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Differential sexual dimorphism: size and shape in the cranium and pelvis of grey foxes (*Urocyon*)

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Patterns of sexual size dimorphism (SSD) and cranial dimorphism are well documented. However, limited examinations exist of the contrasts in the patterns and nature of dimorphism across body regions (e.g. cranium, pelvis), particularly when these regions have different sex-specific functions (e.g. display in mating, locomotion, and reproduction). Using landmark-based morphometric techniques, we investigated size and shape dimorphism variation in the crania and pelves of two closely-related fox species within the genus *Urocyon*. Although we found no significant size and shape dimorphism in the crania of either species, we did find significant dimorphism in the pelvis: its size was dimorphic in *Urocyon littoralis* (but not in *Urocyon cinereoargenteus*) and its shape was dimorphic in both species (though more pronounced in *U. littoralis*). The observation of greater dimorphism in the pelvis than in the cranium suggests that factors such as offspring size and locomotor mode play a greater role in sexual dimorphism than simple 'whole body' allometric affects associated with dimorphism in body size. *Biological Journal of the Linnean Society*, 2009, **96**, 339–353.

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INTRODUCTION

Sexual size dimorphism (SSD) has been studied intensively in mammals. Generally, males are larger than females ('male-dominant'), although a smaller number of 'female dominant' cases also exist (Ralls, 1977; Leutenegger, 1978; Abouheif & Fairbairn, 1997; Weckerly, 1998; Loison *et al.*, 1999). Rensch (1960) observed that in male-dominated species, the magnitude of SSD is greater in larger versus smaller species. This allometric pattern in body size dimorphism has become known as Rensch's rule (Fairbairn & Preziosi, 1994), studies of which are common in both the mammal and the broader animal literature.

The strong focus on Rench's rule has led to an emphasis of body size dimorphism in sexual dimorphism studies. Primarily, studies measure body size with univariate proxies such as skull length or directly as body length or body mass. Although these descriptors of size are useful when discussing overall body size dimorphism, they do not represent shape, and therefore do not fully describe differences between males and females, nor do they typically address sexual differences occurring in specific body regions. The present study examined how the magnitudes of shape and size dimorphism differ in body parts with completely different functions.

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We examined sexual size and shape dimorphism in the cranium and os coxae (one of two paired bones comprising the pelvis) because dimorphism in these body regions is potentially affected by differences in sexual selection. Sexual size dimorphism in the crania and dentition of carnivores is common and strongly associated with forms of social structure and their effect on the magnitude of sexual selection (Gittleman & Van Valkenburgh, 1997; Van Valkenburgh & Sacco, 2002). Despite numerous studies of sexual dimorphism in carnivore skull size, only a few studies have attempted to study dimorphism in overall cranial shape (Lynch & O' Sullivan, 1993; Lynch *et al.*, 1996; Lynch, 1996), and their results on limited taxa suggest that cranial shape dimorphism has an allometric scaling component such that shape differences are driven by size differences.

Whereas cranial dimorphism appears to be closely associated with mating system, pelvic dimorphism may be influenced by different causal factors, and thus exhibit different allometric patterns. Many studies attribute pelvic dimorphism (both in size and shape) to functional pressures on the pelvis produced by weight bearing, parturition, and locomotion (Schultz, 1949; Leutenegger, 1974; Rosenberg & Trevathan, 2002; Berdnikovs, 2005; Carrier, Chase & Lark, 2005; Rosenberg & Trevathan, 2005). These three biomechanical roles affect pelvic form (size and shape) in the following ways: weight-bearing affects pelvic form due to the stress that body mass places on the rear limbs (Carrier *et al.*, 2005); parturition affects pelvic form by requiring an ample aperture for the passage of offspring (Washburn, 1948; Schultz, 1949; Leutenegger, 1974; Leutenegger & Larson, 1985; Ridley, 1995; Rosenberg & Trevathan, 2002); and, finally, locomotion affects pelvic form through requirements for limb orientation and muscle attachment (Gregory, 1912; Jenkins & Camazine, 1977; Hildebrand & Goslow, 2001; Carrier *et al.*, 2005). Because these three functions can simultaneously affect pelvic form, the potential exists for them to conflict with one another. In modern humans, for example, bipedal locomotion is made more efficient by a narrow pelvis, whereas the characteristically large-brained *Homo sapiens* neonate requires an ample birth canal, which necessitates a broader pelvis (Leutenegger, 1974; Leutenegger & Larson, 1985; Hager, 1989; Rosenberg & Trevathan, 2002).

Current knowledge of pelvic sexual dimorphism in mammals suggests that pelvic size and shape do not conform to the same patterns seen in cranial and body size dimorphism. Males in male-dominated SSD species often have larger pelves than females in the absolute sense because of their greater body size, but females often have relatively larger pelves than males, and, for some measurements, even have absolutely larger ones (Dunmire, 1955; Iguchi *et al.*, 1989; Uesugi *et al.*, 1992; Tague, 2003). The latter observation implies that there is sexual dimorphism in the shape of the pelvis, even in cases when size differences between males and females are very slight. Thus, pelvic dimorphism may be related not only to differences in body size between the sexes, but also to the unique biomechanical limitations placed on females by parturition and the relationship between neonatal and maternal size, a different form of sexual selection.

We used the genus *Urocyon* as a system to study allometric patterns in the size and shape of the cranium and pelvis for several reasons. First, the genus contains two closely-related extant species, the grey fox *Urocyon cinereoargenteus* and the island fox *Urocyon littoralis* (Hall, 1981). The Southern California grey fox populations are considered to be the source for the ancestor of the island fox (Gilbert *et al.*, 1990; Wayne *et al.*, 1991; Goldstein *et al.*, 1999). In addition to this close relationship, both species are known to show slight but significant sexual size dimorphism both in terms of body size and linear cranial measures (Grinnell, Dixon & Lindsdale, 1937; Rohde, 1966; Collins, 1993) and both are considered as primarily monogamous (Fritzell & Haroldson, 1982; Crooks & van Vuren, 1996; Roemer *et al.*, 2001). Consequently, any differences in the magnitude of dimorphism between these species should not be associated with variations in mating system. Finally, there is also a marked difference in body size between the two species, with *U. littoralis* being approximately 25% smaller in numerous linear measurements than *U. cinereoargenteus* (Collins, 1982).

