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RESEARCH

On the importance of body-size proxies when scaling sexual dimorphism: A case study in Mustelidae

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Abstract
Sexual dimorphism in a focal trait can arise from sex-specific selection acting directly on this trait. Alternatively, it may result from sex-specific selection acting on body size, to which the focal trait is genetically correlated. Quantifying the allometric relationship between trait size and body size is therefore essential for distinguishing between these different causes of sexual dimorphism. However, body size is often estimated by proxy measurements, and the choice of these proxies can influence the results of the analysis. We illustrate these issues by estimating sexual dimorphism in three craniodental traits in four mustelid species, the Eurasian otter, the European badger, the beech marten and the stoat. Depending on the trait, 16% to 100% of intersexual differences in trait size can be attributed to the allometric effects of body size dimorphism. This suggests that a large part of the sexual dimorphism in the focal traits is often caused by sex-specific selection on body size. For canine size, however, we find a consistent sexual dimorphism independent of body size, suggesting that this trait is under sexual selection. Using two different body size proxies produces estimates of size-independent sexual dimorphism that differ by up to 69%. We discuss the criteria for choosing body-size proxies in such analyses.

Keywords Allometry · ANCOVA · Mean-centring · PCA

Introduction

Sexual dimorphism, the phenotypic differences between the sexes, is widespread among animals and plants (Short and Baladan 1994; Barrett and Hough 2013). It is typically thought to result from differences in selection pressures between the sexes, generated either by sex-specific interactions with the environment or by sexual selection resulting from interactions within and between the sexes (Slatkin 1984; Shine 1989; Andersson 1994). In mammals, the higher variance in male reproductive success often leads to stronger selection on traits that increase male mating success, such as ornaments or weapons (Andersson 1994). Consequently, morphological traits that influence male-male interactions, such as horns, antlers or canines, or traits that influence female mating preferences, such as ornaments and courtship behaviour, are expected to be more pronounced in males than in females, or to be present only in males (Berglund et al. 1996; Hill and Yasukawa 2014).

However, sexual dimorphism in a trait does not necessarily result from selection acting on that particular trait. It may instead result from a correlated response to sex-specific selection acting on genetically correlated traits (Lande 1979). For example, if a trait is correlated with overall body size, the sexual dimorphism observed in this trait may result from direct selection on it, but it may as well result from sex-specific selection on body size with a correlated response in the trait. The sexual dimorphism in canine teeth, widely observed in many primates (Plavcan 2001) and carnivores (Gittleman and Van Valkenburgh 1997), may represent an instance of correlated evolution between a specific trait and overall body size. This is supported by the fact that teeth, and particularly canines, often scale allometrically with body size both within and across mammalian species (Christiansen 2008; Plavcan and Ruff 2008). Consequently, between-sex differences in canine size in these species may largely reflect underlying body size variation and the

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associated correlated response of dental traits. Nonetheless, sexual dimorphism may also result from a combination of selection acting directly on the trait itself as well as selection acting on overall body size (Leutenegger and Kelly 1977). Identifying the drivers of sexual dimorphism in a particular trait therefore requires separating the component of dimorphism that covaries with sexual dimorphism in body size from the component that is independent of body size.

Such a distinction can be achieved by analysing the allometric relationship between trait size and body size in both sexes (Fig. 1). The total sexual dimorphism SD_T in a trait Y, can be measured as the proportional size difference between the sexes: $SD_T = ln(\overline{Y}_{male}) - ln\left(\overline{Y}_{female}\right)$, where $\overline{Y}$ is the mean trait size for males or females, and *ln* is the natural logarithm (see Smith 1999 for a justification of this measure of sexual dimorphism). In the absence of allometric relationship between Y and the body size X (Fig. 1a), SD_T is expected to result solely from between-sex differences in the selection directly acting on the trait. The trait Y may instead exhibit an allometric relationship with body size X that can be expressed as: $ln\,(Y) = \alpha + \beta\, ln\,(X)$, where β and α are the allometric slope and intercept, respectively (Pélabon et al. 2014). In this case, the total sexual dimorphism in the trait, SD_T, may be entirely

