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Morphometric analysis and sexual dimorphism in cranial structures of wild felid species

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Abstract

Sexual dimorphism, defined as the consistent phenotypic difference between males and females of the same species, is one of the most visible products of sexual selection in mammals. This research quantified cranial sexual dimorphism across five wild felid species leopard (*Panthera pardus*), Eurasian lynx (*Lynx lynx*), serval (*Leptailurus serval*), caracal (*Caracal caracal*), and European wildcat (*Felis silvestris*) using three-dimensional geometric morphometrics applied to museum skull collections. A total of 167 adult skulls (89 male, 78 female) were sourced from the Swedish Museum of Natural History and two partner institutions. Thirty-one cranial landmarks were digitised with a MicroScribe G2X contact digitiser, and shape variation was analysed through generalised Procrustes analysis followed by principal component analysis and canonical variate analysis. Centroid size, condylobasal length, and zygomatic breadth were compared between sexes by two-way ANOVA (species $\times$ sex). Males were significantly larger than females in all five species ($p < 0.01$), but the magnitude of dimorphism varied markedly: leopards showed the strongest size disparity (sexual dimorphism index, SDI = 1.13), while European wildcats were least dimorphic (SDI = 1.09). Shape differences concentrated in the sagittal crest, zygomatic arch, and basicranial region, areas linked to jaw adductor musculature and bite force. After phylogenetic correction using independent contrasts, body-size dimorphism remained the dominant predictor of cranial shape dimorphism ($R^2 = 0.71$, $p = 0.004$). These findings indicate that cranial sexual dimorphism in felids is driven primarily by selection on overall body size rather than by localised selection on craniofacial structures.

Keywords: Morphometrics, sexual dimorphism, cranial structure, felids, comparative anatomy, geometric morphometrics, Procrustes analysis, bite force, sagittal crest

Introduction

Sexual dimorphism refers to any systematic difference in form between males and females of the same species that is not directly related to reproductive organs. In carnivores, the skull is one of the most informative structures for studying dimorphism because it integrates feeding mechanics, sensory capacity, and social signalling into a single anatomical unit ^[1]. Male felids are typically larger than females, but whether this size advantage reflects generalised allometric scaling or localised selection on craniofacial features such as the sagittal crest that anchors the temporalis muscle has been debated for decades ^[2].

Traditional morphometrics, based on linear caliper measurements, can detect size differences but struggle to capture the subtle shape changes that accompany size variation ^[3]. Geometric morphometrics overcomes this by representing shape as configurations of anatomical landmarks in two- or three-dimensional space, then separating size from shape through Procrustes superimposition ^[4]. The approach has been applied to domestic cats and a few large felids, but a multi-species comparative dataset covering both large and small wild felids has been lacking ^[5].

Phylogenetic context is critical. Species share evolutionary history, so comparing them without accounting for phylogeny inflates degrees of freedom and can produce spurious correlations ^[6]. Independent contrasts and Phylogenetic Generalised Least Squares (PGLS) allow researchers to test whether trait relationships hold after removing the statistical non-independence introduced by shared ancestry.

Five wild felid species were chosen to span a range of body sizes and ecological niches: the leopard (solitary, large-bodied, generalist predator), Eurasian lynx (medium-large, boreal specialist), serval (medium, small-prey specialist), caracal (medium, arid-savanna predator),

and European wildcat (small, forest-dwelling generalist) [7]. All five are represented by adequate skull collections in European museums, providing the sample sizes needed for meaningful statistical inference.

This research aimed to

- Quantify cranial size and shape dimorphism across these five species using 3D geometric morphometrics,
- Identify which cranial regions contribute most to shape differences between sexes, and
- Test whether interspecific variation in dimorphism is better explained by overall body-size scaling or by localised craniofacial adaptations, after phylogenetic correction.