The present study examined how patterns of size and shape dimorphism varied between the cranium and pelvis, and how within each element, size and shape dimorphism differed between two closely-related species. We tested two hypotheses. First, we tested the hypothesis that cranial shape and size dimorphism would be of relatively low overall magnitude and differ little between the two species due to their monogamous mating system. This hypothesis was based on previous studies that indicate low dimorphism in monogamous species and no correlation between cranial size or body size and SSD in carnivores (Van Valkenburgh & Wayne, 1994; Van Valkenburgh & Sacco, 2002).

Second, we tested the hypothesis that pelvic shape and size dimorphism would differ in magnitude from that of cranial shape and size dimorphism overall, and that the patterns of dimorphism would also differ between these two differently sized species. In particular, we predicted that the magnitude of pelvic shape and size dimorphism would be greater in *U. littoralis* than in *U. cinereoargenteus* because of the

smaller body size of the former. This hypothesis was based on previous studies in primates showing that pelvic dimorphism increases in magnitude as body size decreases (Schultz, 1949; Leutenegger, 1974; Mobb & Wood, 1977).

MATERIAL AND METHODS

Samples

We took high resolution digital images of 68 crania and 68 ossa coxae (1/2 of the pelvis) of *U. cinereoargenteus* and 64 crania and 82 ossa coxae of *U. littoralis* at a distance of at least 1 m to reduce distortion (Cardini & Tongiorgi, 2003) and using the acetabulum to position the specimen at the center of the focal plane. All data were collected from adult specimens found at the following institutions: American Museum of Natural History (AMNH), Los Angeles County Museum of Natural History (LACM), Santa Barbara Museum of Natural History (SBMNH), and University of Kansas Museum of Natural History (UKMNH). Age was determined by full cranial suture closure and eruption of all adult dentition. Crania and ossa coxae samples for each species were evenly divided between males and females. Landmarks were recorded as fourteen two-dimensional Cartesian coordinates along with scales on the digital images utilizing tpsDIG (Rohlf, 2006). Landmarks are shown in Figure 1A, B. Previous work on mammal crania has shown that two- and three-dimensional analyses yield highly correlated results even though the structure is three-dimensional and this can increase measurement error (Cardini & Thorington, 2006). Our choice of primarily co-planar landmarks and use of an appropriate photographic distance is concordant with those studies and measurement error should therefore be low (Cardini & O'Higgins, 2004). However, the pelvis, another three-dimensional structure has not received as much attention in terms of landmark measurement error. Consequently, we decided to calculate percent measurement error (ME) for our os coxae samples.

We assessed measurement error in our os coxae sample due to specimen rotation and parallax following Bailey & Byrnes (1990) and further described in Polly (2001). To calculate percent ME in our dataset, a representative sub-sample was photographed and digitized multiple times so that we could assess within-specimen variation relative to between specimen variation. In the os coxae, the %ME for the entire *Urocyon* sample was 9.11% and, within each species, %ME was 11.56% (*U. littoralis*) and 7.83% (*U. cinereoargenteus*). In all cases, the within specimen variance was significantly less than the between specimen variance ($P < 0.001$).

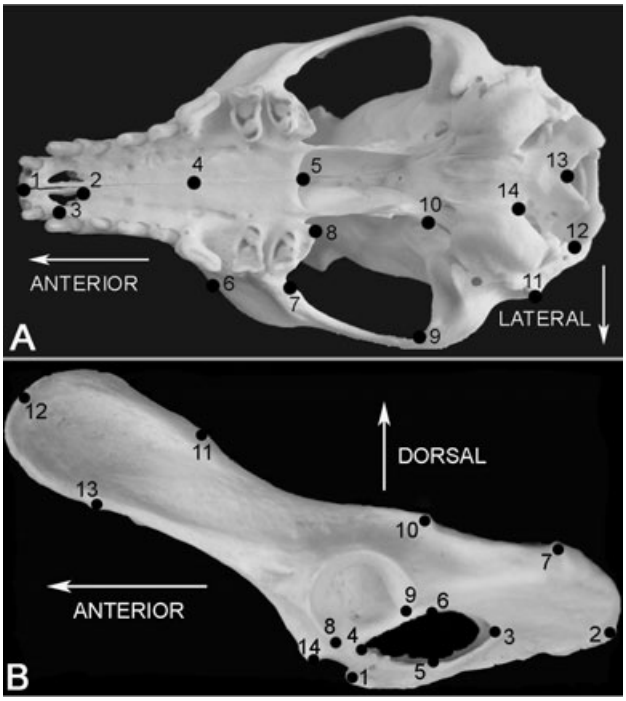

Figure 1. Landmark placement of 14 landmarks. A, the ventral view of the cranium. B, lateral aspect of the os coxae. Cranium landmark positions: 1, rostral-most point of pre-maxilla suture; 2, caudal-most point of palatine fissure; 3, lateral-most point of pre-maxilla/maxilla suture at canine alveolus; 4, medial-most point of palatine/maxilla suture; 5, caudal-most point of palatine at palatine suture; 6, rostral-most point of jugal/maxilla suture; 7, caudal-most point of jugal/maxilla suture; 8, caudal-most projection of maxillary tuberosity; 9, medial-most point of jugal/temporal suture; 10, rostral-most opening of alisphenoid canal; 11, lateral-most projection of mastoid process; 12, rostral and lateral-most projection of occipital condyle; 13, midpoint of rostral-most border of foramen magnum; 14, medial-most point of jugal foramen. Os coxae landmark positions: 1, pubic tubercle; 2, caudal-most point of ventral ramus of ischium; 3, caudal-most point on border of obturator foramen; 4, obturator goove: rostral-most point on border of obturator foramen; 5, midpoint of landmarks 3 and 4 at ventral border of obturator foramen; 6, midpoint of landmarks 3 and 4 at dorsal border of obturator foramen; 7, dorsal-most point of ischial tuberosity; 8, ventral tubercle of acetabular lunate surface; 9, dorsal tubercle of acetabular lunate surface; 10, ischial spine; 11, dorso-caudal iliac spine; 12, rostral-most projection of iliac crest; 13, ventro-caudal iliac spine; 14, ilio-pubic tubercle.