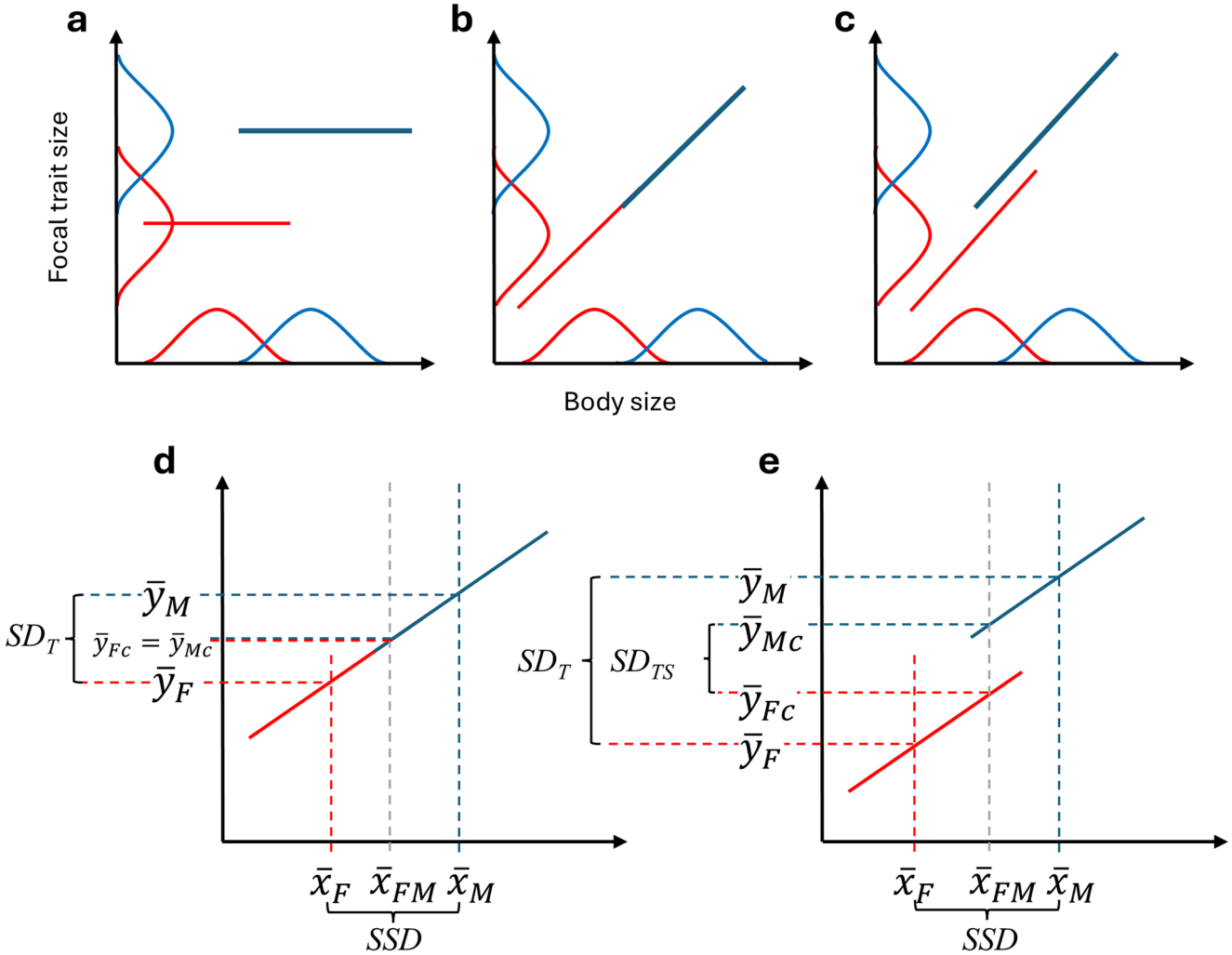

Fig. 1 Expected effect of an allometric relationship between a focal trait (y axis) and body size (x axis) on the measurement of sexual dimorphism. **a–c**. Different scenarios for the effect of allometry on sexual dimorphism. In **a**, there is no allometric relationship between the trait and body size and the sexual dimorphism in the trait is most likely due to sex-specific selection directly acting on the trait. In **b**, there is an allometric relationship between the trait and body size and the sexual dimorphism in the trait can be entirely explained by the sexual dimorphism in body size and the correlated effect on the trait. This may indicate that sexual dimorphism in the trait is generated by sex-specific selection on body size. In **c**, sexual dimorphism in the trait is a combination of the correlated effect of the sexual dimorphism in body size and a size-independent component of sexual dimorphism. In **d** and **e**, we show how the total sexual dimorphism in the trait corresponds to a single allometric component (in **d**) or two additive components, an allometric (size-dependent) and non-allometric (size-independent, noted SD_{TS}) sexual dimorphism (in **e**). We consider here a species with male biased sexual dimorphism with the red and blue lines representing the allometric relationship for females and males, respectively

explained by the sexual dimorphism in body size (Fig. 1b). Sexual dimorphism in the trait SD_T is then allometrically related to the sexual dimorphism in body size (SSD) such that: $SD_T = \beta \times SSD$ (Fig. 1d). Such a pattern may result from sex-specific selection acting on body size with a correlated response in the trait, from sex-specific selection acting on the trait with a correlated response in body size, or from sex-specific selection acting similarly on the trait and body size. Given the central importance of body size in mammals (Peters 1986; Sibly and Brown 2007), the widespread occurrence of sexual size dimorphism (Ralls 1977; Loison et al. 1999; Lindenfors et al. 2007), and the many mechanisms proposed to generate divergent selection on male and female body size in mammals in general (Weckerly 1998; Isaac 2005) and in mustelids in particular (Erlinge 1979; Moors 1980), we consider the first scenario to be the most likely. We note, however, that distinguishing between these different scenarios in natural populations may be particularly difficult. Nevertheless, in most cases corresponding to the scenario described by Fig. 1b, it may not be necessary to invoke sex-specific selection on the trait itself to explain the evolution of its sexual dimorphism.

Alternatively, sexual dimorphism may result from a combination of sex-specific selection on both body size and trait size (Fig. 1c). In this case, sexual dimorphism in the trait would have two components, an allometric component (i.e. body-size dependent) generated by the correlated response to sex-specific selection on body size, and a non-allometric component (i.e. body-size independent) generated by the sex-specific selection on the trait itself. These components are additive: $SD_T = \beta \times SSD + SD_{TS}$, where SD_{TS} denotes the trait-specific component of the sexual dimorphism resulting from the trait-specific selection (Fig. 1e). These two components can be estimated statistically using an analysis of covariance (ANCOVA). In the Discussion, we outline how this approach differs conceptually from principal component analyses (PCAs) routinely applied to quantify trait sexual dimorphism while controlling for sexual size dimorphism.

While this statistical analysis is straightforward, it assumes that we have a reliable measure of body size. This may prove problematic in many cases. Although body size can be estimated from lean body mass, this measure is often difficult to estimate in living organisms because it can vary significantly between seasons or over shorter timescales (e.g., Lovegrove 2005; Szafrańska et al. 2013). Fresh specimens can also be difficult to obtain, or even impossible for extinct species. Therefore, skeletal measures are widely employed to estimate body size. However, these measures also have limitations, because overall body size is often estimated using single skeletal elements as proxies. Because different elements may have different scaling relationships with body size, discrepancies may result among body size estimates inferred from different skeletal or dental elements (e.g., Jungers 1990; Ruff and Niskanen 2018). In mammals, various craniodental measurements such as condylobasal length, basicranial axis length, and occipital condyle width are traditionally used as proxies for overall body size. Unlike postcranial skeletal elements, crania are often easier to identify at the species level and are more readily available. While the variation in body-size estimation introduced by different proxies may be negligible for interspecific comparisons, it can significantly impact within-species analyses such as estimating allometric relationships, and consequently the distinction between the allometric and the non-allometric components of sexual dimorphism.

To illustrate these different issues, we study sexual dimorphism in three craniodental traits (upper canine diameter, occiput surface area, and temporalis surface area) in four species of Mustelidae, a family in which sexual dimorphism has been studied extensively (e.g., Wiig 1986; Dayan et al. 1989; Dayan and Simberloff 1994; Johnson and Macdonald 2001; Abramov and Puzachenko 2005). In each species, we estimate the two components of the sexual dimorphism for each trait using two different body-size proxies and then compare the results. In addition to demonstrating the importance of the body-size proxy in estimating the allometric and non-allometric components of the sexual dimorphism in each trait, we also show that estimating the non-allometric component of sexual dimorphism reveals specific patterns of selection that have been previously overlooked.

Methods

Study species

Sexual dimorphism of craniodental traits was quantified in four mustelid species, the European badger *Meles meles*, the Eurasian otter *Lutra lutra*, the beech (or stone) marten *Martes foina*, and the stoat *Mustela erminea*. These species were selected to represent a broad range of lifestyles within the Mustelidae, including subterranean (badger), aquatic (otter), terrestrial (stoat) and arboreal (beech marten) lifestyle. They also display different social structures, from being territorial and mostly solitary for the otter (Kruuk and Moorhouse 1991; but see Quaglietta et al. 2014 and Lodé et al. 2021), the beech marten (Genovesi et al. 1997) and the stoat (Sandell 1986), to living in groups for the badger (although badgers have also been found to live solitarily or in pairs, Dugdale et al. 2007). These different social structures could also lead to different levels of sexual size dimorphism. For example, in group-living species such as the badger, where males have easy access to females, the mating system characterized by

polygynandry (Dugdale et al. 2007) may limit male-male competition. Accordingly, badgers should exhibit less sexual dimorphism in traits involved in male-male competition such as the upper canine (Noonan et al. 2016). Differences in diet could also affect sexual size dimorphism. For example, the niche partitioning hypothesis posits that sexual size dimorphism may evolve to avoid competition between the sexes during periods of food scarcity (e.g., Slatkin 1984; Johnson and Macdonald 2001; Thom et al. 2004). Among the species examined, the beech marten exhibits a broad and opportunistic diet (Papakosta et al. 2014), whereas the otter specializes on fish (Carss 1995). In both cases, these diets constitute relatively stable food resources. In contrast, the badger feeds on insects (Cleary et al. 2009), and the stoat is a specialist that feeds on birds, insects and mice (Powell and King 1997). Because periods of food scarcity are more likely for these latter feeding regimes, sexual size dimorphism may evolve in badger and stoat as a result of niche partitioning.

Measurements

Skulls were obtained from the dry specimen collections of the Naturalis Biodiversity Center and the Natuurhistorisch Museum Rotterdam (Online Resource 1: Table S1). Digital photographs were taken of 50 individuals per species, 25 of each sex, except for *L. lutra*, for which only 15 males and 16 females were available. These sample sizes are limited, but we preferred to measure individuals from a restricted area (all specimens have been collected in the Netherlands) rather than pooling individuals from geographically distant populations that may display different sizes or degrees of sexual dimorphism (e.g., Dayan and Simberloff 1994). When more than 25 individuals of each sex were available, skulls were randomly selected. Only complete skulls from adult individuals were included in the analysis. The collection tag indicated the sex and whether the individual was adult or not. We discarded one *M. foina* individual suspected to be a juvenile due to the presence of unfused cranial sutures observed during the analysis of the photographs. For two individuals (one female badger, one female stoat), not all traits could be measured, and these individuals were excluded from the analysis of the sexual dimorphism (Online Resource 1: Table S1).