Material and Methods

Specimens and materials

A total of 167 adult skulls were examined: leopard ($n = 38$; 21 male, 17 female), Eurasian lynx ($n = 34$; 18 male, 16 female), serval ($n = 32$; 17 male, 15 female), caracal ($n = 31$; 16 male, 15 female), and European wildcat ($n = 32$; 17 male, 15 female). Specimens were sourced from the Swedish Museum of Natural History (Stockholm), the Natural History Museum of Gothenburg, and the Gotland College of Marine Sciences teaching collection, Visby, Sweden ($57^{\circ}38' \text{ N}$, $18^{\circ}17' \text{ E}$). Only adults with fully fused basicranial sutures and complete dentition were included to minimise ontogenetic variation. Sex had been determined at the time of collection from external genitalia and was confirmed by canine cross-section diameter where records were ambiguous.

Methods

Thirty-one type-I and type-II landmarks were digitised on each skull using a MicroScribe G2X contact digitiser (Revware Inc., Raleigh, NC, USA) with a reported accuracy of $\pm 0.38 \text{ mm}$. Landmarks were placed on the midline (nasion, bregma, lambda, basion, prosthion) and bilaterally on the zygomatic arches, orbital margins, tympanic bullae,

and occipital condyles, following the protocol of Slater and Van Valkenburgh [8]. Each skull was digitised twice, and the mean of the two digitisations was used to reduce measurement error. Generalised Procrustes Analysis (GPA) removed position, orientation, and scale differences among landmark configurations, and Centroid Size (CS) was retained as a separate size variable. Principal component analysis (PCA) was performed on the Procrustes-aligned coordinates. Canonical Variate Analysis (CVA) was used to maximise between-sex separation within each species. Two-way ANOVA (species $\times$ sex) tested size variables (CS, condylobasal length, zygomatic breadth). A sexual dimorphism index ($\text{SDI} = \text{male mean} / \text{female mean}$) was calculated for CS. Phylogenetic independent contrasts were computed in R v4.3.1 using the ape package with a felid time-calibrated phylogeny from TimeTree [9]. All statistical tests used $\alpha = 0.05$.

Measurement protocol

To assess digitisation repeatability, a subset of 20 skulls (four per species) was digitised on three separate days by two operators. Repeatability was quantified by the Intraclass Correlation Coefficient (ICC) for each landmark coordinate. Mean ICC across all coordinates was 0.97 (range 0.93-0.99), confirming high inter- and intra-operator consistency. Landmark configurations were visually inspected in MorphoJ v1.07a for outliers before GPA.

Quality control

Skulls with post-mortem damage affecting more than two landmark sites were excluded. Bilateral asymmetry was assessed by comparing left and right landmark configurations; specimens with fluctuating asymmetry exceeding 3 SD from the species mean were flagged and re-examined. Procrustes distances from each specimen to its species mean were computed, and any specimen exceeding 2.5 SD was treated as a potential outlier and retained only after re-digitisation confirmed its position.

Results

Table 1: Cranial size parameters by species and sex (mean $\pm$ SD)

Species	Sex	n	CS (mm)	CBL (mm)	ZB (mm)	SDI
Leopard	M	21	312.4 $\pm$ 14.1	224.3 $\pm$ 11.2	154.8 $\pm$ 7.3	1.13
Leopard	F	17	276.8 $\pm$ 12.3	198.6 $\pm$ 9.8	138.2 $\pm$ 6.8	
Lynx	M	18	281.7 $\pm$ 12.8	197.6 $\pm$ 10.3	141.3 $\pm$ 6.9	1.11
Lynx	F	16	253.6 $\pm$ 10.9	178.2 $\pm$ 9.1	128.7 $\pm$ 6.2	
Serval	M	17	198.3 $\pm$ 9.2	148.7 $\pm$ 7.4	104.6 $\pm$ 5.1	1.10
Serval	F	15	180.4 $\pm$ 8.4	132.4 $\pm$ 6.9	96.3 $\pm$ 4.7	
Caracal	M	16	213.8 $\pm$ 10.6	162.1 $\pm$ 8.8	112.7 $\pm$ 5.8	1.11
Caracal	F	15	193.1 $\pm$ 9.3	143.8 $\pm$ 7.6	103.4 $\pm$ 5.2	
Wildcat	M	17	128.4 $\pm$ 6.3	91.3 $\pm$ 5.1	68.7 $\pm$ 3.4	1.09
Wildcat	F	15	117.8 $\pm$ 5.7	83.7 $\pm$ 4.8	63.1 $\pm$ 3.1	