Morphometric data

A generalized least squares Procrustes fit was performed on the raw landmark data and then the partial warps (PW) and the uniform component were saved, using tpsRelw software (Rohlf, 2007).

Using the same software, we extracted centroid size, the square root of the sum of squared distances from the centroid (Bookstein, 1991) and log-transformed it to meet the assumption of homoscedasticity for regression analyses (Sokal & Rohlf, 1981; Kachigan, 1991). Centroid size is a geometrically-based measure of size that in the absence of allometry is statistically uncorrelated with shape variables (Bookstein, 1991) and thus is an excellent size metric to use in this study. Furthermore, cranial centroid size is known to be a good proxy for body mass, a commonly used size measure (Hood, 2000).

Indices of size and shape dimorphism

Indices of sexual size dimorphism

To asses the magnitude of sexual size dimorphism, we calculated two indices of size dimorphism (hereafter labeled size index 1 and size index 2). We developed size index 1 as the univariate version of the shape index 1 metric described below, except that we used centroid size in the equation instead of Procrustes distance. Consequently, size index 1 is the difference in size between the sexes divided by the sum of the variance in size within the sexes and is expressed as.

$$\text{Size index 1} = \frac{\left(\bar{S}_{\text{m}} - \bar{S}_{\text{f}}\right)^2}{Var_{\text{m}} + Var_{\text{f}}}$$

where $\bar{S}_{\text{m}}$ and $\bar{S}_{\text{f}}$ are the mean male and mean female centroid sizes and Var_{m} and Var_{f} are the sample variances in male and female centroid size, respectively.

Size index 2 is the size metric described by Lovich & Gibbons (1992) and further discussed by Smith (1999). Size index 2 is calculated by dividing the mean size of the larger sex by the mean size of the smaller sex, subtracting 1 so that size index 2 = 0 when there is no difference in size, and arbitrarily assigning a negative sign if males are larger or a positive sign if females are larger. Size index 2 is given by:

$$\text{Size index 2} = (+/-)1 \times \left(\frac{S_{\text{l}}}{S_{\text{s}}} - 1\right)$$

where S_{l} and S_{s} are the mean centroid sizes of the larger and smaller sexes, respectively.

Indices of sexual shape dimorphism

To measure sexual shape dimorphism, we developed two new indices (shape index 1 and shape index 2) based on the Procrustes distance (the square root of the sum of squared differences in the positions of the landmarks in two shapes) (Rohlf & Slice, 1990; Dryden & Mardia, 1998). Both indices are univariate, independent of sample size and are comparable across taxa and anatomical structures. In shape index 1, the difference in shape between the sexes is divided by the sum of the variances within the sexes and is expressed as:

$$\text{Shape index 1} = \frac{D^2_{\bar{\text{m}}\bar{\text{f}}}}{Var_{\text{m}} + Var_{\text{f}}}$$

where $D^2_{\bar{\text{m}}\bar{\text{f}}}$ is the squared Procrustes distance between the mean male and female landmark configuration; and Var_{m} and Var_{f} are the sample variances in male and female shape respectively. Thus, size index 1 and shape index 1 use the exact same computation with the only difference being that one (size index 1) uses centroid sizes and the other (shape index 1) uses Procrustes distances.

We also formulated a second index that is built upon the univariate index of sexual dimorphism (size index 2 above) developed by Lovich & Gibbons (1992) and has many of the same properties. Similar to the shape index 1, shape index 2 uses Procrustes distance instead of centroid size. This index is given as:

$$\text{Shape index 2} = (+/-)1 \times \left(\frac{\sum {D^2}_{\text{mf}}}{\sum {D^2}_{\text{j}}} - 1\right)$$

Where the numerator ${D^2}_{\text{mf}}$ is the mean pairwise squared-Procrustes distance between individuals i and j where all i are male and all j are female. The denominator is the mean pairwise Procrustes distance between individuals of whichever sex has the greatest mean distance (measured as the mean of the pairwise Procrustes distances among individuals of that sex). Where ${D^2}_{\text{l}}$ is the squared-Procrustes distance between individuals i and j where $i \neq j$, both i and i are in the same sex, and the sex used is the one with the larger value of $\Sigma {D_{\text{ij}}}^2$. One is subtracted from the ratio to create an index that goes from zero (if the Procrustes distance between sexes is equal to that within sexes) to infinity (as the Procrustes distance between sexes increases relative to the more disparate sex). The ratio is multiplied by –1 if males are more disparate (have greater within-sex Procrustes distances) or +1 if females are more disparate, as was done for the size metric size index 2 *sensu* Lovich & Gibbons (1992).

Similar to the univariate size indices described above (size index 1, size index 2), our shape indices (shape index 1, shape index 2) produce a single number that is independent of sample size and is comparable across taxa and anatomical structures. However, unlike size index 2 and shape index 2, size index 1 and shape index 1 are not ratios, and the magnitude of dimorphism is not interpreted as a negative or positive deviation from 0. Rather, size index 1 and shape index 1 range upward from zero as

dimorphism between the two sexes increases. Size index 2 and shape index 2 also range from 0 and infinity, but the indices are then multiplied by –1 if males are the more disparate sex, which makes them directional in regard to which sex is more variable in shape. Thus, shape index 2 is quite similar to the index of size dimorphism proposed by Lovich & Gibbons (1992) and which we term size index 2.