Table 1 Definitions and abbreviations of the cranial and dental characters of Mustelidae skulls measured

Abbreviation	Measurement name	Definition
CAN	Upper canine diameter	Distance from the most anterior to the most posterior part of the canine, from a lateral perspective, at the base where the tooth meets the maxilla.
CBL	Condylobasal length	Distance from the most posterior part of occipital condyles to the most anterior part of the premaxilla on the skull.
OCC	Surface area of the occiput	Surface area of attachment of the neck muscles. Pink area in Fig. 2.
OCW	Occipital condyle width	Distance between the most distal ends of the lateral parts of the occipital condyles.
TEM	Surface area of lateral cranium	Part of the lateral cranium to which the temporalis muscle attaches. This includes the temporal and parietal bone, and part of the frontal bone. Blue area in Fig. 2.

Each specimen was photographed from a lateral (left or right, depending on skull damage) and a caudal view. The skulls were stabilised using kneadable rubber. To avoid scale distortion, a ruler was placed in the centre of each photograph. We used ImageJ (Schneider et al. 2012) to measure five different traits: condylobasal length (CBL), occipital condyle width (OCW), canine diameter (CAN), occiput surface area (OCC), and temporalis surface area (TEM, see Table 1; Fig. 2). Areas were measured using the Freehand Selection tool in ImageJ. To quantify measurement error, the whole measurement procedure was repeated on ten skulls of each species. Two photographs were taken and measured by two different observers (XB and GVDV). All data are available in the supplementary file (Online Resource 2).

We used condylobasal length (CBL) and occipital condyle width (OCW) as proxies for body size. CBL measures skull length by taking the distance between the most caudal part of the occipital condyles to the most rostral point of the incisive bone. It is a simple and commonly used proxy for body size that can be measured precisely (see Results). It is used to estimate body mass in a wide range of mammals (Van Valkenburgh 1990). Occipital condyle width (OCW) is an indirect measure of the size of the foramen magnum, through which neurons exit the brain. Because the number of neurons per unit mass of postcranial body tissue is relatively constant among mammals (Radinsky 1967), Engelman (2022) suggests that the size of the foramen magnum, and therefore OCW, is closely correlated with body mass. Accordingly, OCW is a good predictor of body mass among mammalian species (Engelman 2022).

Statistical analyses

All analyses were performed using R (version 4.4.2; R Core Team, 2024). For each trait in each species, measurement variance was estimated using a mixed-effects model

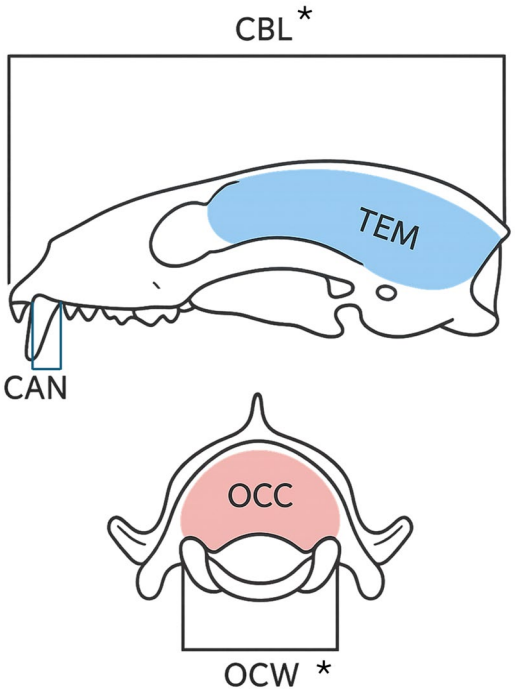

Fig. 2 Representation of the cranial and dental characters measured on the skull of males and females in four species of mustelids. The two traits identified with * are the body-size proxies. Abbreviations: **CAN**, upper canine diameter; **CBL**, condylobasal length; **OCC**, surface area of the occiput; **OCW**, occipital condyle width; **TEM**, surface area of lateral cranium (see Table 1 for descriptions)

in the LME4 package (Bates et al. 2015). All models were run on natural ln-transformed data (same scale as the analysis of sexual dimorphism) and fitted with only an intercept and individual identity as a random factor to estimate the amount of within (residual) and among-individual variance. Measurement error is presented as the percentage of the total variance due to measurement variance: ME = 100 × *var within*/ (*var within* + *var among*), where *var within* and *var among* designate the components of the total variance due to within- and among-individual variation (Table 2).

For all traits including the two body-size proxies, CBL and OCW, we first estimated the total sexual dimorphism (i.e. not corrected for the allometric relationship with body size), as: $ln(\overline{Y}_{male}) - ln\left(\overline{Y}_{female}\right)$ where $\overline{Y}$ denotes the mean trait value. We obtained these measures and their standard error from linear models on ln-transformed data with sex as the predictor variable.

To estimate the non-allometric component of the sexual dimorphism (SD_{TS} in Fig. 1), we analysed the allometric relationship between each focal trait and the two body-size proxies using ANCOVAs on ln-transformed data (see Pélabon et al. 2018 for a justification of using a ln-ln scale to estimate allometric relationships). In these models, the focal trait was the response variable (CAN, TEM, or OCC), and CBL or OCW, sex, and their interactions were the predictor

Table 2 Components of the variance (including ind, among-individual and res, residual/measurement) and percent measurement error (ME%). Abbreviations: **CBL**, condylobasal length; **OCW**, occipital condyle width; **CAN**, upper canine diameter; **TEM**, surface area of lateral cranium; **OCC**, surface area of the occiput

	CBL			OCW			CAN			TEM			OCC		
	ind*	res*	ME%	ind*	res*	ME%	ind*	res*	ME%	ind	res	ME%	ind	res	ME%
L. lutra	6824.14	5.99	0.09	687.35	0.78	0.11	29.41	0.23	0.77	32724.72	1047.43	3.1	11996.73	339.63	2.75
Me. meles	4104.89	22.70	0.55	192.13	4.23	2.16	21.63	2.69	11.06	57903.59	9366.07	13.92	3556.94	96.05	2.63
Ma. foina	1750.26	3.88	0.22	86.27	0.21	0.24	18.34	0.57	3	1629.79	711.24	30.38	747.89	58.91	7.3
Mu. erminea	431.72	1.10	0.25	21.23	0.17	0.81	4.05	0.26	5.94	991.67	64.86	6.14	108.08	4.75	4.21

*Variance estimates ×100

variables. The covariate, CBL or OCW, was centred on the species mean after ln-transformation. By doing so, the intercepts of the ANCOVA model (one for each sex) represent the expected trait value on a ln-scale for a male and a female sharing the same body size, set to the population mean ($\bar{x}_{FM}$ in Fig. 1e). Consequently, the difference between the two intercepts, expressed as the contrast between sexes in the model, represents an estimation of the body-size-corrected sexual dimorphism, that is, the non-allometric component of the sexual dimorphism (SD_{TS} in Fig. 1e). Note that most statistical programs provide the standard error of the contrasts, which therefore corresponds to the standard error of the non-allometric component of the sexual dimorphism (the R script for this analysis is provided in Online Resource 3). By directly estimating the sexual dimorphism and its standard error from the model, this approach appropriately incorporates the uncertainty of the model parameters into the estimation (Garcia-Berthou 2001). The difference between the total and the size-corrected sexual dimorphism represents the allometric component of the sexual dimorphism, that is, the part that is generated by the correlation between the trait size and body size. Because both trait size and body size proxy are ln-transformed, these different measures of sexual dimorphism multiplied by 100 can be interpreted as percent differences in size between the sexes. Estimates of the sexual dimorphism are considered statistically different from zero when their 95% confidence intervals ($\pm 1.96 \times$ SE) do not overlap zero.