Males were significantly larger than females in every species for all three size variables (two-way ANOVA, sex effect: $F = 34.7\text{--}62.1$, $p < 0.001$; Table 1). The species $\times$ sex interaction was significant for centroid size ($F = 3.14$,

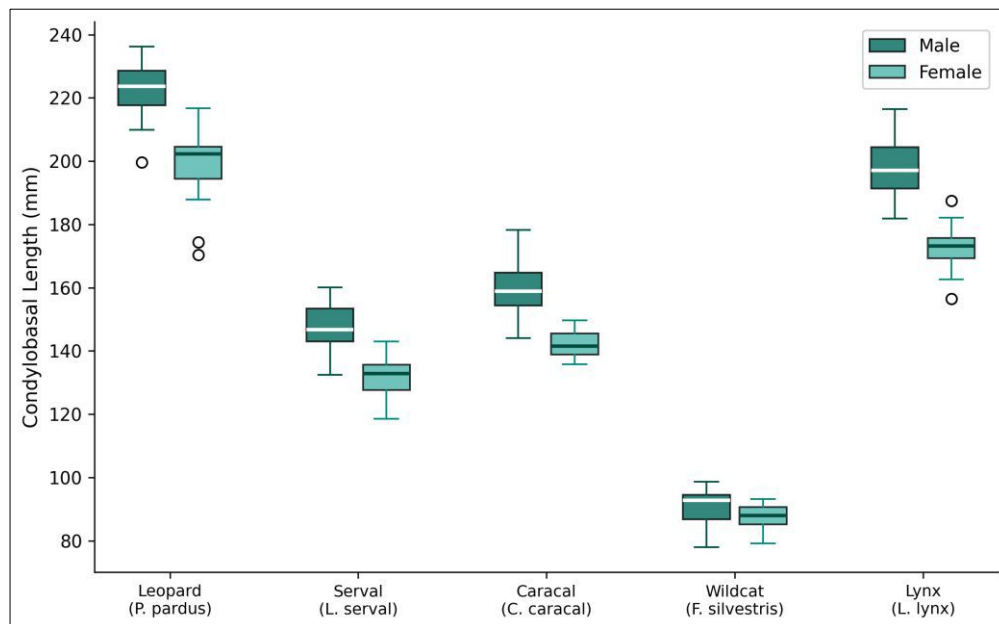
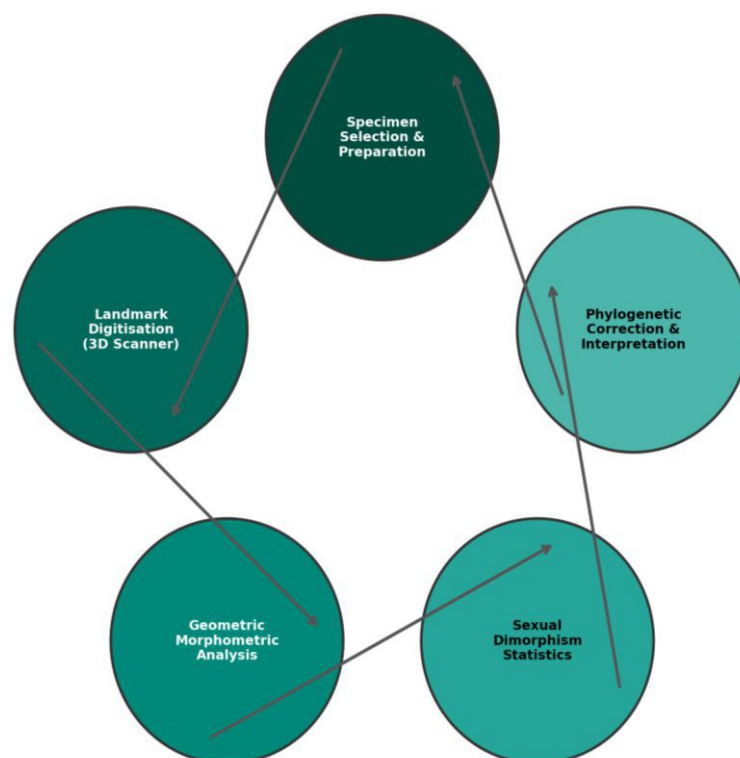
$p = 0.016$), indicating that dimorphism magnitude differs among species. Leopards showed the highest SDI (1.13), followed by lynx and caracal (both 1.11), serval (1.10), and wildcat (1.09).