We determined significance for all four indices (size and shape) by performing 10 000 randomization runs for each element, where individuals were randomly assigned without replacement to equal sized male and female groups and the index was re-calculated. This generated a null distribution of random differences between two groups against which to test our observed index. The sexes were considered significantly dimorphic if the measured dimorphism metric was greater than 95% (0.05 level of significance) of the randomly generated metrics (Manly, 2006). All index calculations, including the generation of Procrustes distances, calculation of the index and the necessary re-alignment of specimens after each randomization for the multivariate indices (shape index 1 and shape index 2), were performed in MATHEMATICA, version 6.0 (Wolfram Research, 2005).

Statistical analysis

For all statistical analyses, we examined the crania and ossa coxae of each species separately. First, we examined size differences in both structures between the sexes. To test for significant sex differences in the cranium and the os coxae, we performed an analysis of variance (ANOVA) with log centroid size as the dependent variable and sex as the independent variable. Finally, to evaluate how sexual size dimorphism in both structures varied between the mainland and island species, we performed a two-way ANOVA with log centroid size as the dependent variable and sex and species as the independent variables.

To test for significant sexual dimorphism in shape, we performed a multivariate analyses of variance (MANOVA) using the PW scores and uniform component as the dependent variables, and sex as the independent variable. We then compared the randomization results of the shape indices to the results of the MANOVA. To test for differences in shape between the sexes while holding log centroid size constant, we conducted two multivariate analyses of covariance (MANCOVAs) using the PW scores and the uniform component as the dependent variables, sex as the independent variable and log centroid size as a covariate. Before interpreting the main effects of sex, we performed an analysis including the interaction term (sex × centroid size). A significant interaction between body size and sex would suggest a difference in allometry between sexes within each species and prevent us from interpreting the main effects. Finally, for all of these multivariate analyses, we also report the partial eta squared (η_p^2), defined as the proportion of the effect + error variance attributed to each effect (Tabachnick & Fidell, 1996).

To evaluate how sexual shape dimorphism in both structures varied between the two species, we performed a two-way MANOVA with the PW scores and the uniform component as the dependent variables and sex and species as the independent variables.

Finally, to describe the patterns of variation between the sexes, we used the CVAGen6l (Sheets, 2006) software package to perform a canonical variates analysis (CVA) of the unweighted partial warps scores matrix for each element in the two species. The partial warp scores were then regressed onto the significant canonical axes (0.05 level of significance) to produce deformation grids representing shape changes associated with each axis (Rohlf, Loy & Corti, 1996). The CVA analyses also generate assignments of group membership and assess the level of accurate group membership prediction from shape data using a jackknife procedure (Nolte & Sheets, 2005). We report these group assignments as well.

RESULTS

Size and shape dimorphism in the cranium

Cranial size dimorphism

In the cranium, size dimorphism metrics for both species were quite low in *U. littoralis* but higher by contrast in *U. cinereoargenteus* and nonsignificant based on the randomiozations except for size index 2 in *U. cinereoargenteus* (Table 1). Our ANOVA results also indicated that cranial sexual size dimorphism was not significant in either species (Table 2).

When the cranial size data for both species were grouped and used in a two-way ANOVA of cranial log centroid size, we found that sex was not a significant factor, but that species was, indicating that size differs between species, but not as a function of sex (Fig. 2, Table 2).

Cranial shape dimorphism

The magnitude of shape dimorphism in each species, although slightly greater in *U. cinereoargenteus* than in *U. littoralis* (Table 1), was not significant for either species based on the randomizations. The within-species MANOVA results also indicated that sexual shape dimorphism was not significant in the crania of either species (Table 3). In addition, the within-species MANCOVA results (Table 3) indicated that allometric trends do not differ between males and females in either species (the sex × log centroid inter-

Table 1. Comparisons of indices of size (1 and 2) and shape (1 and 2) dimorphism for the cranium and pelvis for both species

	Size dimorphism					Shape dimorphism				
	Overall size	♀ Size	♂ Size	Size index 1	Size index 2	Variance	♀ Variance	♂ Variance	Shape index 1	Shape index 2
Urocyon cinereoargenteus										
Crania	16.754 (3.067)	16.375 (2.850)	17.133 (3.077)	0.097 (93%)	–0.046 (96%)*	0.001	0.001	0.000	0.473 (90%)	–0.008 (60%)
Os coxae	9.752 (0.457)	9.641 (0.462)	9.864 (0.439)	0.055 (83%)	–0.023 (92%)	0.004	0.004	0.004	0.055 (93%)	–0.007 (55%)
Urocyon littoralis										
Crania	13.115 (0.780)	13.102 (0.783)	13.129 (0.801)	0.000 (10%)	–0.002 (55%)	0.000	0.000	0.000	0.038 (73%)	–0.005 (55%)
Os coxae	8.864 (4.450)	7.804 (0.448)	9.924 (6.42)	0.671 (100%)*	–0.272 (100%)*	0.003	0.003	0.003	0.637 (99%)*	0.020 (72%)

Descriptive statistics for size in the overall sample and for each sex are included: mean centroid sizes (cm) and their variances in parentheses. For the shape data, we include the variances in the overall sample and for each sex. Significance for all indices was determined using 10 000 permutations. The number in parentheses is the percent of runs with a lower value than the calculated index; values greater than 95% are significant at the 5% level (*$P < 0.05$).

action was not significant) and cranial shapes do not differ between the sexes (the main effect of sex was not significant). However, in *U. cinereoargenteus*, the main effect of centroid size was significant; indicating that, in this species shape varies as size changes when sex is controlled for.

When the cranial shape data for both species was grouped and used in a two-way MANOVA of shape with sex and species as fixed factors (Table 3), we found that both sex and species were significant, but not their interaction, indicating sexual cranial shape differences exist when controlling for species and that species shape differences occur when controlling for sex. The lack of significance in the interaction term indicates that the degree of sexual shape dimorphism does not differ between the two species.