Fitting a model with an interaction between the two predictor variables ($Y = \beta_1$ Body size $+ \beta_2$ Sex $+ \beta_3$ Body size $\times$ Sex), allows estimating between-sex differences in the allometric relationship between the trait size and body size (i.e. different allometric slopes between sexes represented by the parameter β_3 in the model). If the allometric relationship differs between sexes, and the two sexes have different average body sizes, including this interaction will affect the estimation of the non-allometric sexual dimorphism. We provide estimates of the non-allometric sexual dimorphism obtained from models fitted with and without interaction between the predictor variables, that is, with different or similar allometric slopes in the two sexes, respectively.

Results

Measurement error

For both body-size proxies, the measurement error ME is low, ranging among species between 0.09 and 0.55% of the total variance for condylobasal length, and between 0.11 and 2.16% for occipital condyle width (Table 2). Considering the limited measurement variance in these two traits, we did not correct the allometric slopes for ME. For the focal traits, the measurement error is more substantial for occiput surface area and canine diameter, ranging from 2.6 to 7.3% and 0.8–11% across species, respectively. For temporalis surface area, ME reaches 14% in the badger and 30% in the beech marten. The larger ME for temporalis surface area may be explained by the difficulty to precisely define and measure the surface of a 3D object on a 2D image.

Allometric relationships

The allometric relationships between focal traits and body size proxies tend to be similar between sexes for most traits (Table 3; Figs. 3, 4 and 5). Notable exceptions, however, are for the badger and the beech marten where allometric relationships tend to differ between sexes. Differences in allometric slopes between sexes increase with a decrease in the R^2 of the model. This suggests that these differences primarily result from sampling variance, that may be partly associated with the higher ME in the focal traits reported for these two species.

The allometric relationships between occiput surface area or temporalis surface area and body size proxies are steeper on average than for canine diameter. This is expected for morphological traits expressed as surface compared with linear measurements. Finally, we note that the allometric relationships between the focal traits and condylobasal length have consistently higher R^2 than the relationships with occipital condyle width, except for occiput surface area in the otter and the badger.

Sexual dimorphism

In Table 4, we report the total sexual dimorphism for all traits including the two body-size proxies, as well as the non-allometric sexual dimorphism in the focal traits estimated using both body-size proxies with or without sex-specific allometric slope. The total sexual dimorphism of the two body-size proxies suggests that sexual size dimorphism (SSD) in these species ranges from ca. 2.7% in the badger to ca. 7% in the otter, with males larger than females in all species. Both proxies give similar estimates. For the focal traits, the total sexual dimorphism ranges from 3% for occiput surface area in the badger up to more than 14% in temporalis surface area in the stoat, with an average value of 9.2%. Trait size is consistently larger in males than in females for all traits in all species.

Correcting for the effect of the allometric relationship between trait size and body size strongly affects the sexual dimorphism of the focal traits. The average size-corrected (non-allometric) sexual dimorphism is about 1.7% and

Table 3 Slopes ± SE and R^2 for the allometric relationships between the focal traits and the two body size proxies, CBL and OCW, for each sex. Slopes and R^2 values are estimated from models including an interaction effect between body size proxy and sex. Abbreviations: **CBL**, condylobasal length; **OCW**, occipital condyle width; **CAN**, upper canine diameter; **TEM**, surface area of lateral cranium; **OCC**, surface area of the occiput

Species	Sex	CAN				TEM				OCC			
		CBL	R^2	OCW	R^2	CBL	R^2	OCW	R^2	CBL	R^2	OCW	R^2
L. lutra	Male	1.07 ± 0.13	0.89	0.84 ± 0.16	0.77	1.65 ± 0.26	0.71	1.43 ± 0.24	0.65	1.61 ± 0.28	0.64	1.38 ± 0.23	0.66
	Female	0.93 ± 0.16		0.78 ± 0.29		1.53 ± 0.31		1.62 ± 0.44		0.85 ± 0.34		1.11 ± 0.42	
Me. meles	Male	1.27 ± 0.33	0.51	1.25 ± 0.32	0.49	1.29 ± 0.44	0.42	1.10 ± 0.46	0.31	1.01 ± 0.32	0.40	1.14 ± 0.30	0.43
	Female	0.61 ± 0.34		0.32 ± 0.33		1.30 ± 0.45		0.50 ± 0.47		1.42 ± 0.34		1.29 ± 0.31	
Ma. foina	Male	0.64 ± 0.45	0.66	-0.17 ± 0.34	0.65	1.27 ± 0.58	0.45	-0.39 ± 0.47	0.32	0.22 ± 0.52	0.49	0.71 ± 0.42	0.39
	Female	1.09 ± 0.45		0.85 ± 0.35		1.53 ± 0.58		0.21 ± 0.50		2.41 ± 0.52		1.23 ± 0.44	
Mu. erminea	Male	1.36 ± 0.28	0.71	0.98 ± 0.30	0.55	2.41 ± 0.27	0.79	1.70 ± 0.29	0.69	2.11 ± 0.32	0.70	1.96 ± 0.33	0.66
	Female	1.33 ± 0.28		0.65 ± 0.43		1.08 ± 0.27		1.46 ± 0.42		1.79 ± 0.32		2.08 ± 0.43	

4.4% when the effect of size is corrected using the condylobasal length and occipital condyle width, respectively. In some cases, sexual dimorphism in the focal traits vanishes or changes direction (i.e. females showing a proportionally larger trait than males – negative numbers in Table 4) when the allometric component of sexual dimorphism is accounted for. This is the case for occiput surface area in all species, although these results are generally not supported statistically. A notable exception, however, is for temporalis surface area in the otter where the non-allometric component of sexual dimorphism is always female biased and statistically different from zero.

Size-corrected measures of sexual dimorphism estimated with condylobasal length or occipital condyle width are correlated, but the values estimated using the latter tend to be higher than the values estimated with the former (Table 4). The largest discrepancies are observed for temporalis surface area in the beech marten and the stoat and for canine diameter in the stoat, where the size-corrected sexual dimorphism is more pronounced when correction is performed using occipital condyle width. As illustrated in Figs. 3 and 4, these discrepancies are generated by the differences in allometric relationship between the focal traits and the body-size proxies. In the case of the occipital condyle width, the shallower allometric relationships with the focal traits decrease the part of the total sexual dimorphism due to the correlation with body size, which produce larger estimates of the non-allometric sexual dimorphism (Table 4). Finally, we note that there are only small differences in the estimates of the non-allometric sexual dimorphism in the focal traits when the size correction is performed using the same slope for both sexes (model without interaction) or different slopes (model with interaction, Table 4).

Canine diameter is the only trait that consistently display non-allometric sexual dimorphism in the four species with the canine diameter being on average 5.6% larger in males than in females of similar body size. In contrast, size corrected sexual dimorphism in occiput surface area is weak and never statistically different from zero in all species.

