifinality
- Tooth marks on medium/large and small-sized animals present the largest magnitude of differences. These, however, are not always significant.
- Geometric morphometric data are the least effected by prize size as opposed to standard metric data.

These results may implicate careful planning involved when comparing experimental tooth samples with archaeological,

palaeontological or modern-day tooth marks found on animal carcasses. While an ideal situation would hope for similar results to those presented by Maté-González et al. (2019), the present study has been able to reveal the physical properties of tooth-mark formation to be much more complex than those of cut marks. Nevertheless, data of this type is highly useful for future experimental programmes in tooth-mark studies of both a palaeoecological and modern-day ecological nature.

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## Author contributions

L.A.C. Conceptualization, Methodology, Software, Validation, Formal Analysis, Investigation, Data Curation, Visualization, Writing – Original draft, review and editing. J.Y. Conceptualization, Methodology, Investigation, Project Administration, Resources, Supervision, Writing – Review and Editing. M.Á. M.G. Funding Acquisition. J.M.V.R. Resources. M.F.F. Funding Acquisition. D. G.A. Project Administration, Supervision, Funding Acquisition, Writing – Review and Editing. All authors have given final approval for publication.

## Data availability

All measurements and geometric morphometric landmark data have been included as supplementary files.

## Disclosure statement

We have no conflicts of interests to declare. All authors have read and approved the present study and take full responsibility for its content.

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