Patterns of cranial shape dimorphism

The CVAs of the unweighted PW scores matrices for the crania in each species using sex as the independent variable all parallel the results of the MANOVAs as expected. Although CVA describes the maximum variance between groups (Zelditch *et al.*, 2004; Nolte & Sheets, 2005), a significant canonical variates axis differentiating cranial shape between the sexes was not generated for either species. In *U. cinereoargenteus*, for group membership prediction, female crania were correctly assigned 100% of the time but males were incorrectly assigned as females 100% of the time. In *U. littoralis*, for group membership prediction, female crania were correctly assigned 100% of the time and males were incorrectly assigned as females 100% of the time. Thus, for both species, reliable prediction as to sex could not be made using cranial shape data.

Overall, when CV 1 was plotted against CV 2 for both cranium datasets and we examined these along with the associated deformation grids of each sex relative to the reference, little to no differentiation in cranial shape between the sexes is apparent (Fig. 3A, C). In terms of shape differences, the little differentiation that is present, is seen primarily in *U. cinereoargenteus* (Fig. 4A) centered around the narrower and slightly shorter pre-maxilla (landmarks 1, 2, and 3) and narrower palate (landmarks 4–8) and zygomatic region (landmarks 9 and 10) of females versus males. These patterns of differentiation are also seen in *U. littoralis* males and females but at a lesser magnitude such that even the ×20 magnification in deformation cannot pick up discernible shape differences (Fig. 4B).

Size and shape dimorphism in the os coxae

Os coxae size dimorphism

In the os coxae, size dimorphism metrics varied considerably between species (Table 1) with *U. littoralis*

Table 2. Tests for sex dimorphism in size of the cranium and os coxae using log centroid size

Element	ANOVA summary statistics for *Urocyon cinereoargenteus*	
Cranium	Sex:	$F_{1,66} = 3.144$, $P = 0.081$, Adjusted $R^2 = 0.031$
Os coxae	Sex:	$F_{1,66} = 1.889$, $P = 0.174$, Adjusted $R^2 = 0.013$
Element	ANOVA summary statistics for *Urocyon littoralis*	
Cranium	Sex:	$F_{1,62} = 0.130$, $P = 0.908$, Adjusted $R^2 = -0.016$
Os coxae	Sex:	$F_{1,80} = 31.697$, $P < 0.01$, Adjusted $R^2 = 0.275$*
Element	ANOVA summary statistics for combined species datasets	
Cranium	Sex:	$F_{1,128} = 2.332$, $P = 0.129$, Adjusted $R^2 = 0.653$
	Species:	$F_{1,128} = 244.71$, $P < 0.01$*
	Sex × species:	$F_{1,128} = 1.966$, $P = 0.163$
Os coxae	Sex:	$F_{1,146} = 28.408$, $P < 0.01$*, Adjusted $R^2 = 0.336$
	Species:	$F_{1,146} = 26.626$, $P < 0.01$*
	Sex × species:	$F_{1,146} = 18.492$, $P < 0.01$*

F- and *P*-values for analysis of variance (ANOVA) on the cranium and os coxae within each species and with both species combined. Dependent variable = centroid size, independent variable = sex.
*$P < 0.05$.

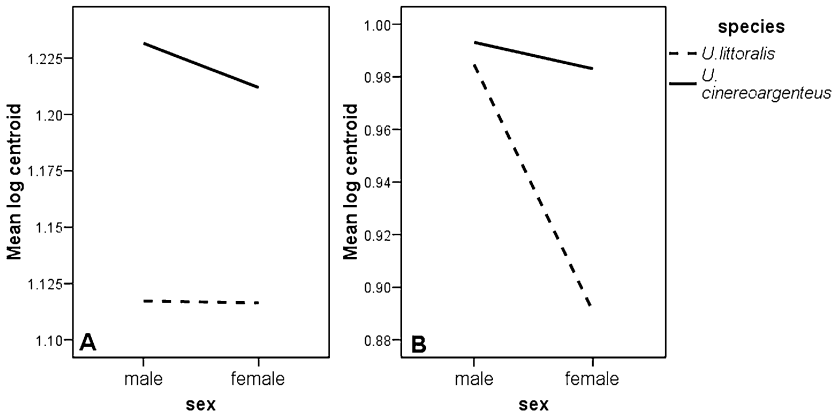

Figure 2. Bivariate plots of mean log centroid size by sex, separated by species for cranium (A) and os coxae (B). Solid lines represent *Urocyon cinereoargenteus* and dashed lines represent *Urocyon littoralis*.

exhibiting a much greater magnitude of sexual size dimorphism than *U. cinereoargenteus*. Size dimorphism was significant in the former but not in the latter species based on the randomizations. Our ANOVA results also indicated that size dimorphism was significant in *U. littoralis* but not *U. cinereoargenteus* (Table 2).

When the data for both species were grouped and used in a two-way ANOVA of log os coxae centroid size, we found that the sex × species interaction was significant along with the main effects of sex and species. This result indicates that the size of the os coxae differs between the sexes, more so in *U. littoralis* than in *U. cinereoargenteus* (Fig. 2, Table 2).

Os coxae shape dimorphism

The magnitude of shape dimorphism, when compared between species, was greater in *U. littoralis* than in *U. cinereoargenteus* with os coxae shape dimorphism marginally insignificant in *U. cinereoargenteus* for shape index 1 and significant in *U. littoralis* only for shape index 1 based on the randomizations (Table 1). The within species MANOVA results indicated that os coxae shape dimorphism was significant in both species (Table 3).

The within species MANCOVAs (Table 3) demonstrated that, in *U. littoralis*, allometric trends differed between male and female os coxae shapes (the sex × centroid size interaction was significant). In *U. cinereoargenteus*, allometric trends did not differ between males and females, and the full MANCOVA showed a significant difference in shape between the sexes when centroid size was controlled for.