Discussion

Sexual dimorphism in a particular trait does not necessarily result from differences in selection acting directly on that trait. It may instead be the result of selection acting on body size with which the trait is genetically correlated (Lande 1979). Consequently, inferring sex-specific selection from measures of sexual dimorphism that have not been corrected for the allometric relationship between trait size and body size may overestimate the role of such a selection. In some cases, it may even lead to an error in the direction of the

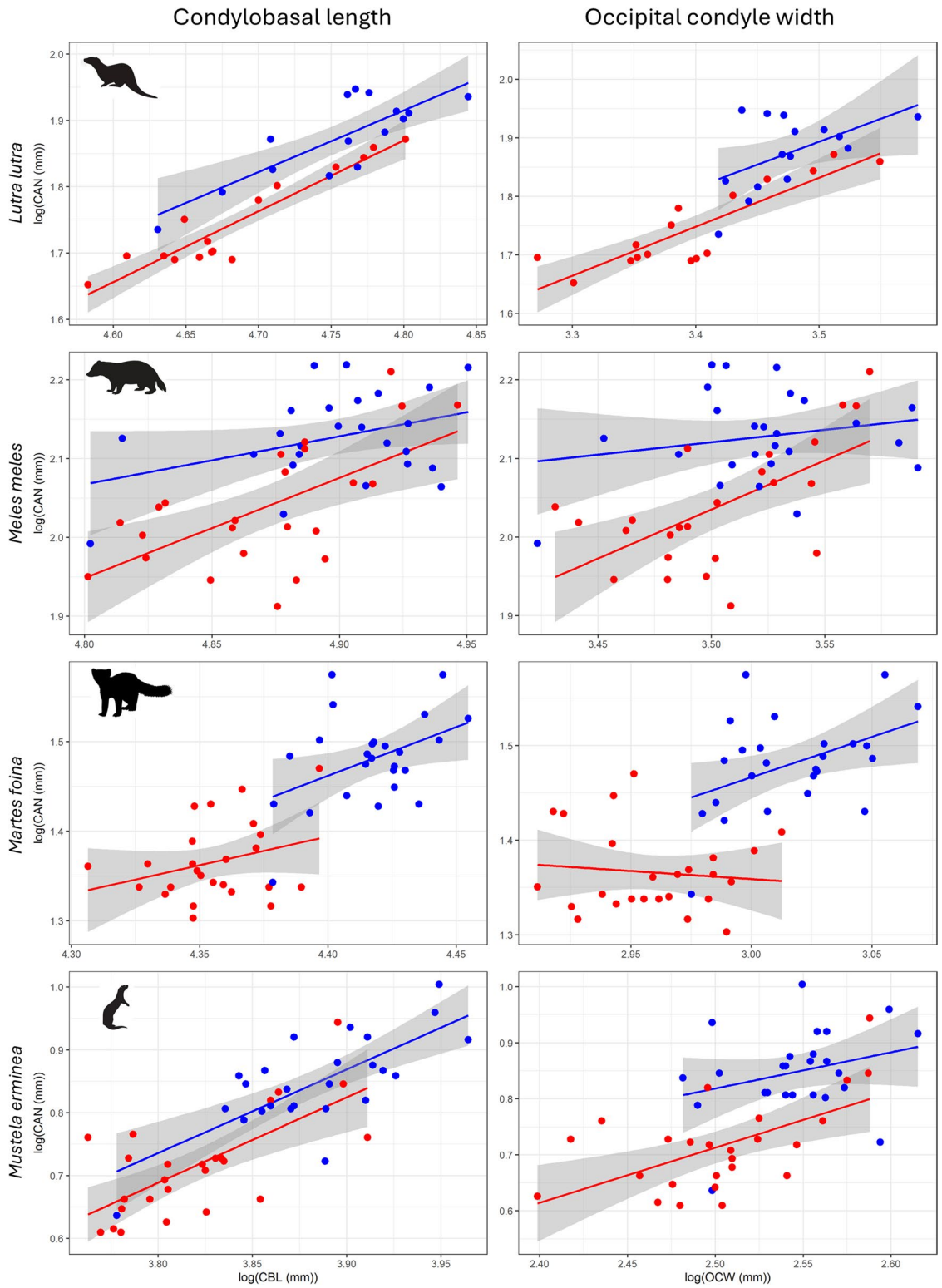

Fig. 3 Allometric relationships between upper canine diameter (CAN) and two proxies of body size, condylobasal length (CBL; left panels) and occipital condyle width (OCW; right panels), for males (blue lines and symbols) and females (red lines and symbols) in *Lutra lutra* (first row), *Meles meles* (second row), *Martes foina* (third row) and *Mustela erminea*. Sex-specific allometric slopes are displayed in all graphs, regardless of whether differences in the slope between sexes were statistically significant. Estimates of the non-allometric component of sexual dimorphism derived from these analyses are presented in Table 4. Shaded areas represent the 95% CI of the regression lines