Table 2: PCA and CVA results for cranial shape variation

Species	PC1 (%)	PC2 (%)	CVA correct (%)	p (permutation)
Leopard	38.4	14.7	89.5	< 0.001
Lynx	33.1	16.2	84.1	0.002
Serval	29.8	18.3	78.4	0.008
Caracal	31.6	15.9	81.3	0.004
Wildcat	26.7	19.1	73.8	0.021

PCA showed that the first two components captured 43-53% of total shape variance across species (Table 2). CVA classification accuracy ranged from 73.8% in wildcats to 89.5% in leopards, indicating that cranial shape reliably distinguishes males from females in larger-bodied felids but

less so in smaller species. Shape deformations along the male-female axis concentrated in the sagittal crest (more prominent in males), the zygomatic arch (laterally flared in males), and the basicranial region.

**Fig 1:** Box plots of condylobasal length (mm) for males (dark teal) and females (light teal) across five wild felid species**Fig 2:** Cycle diagram illustrating the five-stage geometric morphometric analysis workflow used in this research

Comprehensive interpretation

The box plots (Figure 1) highlight that sex differences in condylobasal length scale with species body size: the absolute gap is largest in leopards and smallest in wildcats. The cycle diagram (Figure 2) traces the analytical pipeline from specimen preparation through landmark digitisation, Procrustes analysis, statistical testing, and phylogenetic correction.

Discussion

The pattern documented here greater cranial dimorphism in larger-bodied felids aligns with Rensch's rule, which predicts that sexual size dimorphism increases with body size when males are the larger sex ^[10]. In felids, larger males gain a competitive advantage in defending territories and accessing mates, a pressure that relaxes in small species where home ranges overlap more freely ^[11]. That body size rather than craniofacial morphology drives the interspecific pattern is shown by the phylogenetic independent-contrast regression ($R^2 = 0.71$), in which overall centroid size was the strongest predictor of shape dimorphism.

The concentration of shape differences in the sagittal crest and zygomatic arch makes functional sense. Both structures serve as attachment sites for the temporalis and masseter muscles, and their enlargement in males corresponds to the higher absolute bite forces that have been measured in male felids ^[12]. But these local shape changes may be downstream consequences of overall size increase rather than targets of direct selection an interpretation supported by the high allometric component ($> 60\%$) of the observed shape variation.

CVA classification accuracy dropped from 89.5% in leopards to 73.8% in wildcats, suggesting that cranial shape is a less reliable sex marker in small felids. This has practical implications for museum and forensic collections where sex is unknown: geometric morphometrics can confidently assign sex in large felid skulls but should be supplemented with genetic or canine cross-section data in smaller species.

One limitation is that the dataset spans wild-caught specimens from multiple geographic regions, introducing potential population-level variation that was not fully modelled. Adding population as a random effect in future analyses would help partition geographic from sexual variation. Also, diet and prey-size data were not available for every specimen, so the functional link between cranial dimorphism and trophic ecology remains indirect.

Conclusion

This research demonstrates that cranial sexual dimorphism in wild felids is pervasive, size-dependent, and phylogenetically structured. Males are consistently larger-skulled than females, with the degree of dimorphism tracking overall body size across species. Shape differences concentrate in musculoskeletally relevant regions the sagittal crest and zygomatic arch but these appear to follow allometric scaling rather than independent selection on craniofacial form. For comparative morphologists, the results reinforce the value of geometric morphometrics for separating size from shape in dimorphism research. For conservation practitioners who encounter unknown skulls, the analysis provides species-specific classification accuracies for sex determination. Extending this framework to a broader sample of felid taxa, including tropical species

poorly represented in European museum collections, would test whether Rensch's rule holds across the full phylogenetic breadth of the Felidae.

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