When the os coxae shape data for both species was grouped and used in a two-way MANOVA of shape with sex and species as fixed factors, we found that

Table 3. Tests of shape sexual dimorphism for the cranium and os coxae of both species and for combined species datasets

	Cranium	Os coxae
MANOVA (sex) for *Urocyon cinereoargenteus*	Wilk's $\lambda = 0.682$, $F_{24,43} = 0.841$, $P = 0.670$ $\eta_p^2 = 0.319$	Wilk's $\lambda = 0.490$, $F_{24,43} = 1.860$, $P = 0.037$* $\eta_p^2 = 0.510$
MANOVA (sex) for *Urocyon littoralis*	Wilk's $\lambda = 0.513$, $F_{21,24} = 1.541$, $P = 0.112$ $\eta_p^2 = 0.487$	Wilk's $\lambda = 0.363$, $F_{24,57} = 4.159$, $P < 0.001$* $\eta_p^2 = 0.637$
MANOVA for combined species datasets	Cranium	os coxae
Sex	Wilk's $\lambda = 0.689$, $F_{24,105} = 1.977$, $P = 0.010$* $\eta_p^2 = 0.311$	Wilk's $\lambda = 0.534$, $F_{24,123} = 4.471$, $P < 0.01$* $\eta_p^2 = 0.466$
Species	Wilk's $\lambda = 0.193$, $F_{24,105} = 18.290$, $P < 0.01$* $\eta_p^2 = 0.807$	Wilk's $\lambda = 0.325$, $F_{24,123} = 10.625$, $P < 0.01$* $\eta_p^2 = 0.675$
Sex × species	Wilk's $\lambda = 0.833$, $F_{24,105} = 0.876$, $P = 0.632$ $\eta_p^2 = 0.167$	Wilk's $\lambda = 0.834$, $F_{24,123} = 1.023$, $P = 0.443$ $\eta_p^2 = 0.166$
MANCOVA for *Urocyon cinereoargenteus*	Cranium	os coxae
Sex	Wilk's $\lambda = 0.554$, $F_{24,41} = 1.374$, $P = 0.181$ $\eta_p^2 = 0.446$	Wilk's $\lambda = 0.611$, $F_{24,41} = 1.086$, $P = 0.399$ $\eta_p^2 = 0.389$
Log centroid size	Wilk's $\lambda = 0.385$, $F_{24,41} = 2.733$, $P < 0.01$* $\eta_p^2 = 0.615$	Wilk's $\lambda = 0.515$, $F_{24,41} = 1.612$, $P = 0.087$ $\eta_p^2 = 0.485$
Sex × log centroid size	Wilk's $\lambda = 0.550$, $F_{24,41} = 1.399$, $P = 0.169$ $\eta_p^2 = 0.450$	Wilk's $\lambda = 0.618$, $F_{24,41} = 1.057$, $P = 0.428$ $\eta_p^2 = 0.382$
MANCOVA for *Urocyon littoralis*	Cranium	Os coxae
Sex	Wilk's $\lambda = 0.659$, $F_{24,37} = 0.798$, $P = 0.717$ $\eta_p^2 = 0.341$	Wilk's $\lambda = 0.551$, $F_{24,55} = 1.867$, $P = 0.029$* $\eta_p^2 = 0.449$
Log centroid size	Wilk's $\lambda = 0.589$, $F_{24,37} = 1.074$, $P = 0.414$ $\eta_p^2 = 0.411$	Wilk's $\lambda = 0.385$, $F_{24,55} = 3.668$, $P < 0.01$* $\eta_p^2 = 0.615$
Sex × log centroid size	Wilk's $\lambda = 0.662$, $F_{24,37} = 0.787$, $P = 0.729$ $\eta_p^2 = 0.338$	Wilk's $\lambda = 0.544$, $F_{24,55} = 1.918$, $P = 0.024$* $\eta_p^2 = 0.456$

MANOVA, multivariate analysis of variance. Main effects for the multivariate analyses of covariance (MANCOVA) analyses are provided if the interaction terms between sex and log centroid size, or between sex, species, and log centroid size, were nonsignificant. Otherwise, the results of the original analysis are provided.
*$P < 0.05$.

both sex and species were significant, but not their interaction. This result indicated that the shape of the os coxae differs between the sexes when averaging across species. The lack of significance in the interaction term indicates that the degree of os coxae sexual shape dimorphism does not significantly differ between the two species.

Patterns of os coxae shape dimorphism

The results of CVAs of os coxae shape parallel those of the MANOVA and the axis differentiating os coxae shape between the sexes was significant for both species. Note that at most one axis can be significant in a CVA with two groups.

For the *U. cinereoargenteus* os coxae dataset, the CV axis had significant differentiation between the sexes (Wilk's $\lambda = 0.491$, $\chi^2 = 38.470$, d.f. = 24, $P = 0.031$). For group membership prediction, female ossa coxae were correctly assigned 82.4% of the time and males were correctly assigned 91.2% of the time. In the *U. littoralis* os coxae dataset, the CVA produced a similar result with the CV axis producing significant differentiation between the sexes (Wilk's $\lambda = 0.363$, $\chi^2 = 68.827$, d.f. = 24, $P < 0.001$). For group membership prediction, female ossa coxae were correctly assigned 87.8% of the time and males were correctly assigned 85.3% of the time. These results indicate that sex can be predicted fairly well using os coxae shape in both species.