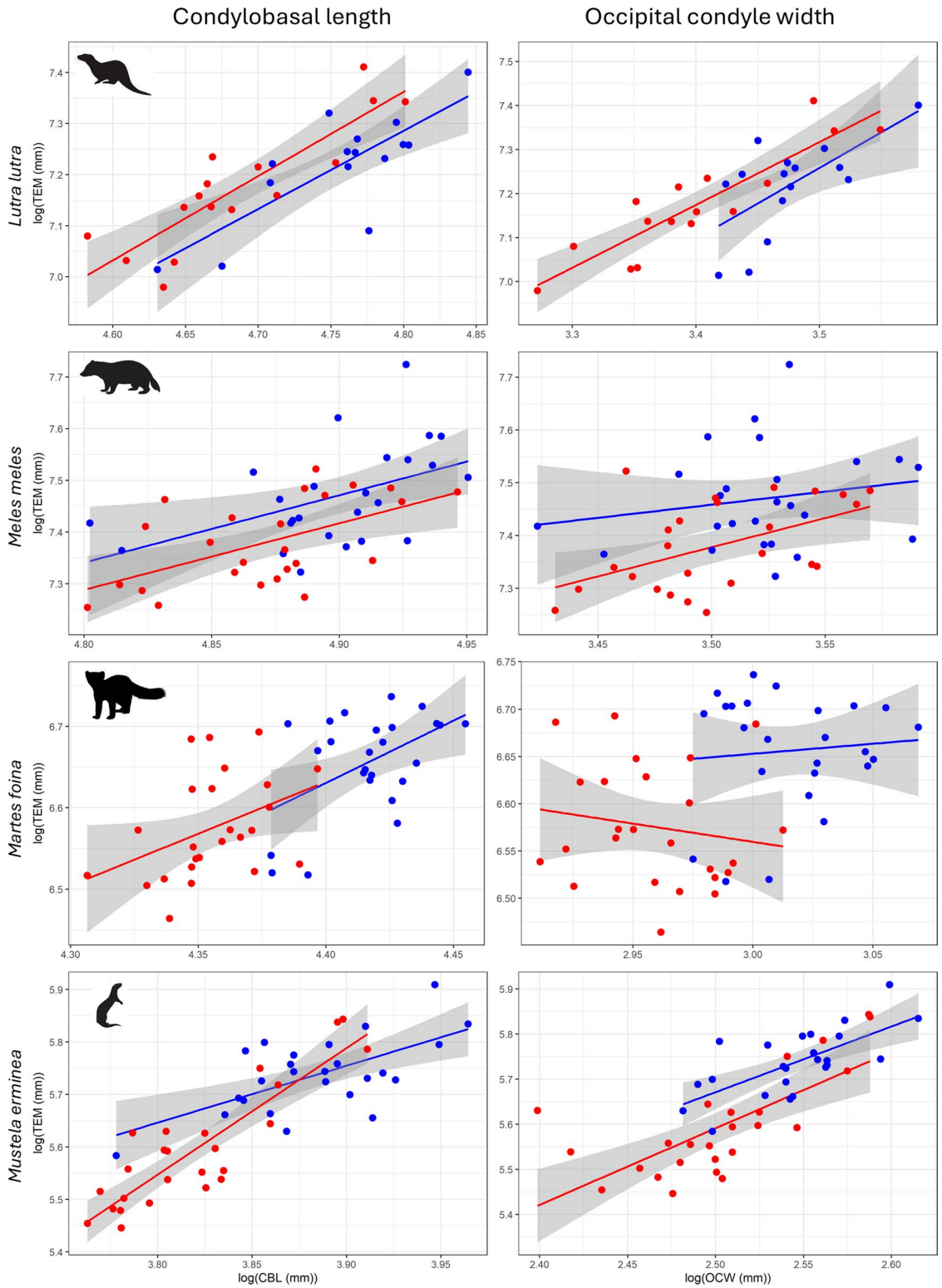

Fig. 4 Allometric relationships between temporalis surface area (TEM) and two proxies of body size, condylobasal length (CBL; left panels) and occipital condyle width (OCW; right panels), for males (blue lines and symbols) and females (red lines and symbols) in *Lutra lutra* (first row), *Meles meles* (second row), *Martes foina* (third row) and *Mustela erminea*. Sex-specific allometric slopes are displayed in all graphs, regardless of whether differences in the slope between sexes were statistically significant. Estimates of the non-allometric component of sexual dimorphism derived from these analyses are presented in Table 4. Shaded areas represent the 95% CI of the regression lines

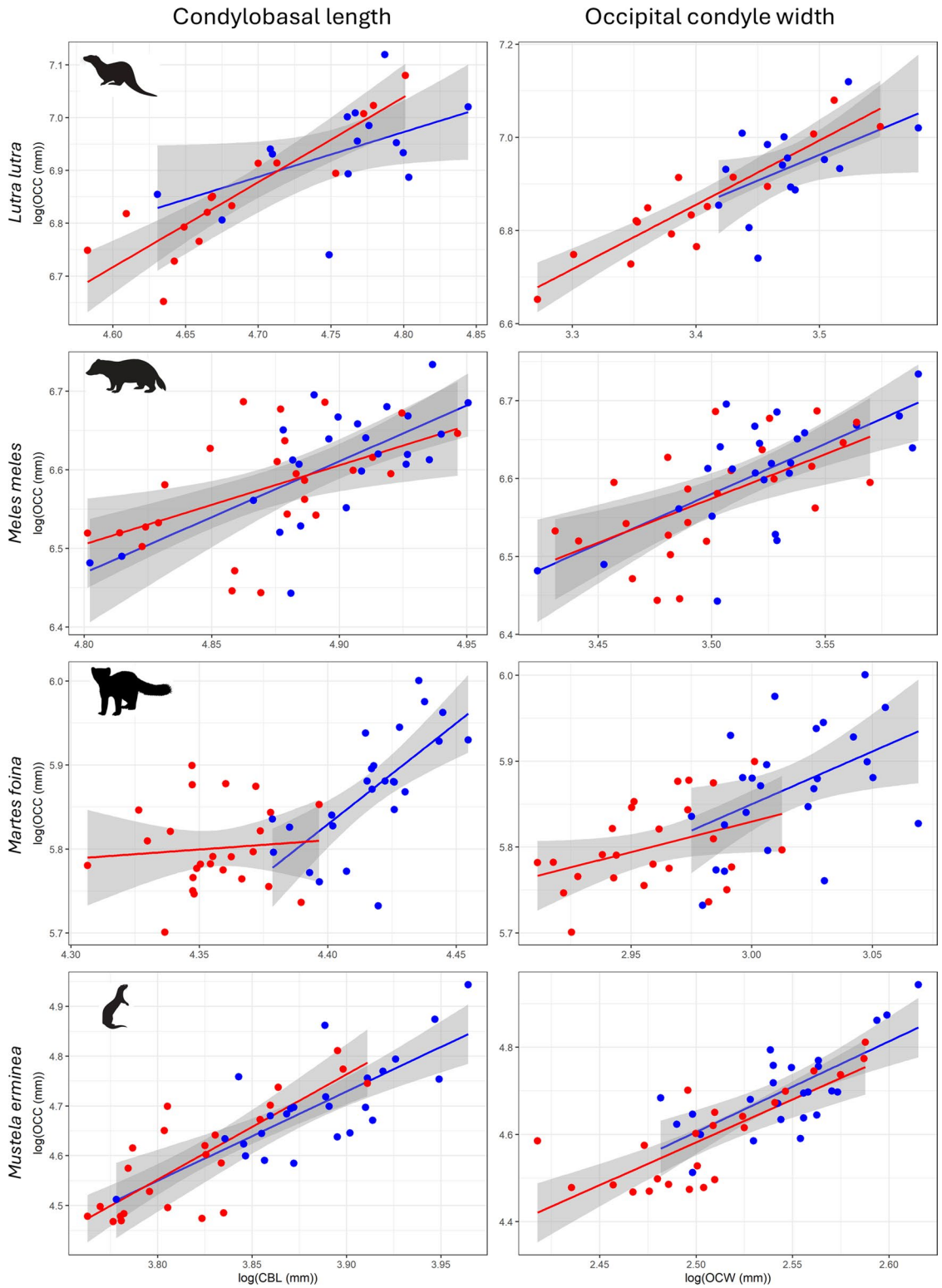

Fig. 5 Allometric relationships between occiput surface area (OCC) and two proxies of body size, condylobasal length (CBL; left panels) and occipital condyle width (OCW; right panels), for males (blue lines and symbols) and females (red lines and symbols) in *Lutra lutra* (first row), *Meles meles* (second row), *Martes foina* (third row) and *Mustela erminea*. Sex-specific allometric slopes are displayed in all graphs, regardless of whether differences in the slope between sexes were statistically significant. Estimates of the non-allometric component of sexual dimorphism derived from these analyses are presented in Table 4. Shaded areas represent the 95% CI of the regression lines

Table 4 Total sexual dimorphism expressed in % in the two body size proxies (CBL and OCW) and in the three focal traits, and non-allometric sexual dimorphism in the focal traits estimated with either CBL or OCW to correct for the allometric effect of body size. The non-allometric sexual dimorphism is estimated from models either with the same slope in males and females or with different slopes. All estimates and standard error (± SE) are in % of the trait size. Abbreviations: **CBL**, condylobasal length; **OCW**, occipital condyle width; **CAN**, upper canine diameter; **TEM**, surface area of lateral cranium; **OCC**, surface area of the occiput

Species	Total sexual dimorphism				Non-allometric (CBL)		Non-allometric (OCW)	
	CBL	OCW	Trait		Same slope	Different slopes	Same slope	Different slopes
L. lutra	6.96 ± 2.12*	7.50 ± 2.20*	CAN	12.57 ± 2.43*	5.53 ± 1.35*	5.63 ± 1.37*	6.38 ± 1.94*	6.49 ± 2.1*
			TEM	4.37 ± 4.06	-6.77 ± 2.66*	-6.68 ± 2.72*	-6.67 ± 2.95*	-7.08 ± 3.19*
			OCC	7.96 ± 3.74*	-1.04 ± 3.02	-0.51 ± 2.93	-1.94 ± 2.82	-1.35 ± 3.04
Me. meles	2.71 ± 1.02*	1.98 ± 1.07	CAN	8.82 ± 1.95*	6.24 ± 1.81*	6.26 ± 1.79*	7.35 ± 1.82*	7.34 ± 1.76*
			TEM	8.91 ± 2.54*	5.4 ± 2.36*	5.40 ± 2.38*	7.31 ± 2.5#	7.32 ± 2.51*
			OCC	3.17 ± 2.04	-0.1 ± 1.76	-0.12 ± 1.77	0.77 ± 1.65	0.77 ± 1.66
Ma. foina	6.11 ± 0.57*	5.70 ± 0.76*	CAN	11.45 ± 1.33*	6.18 ± 2.3*	6.17 ± 2.31*	9.63 ± 1.96*	9.50 ± 1.89*
			TEM	8.08 ± 1.77*	-0.49 ± 2.94	-0.49 ± 2.97	8.65 ± 2.65	8.58 ± 2.65
			OCC	6.91 ± 1.73*	-1.09 ± 2.9	-1.12 ± 2.68	1.44 ± 2.34	1.38 ± 2.35
Mu. erminea	6.46 ± 1.18*	4.34 ± 1.18*	CAN	13.26 ± 2.23*	4.57 ± 2.03*	4.57 ± 2.05*	9.47 ± 2.27*	9.72 ± 2.32*
			TEM	14.27 ± 2.69*	2.98 ± 2.24	2.98 ± 2.02	7.25 ± 2.18*	7.43 ± 2.23*
			OCC	10.56 ± 2.98*	-1.92 ± 2.36	-1.92 ± 2.37	2.72 ± 2.23	2.64 ± 2.28