Os coxae shape was more differentiated between the sexes in *U. littoralis* than in *U. cinereoargenteus* as revealed by plots of CV 1 and CV 2 (Fig. 3C, D). However, the actual shape differences between the sexes were similar in both species (Fig. 5A, B). In

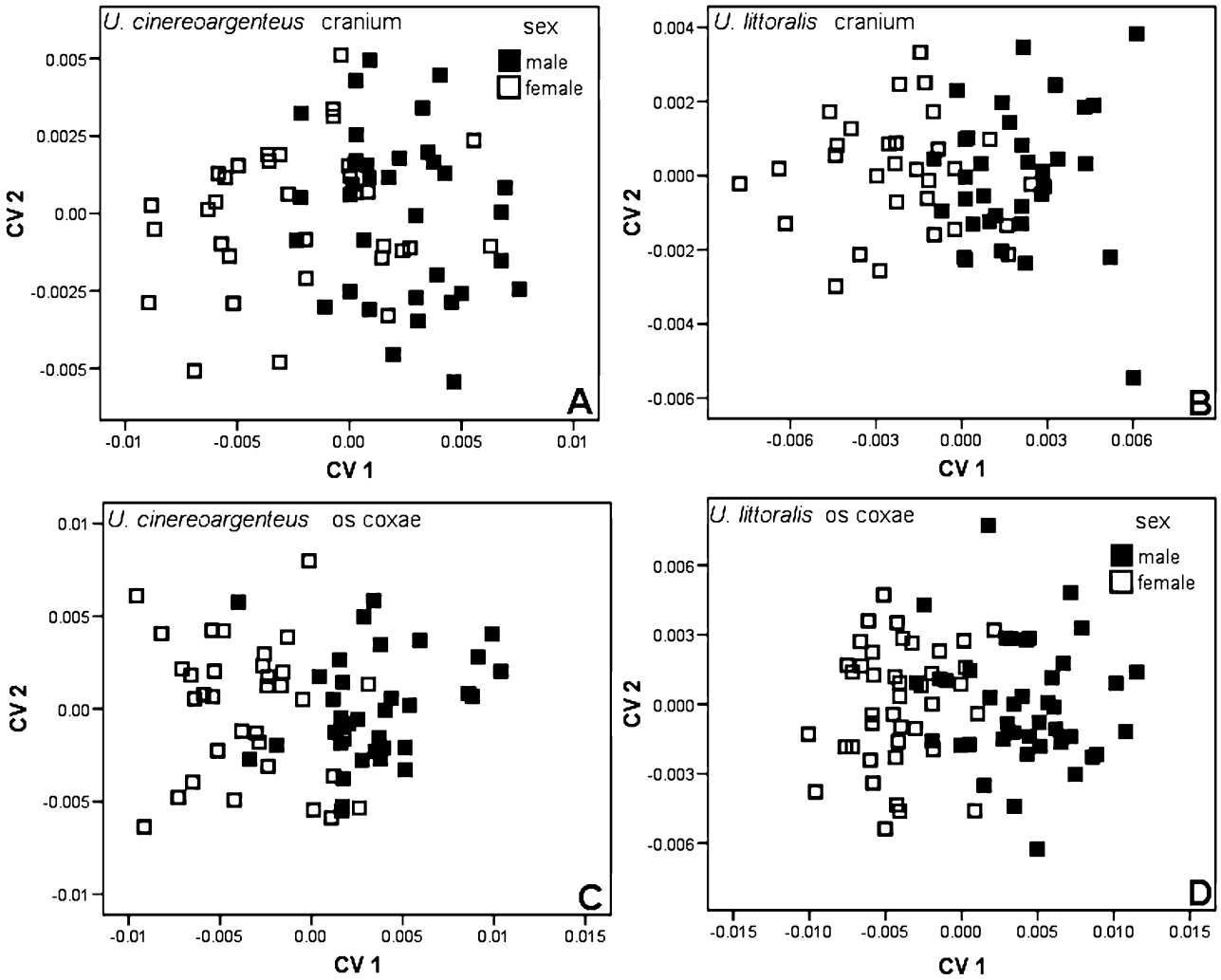

Figure 3. Scatterplot of canonical variates axes 1 and 2 for canonical variates analysis analyses of the cranium and pelves of *Urocyon cinereoargenteus* (A, C) and *Urocyon littoralis* (B, D). Black symbols indicate males; white symbols indicate females.

particular, differentiation was greatest around the acetabulum, obturator foramen and pubic ramus.

Males tend to have a broader (dorsal displacement at landmark 6) and longer (increased distance between landmarks 3 and 4) obturator foramina (landmarks 3–6) than females, with broadening being greater in *U. cinereoargenteus* and lengthening greater in *U. littoralis*. The acetabulum is also proportionately larger in males than in females as demonstrated by the increased distance between landmarks 8 and 9. The iliopubic ramus is relatively longer (landmarks 1 and 14) and wider (landmarks 2, 8, and 14) in females than in males and the pubic symphysis (landmarks 1 and 2) is shorter in females than males. Both of these trends were slightly magnified in *U. littoralis* versus *U. cinereoargenteus*.

DISCUSSION

SIZE AND SHAPE DIMORPHISM IN THE CRANIUM

Our results indicate that, by and large, no significant dimorphism in shape or centroid size exists in the crania of either species, with the exception of size index 2 in *U. cinereoargenteus*. The differences in magnitude of size dimorphism (size indices 1 and 2) are much greater than differences in magnitude of shape dimorphism (shape indices 1 and 2) between the species (Table 1). Consequently, although our analysis of variance results for size and shape confirm that the magnitudes of cranial size and shape dimorphism do not vary significantly between these two species, there is a potential trend of greater cranial size dimorphism in *U. cinereoargenteus* compared to

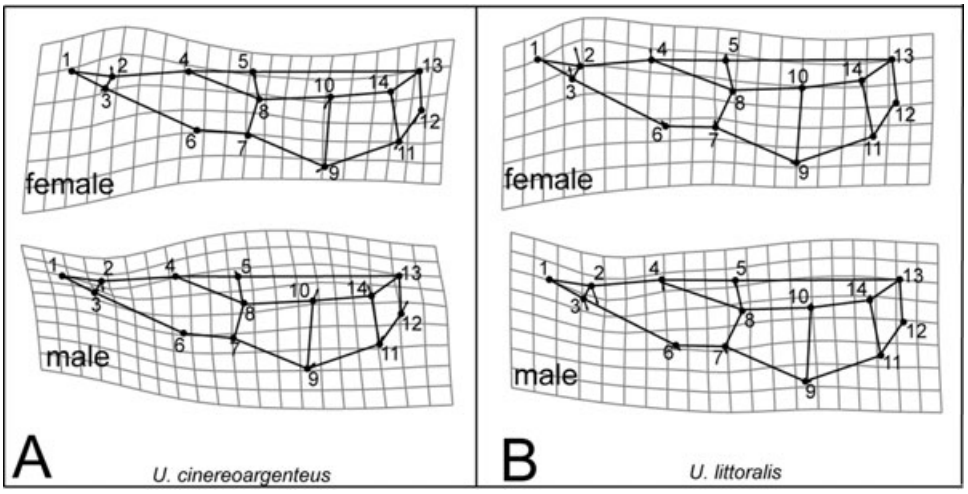

Figure 4. Deformations of cranial shape for the mean female and mean male in *Urocyon cinereoargenteus* (A) and *Urocyon littoralis* (B) along CV 1 and CV 2 produced by the canonical variates analysis analyses. All deformations are shown at a 20× magnification.