*Estimates that do not include 0 in the 95% CI

inferred selection. However, the diversity of methods used to estimate body size, together with the inherent challenges of some of these measurements, means that the correction can be influenced by the proxy chosen to represent body size. We addressed these issues by studying sexual dimorphism in three craniodental traits in four mustelid species, using two different proxy measurements of body size.

Accounting for the allometric relationships between trait size and body size decreased the estimates of sexual dimorphism for the focal traits. For temporalis surface area in the otter, this correction even provided an estimate of sexual dimorphism in the opposite direction (i.e., females having a proportionally larger temporalis surface area). We speculate that in the otter, selection on this character is stronger in females to preserve strong biting force despite their smaller body size (Ito et al. 2024). After correction, canine diameter was the only trait that consistently showed a non-allometric component of sexual dimorphism across all four species, with males having larger canines than females. Therefore, sexual dimorphism in occiput surface area and temporalis surface area appears to be primarily due to a correlated response to selection on overall body size. Consequently, sexual dimorphism in these two traits may solely results from differential selection on body size generated, for example, by character displacement to avoid intersexual competition or different physiological constraints related to the different roles of males and females in reproduction (Erlinge 1979; Moors 1980).

Our findings are consistent with earlier studies showing that sexual dimorphism in the craniodental morphology of various mustelid species generally results from sexual dimorphism in overall body size (e.g., Lynch and O'Sullivan 1993; Rozhnov and Abramov 2006; Abramov et al. 2009; Özen 2020). We also note that the sexual dimorphism in body size estimated from condylobasal length in our study is of similar magnitude as the sexual dimorphism reported in other studies (beech marten 4.5% in Özen 2020; badger 1.7% in Abramov and Puzachenko 2005; *Vormela peregusna*, marbled polecat < 1% in Rozhnov and Abramov 2006; Otter 7.5% in Lynch and O'Sullivan 1993). Rozhnov and Abramov (2006) proposed that the absence of non-allometric sexual dimorphism in the cranium reflects the narrow dietary niche of these species, which constrains the potential for sex-specific dietary specialization. However, sexual dimorphism in various craniodental traits, arising as a correlated response to body size dimorphism, may itself be adaptive. Such dimorphism may facilitate the exploitation of slightly different prey types by males and females or accommodate differing energetic requirements (e.g., Erlinge 1979; Moors 1980; Dayan and Simberloff 1994).

The consistent sexual dimorphism in canine size, independent of body size dimorphism, suggests that sexual selection favouring proportionally larger canines in males is widespread among these species. This result partly contradicts the idea that sexual selection resulting from mating competition among males should be weaker in badgers, because of their social system (Bútora et al. 2018; but see Johnson and Macdonald 2001 for discussion). However, Macdonald et al. (2008) also report that male badgers sustain more wounds than females, and that the frequency of bite wounds increases with the number of badgers living in adjoining territories. Combined with evidence that most extra-group paternities are sired by neighbouring males (Dugdale et al. 2007), these findings suggest that male–male competition in badgers may be stronger than previously assumed.

Effects of body-size proxies on estimates of sexual dimorphism

Estimates of the different components of sexual dimorphism are influenced by the magnitude of sexual dimorphism in body size (SSD) and by the allometric slope, β, which may vary depending on the body-size proxy used. For example, the difference between total sexual dimorphism and size-corrected sexual dimorphism is the smallest on average in the badger, which displays the least sexual size dimorphism. The effect of variation in the allometric slope is generally less pronounced. Still, when occipital condyle width is used as a proxy for body size instead of condylobasal length, the differences between total and size-corrected estimates of sexual dimorphism decrease from an 82% reduction to only a 52% reduction because the allometric relationships between trait size and occipital condyle width are shallower than those with condylobasal length.

These differences demonstrate the importance of the choice of proxy for such analyses. In our study, focal traits display weaker allometric relationships (lower R^2 and shallower slopes) with occipital condyle width than with condylobasal length. Differences in the magnitude of the measurement error between the two proxies are too small to explain the observed differences in allometric relationships. Therefore, these differences in allometric relationships may be genuine, that is, they may reflect weaker size covariation between various craniodental traits and occipital condyle width than between these traits and condylobasal length. While only a careful study of the allometric relationship between the two traits and body mass or other measures of total body size could inform about the validity of each of these measurements as a body-size proxy, other factors may be also considered when choosing a body-size proxy.

The two body-size proxies used in this study may capture different aspects of size, and their accuracy in estimating body size may also vary depending on whether estimates are made within or across species (e.g., Geiman and Long 2023). For example, the use of condylobasal length as a proxy for body size assumes that skull size (mostly length) is proportional to the skeletal body size. This assumption can be criticised when making comparisons among species with different skull shape (e.g., otter vs. badger) or relative proportion of the body size represented by the skull, but it seems more valid when making comparisons within a species, where skull shape is less variable, at least among adults. On the other hand, occipital condyle width is expected to predict body size because it is an indicator of the size of the foramen magnum, and therefore a proxy measure for the number of neurons going to the brain (Engelman 2022), which is itself correlated with body mass among mammal species (Radinsky 1967). Therefore, condylobasal length may represent skeletal size while occipital condyle width is expected to represent body mass. We should thus expect these two measures to display different scaling with the focal traits considered here. We note, however, that occipital condyle width is not expected to accurately measure the size of the foramen magnum because it only measures one dimension of its two-dimensional surface, which varies considerably in shape (Fig. 6). Consequently, depending on the shape of the condyle or its orientation, occipital condyle width can be greater or smaller while the size of the foramen magnum remains the same. These considerations provide more support for the use of condylobasal length than occipital condyle width as a proxy for body size in within-species allometric studies. Yet, condylobasal length of a specimen cannot always be measured because the fragile facial skull is often damaged in specimen collections, while occipital condyle width is less susceptible to damages.

Differences between ANCOVA and PCA for estimating size-corrected sexual dimorphism

The method presented here, in which non-allometric sexual dimorphism is estimated for univariate traits using an ANCOVA, should produce different results to those obtained with principal component analyses in which overall size is expected to be represented by variation along PC1 (e.g., Law et al. 2016). Indeed, in a PCA performed on pooled data for the two sexes, part of the non-allometric sexual dimorphism is captured by the variation along PC1 (Fig. 7). This is because each trait contributes to the variation along PC1 and therefore, contributes to the definition of the overall sexual size dimorphism (SSD measured along PC1 in Fig. 7). This is also the case in geometric morphometrics where size is defined as the centroid size (i.e. the square root of the sum of the squared distances of all landmarks from their average position). This contrasts with the ANCOVA approach, which assumes that the focal trait does not contribute to the definition of the overall size. Both approaches are valid, but their interpretation differs. While the PCA accurately captures variation in shape independent of the variation in size (SShD along PC2 in Fig. 7), the ANCOVA approach better separates the allometric and the non-allometric components of sexual dimorphism if the aim is to estimate the sex-specific selection acting directly on the trait. It assumes, however, that a reliable measure of overall size is available.

We also note that the ANCOVA allows different scaling relationship between trait size and body size in the two sexes (see Fischer and Mitteroecker 2017 for a similar analysis with geometric morphometrics where an independent measure of overall size is available). Testing for such a sex-specific scaling is important if we are to understand the

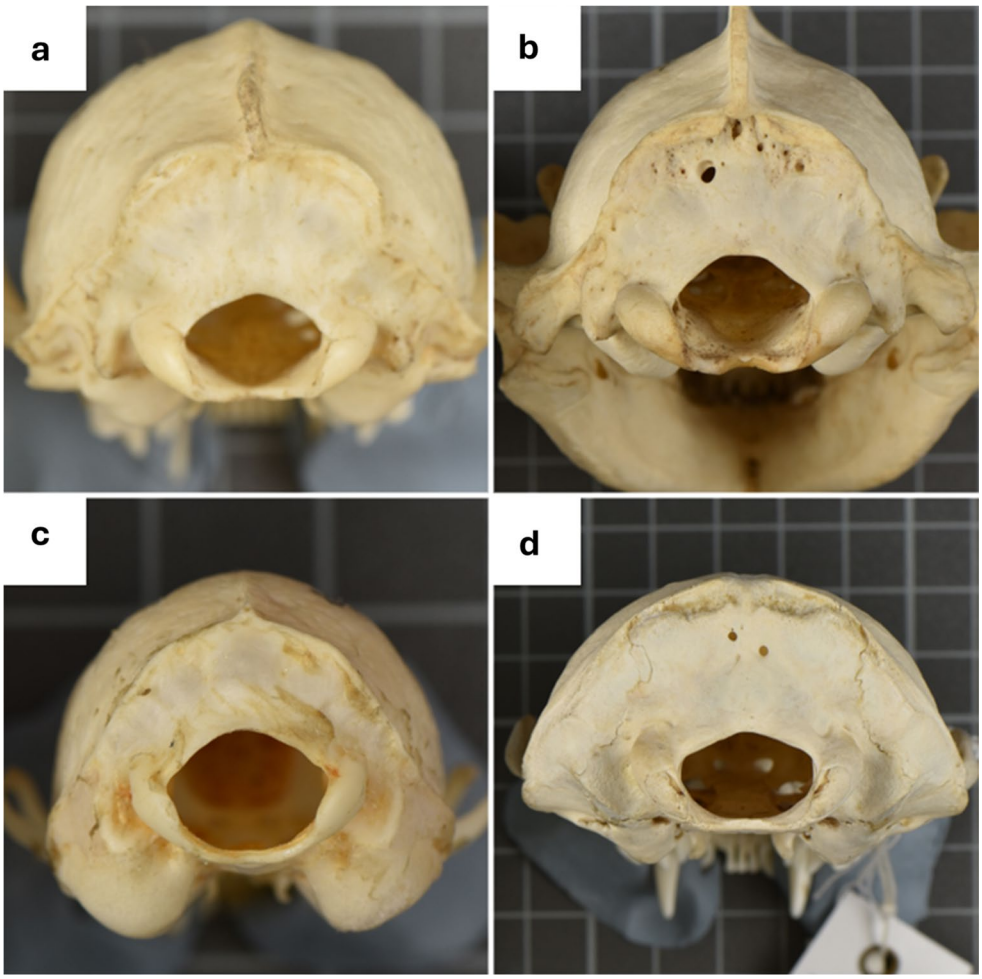

Fig. 6 Comparison of occipital condyle and foramen magnum morphology within Mustelidae. **a**. *Martes foina*; **b**. *Meles meles*; **c**. *Mustela erminea*; **d**. *Lutra lutra*. Condyle orientation and foramen magnum shape can be seen to vary among species within the Mustelidae family. Squares in the background have a 1 cm side

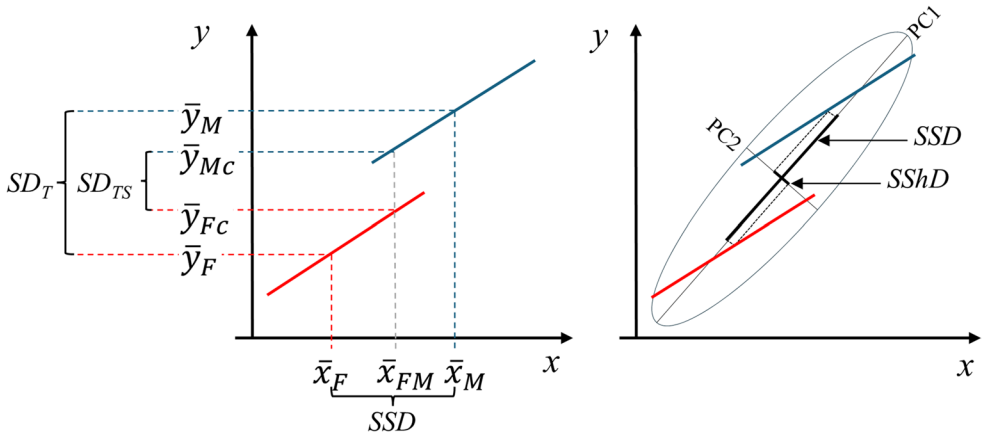

Fig. 7 Difference between an analysis of covariance (ANCOVA, left) and a principal component analysis (PCA, right) for estimating size-dependent and size-independent components of the sexual dimorphism in a trait. In the ANCOVA framework, size-independent sexual dimorphism SD_{TS} is estimated as the difference in the predicted value of the trait between a male and a female of equal (mean) size (see Fig. 1 for details). In the PCA representation (right), the ellipse represents the combined distribution of male and female observations, with its major and minor axes corresponding to the first and second principal components (PC1 and PC2), respectively. Dash lines indicate the projections of the mean male and female values onto each principal component. In this approach, PC1 is expected to capture variation associated to the overall size, whereas PC2 captures shape-related variation. Therefore, sexual size difference (SSD) is represented as the average difference between sexes along PC1 (solid black line along PC1), while the sexual shape dimorphism (SShD) is quantified as the mean difference between sexes along PC2 (solid black line along PC2). Comparing these two figures shows that SD_{TS} is larger than the *SShD*. This is because PC1 incorporates not only body size variation, but also a component of the trait-specific sexual dimorphism that is independent of body size

origin of the sexual dimorphism in the focal trait. Indeed, different scaling between males and females may confirm that the trait plays different roles in both sexes. In our analysis, however, we believe that most of the differences in the scaling relationship between males and females result from sampling variance. We suggest that a better understanding of the origin of sexual dimorphism in the studied species requires further testing of the sex-specific scaling between trait size and body size.

Conclusion

Our results highlight the importance of correcting for body size when estimating sexual dimorphism in a specific trait and demonstrate the impact of using different proxies for this correction. The arguments for and against using condylobasal length or occipital condyle width as proxies for body size illustrate the challenges involved in avoiding bias and imprecision when estimating body size from skeletal remains.

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Author contributions XB, GvdV, FG and AvdG initiated the project, XB and GvdV collected the data, XB, GvdV and CP analyzed the data and prepared the figures, CP and XB wrote the mansucript, All authors reviewed the manuscript.

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Data availability The data are available as supplementary material.

Declarations

Competing interests The authors declare no competing interests

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