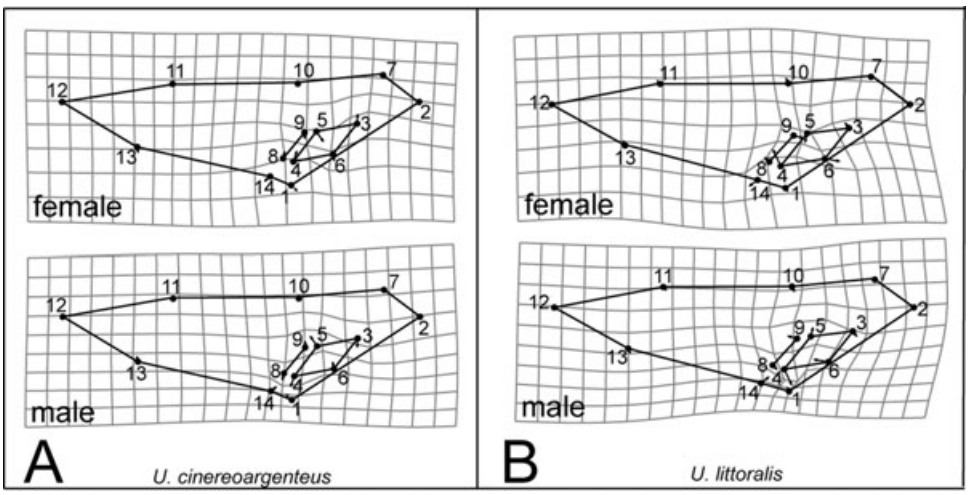

Figure 5. Deformations of os coxae shape for the mean female and mean male in *Urocyon cinereoargenteus* (A) and *Urocyon littoralis* (B) along CV 1 and CV 2 produced by the canonical variates analysis analyses. All deformations are shown at × 20 magnification.

U. littoralis. However, there appears to be no allometric pattern in cranial dimorphism of the genus *Urocyon*.

Our overall finding that cranial size and shape dimorphism is relatively small is consistent with previous studies that investigated dimorphism in other animals and more specifically in other carnivore groups. These studies show that size dimorphism in monogamous species is negligible (Ralls, 1977). In carnivores and canids, in particular, size dimorphism (in terms of individual craniodental measures), although significant, is low compared to other carnivore groups and is uncorrelated with either body size or cranial size (Van Valkenburgh & Wayne, 1994; Gittleman & Van Valkenburgh, 1997). The magnitude of dimorphism measured in canids by those studies was similar to that found in *Urocyon* in the present study.

Although overall cranial size dimorphism is minimal in canids, some cranial features have been shown to vary between the sexes. Previous studies of cranial size dimorphism using linear craniodental measurements meant to assess cranial shape and proportion showed that, in general, males tend to have larger canines and carnassials and longer skulls than females (Gittleman & Van Valkenburgh, 1997; Van Valkenburgh & Sacco, 2002). In a study that quantified both shape and size differences, Lynch

(1996) found that male red foxes (*Vulpes vulpes*) are not only larger than females, but they also have longer skulls and a narrower post-orbital constriction.

Our shape data, although restricted to the ventral cranium, parallel the results from these previous studies. In particular, our results demonstrate that male skulls are slightly more elongate and wider in the rostral region than female skulls. Even though we sampled the canine only superficially (landmark 3), the differences we observed between male and female skulls may be due to larger size of that tooth in males. Canine size has been shown to be an important feature in characterizing dimorphism patterns in carnivores because the magnitude of dimorphism is high and is closely associated with mating system but not body size (Gittleman & Van Valkenburgh, 1997; Van Valkenburgh & Sacco, 2002).

Contrast with other studies

The lack of size dimorphism in the cranium of *Urocyon* in our results differs from previous studies that found significant dimorphism using linear measurements (Collins, 1982; Wayne *et al.*, 1991; Collins, 1993). The difference in our conclusions is probably due to different sampling and not to the fact that we used centroid size instead of specific linear measurements. First, cranial centroid size has been shown to be highly correlated with body mass and body length in mammals (Hood, 2000). Second, a larger number of variables used in a multivariate analysis of linear data may not result in an increase in statistical power, because of the inherently high correlation among linear measurements of the same structure (Zelditch *et al.*, 2004). However, our sample sizes were smaller than those of other studies because we were limited to specimens with postcrania. Consequently, we pooled data from different populations within each species, possibly masking small within population sex differences in cranial size. Indeed, Collins (1993) and Wayne *et al.* (1991) found that sex differences varied as a function of population in two-way MANOVA of sex and population.

We tested whether our data might contain sexual size dimorphism at the population level for both the cranium and os coxae using a two-way ANOVA of log centroid size for *U. littoralis*, where our samples were larger, with sex and sub-species as independent variables. We still found no significant size difference between sexes in the cranium ($F_{1,52} = 0.146$, $P = 0.704$), but we did find significant size differences between sub-species ($F_{5,52} = 2.754$, $P = 0.028$). Because we found no sex × sub-species interaction ($F_{1,52} = 0.146$, $P = 0.704$), it is unlikely that the sub-species differences were due to biased sex ratios in our samples.

In the os coxae we did find significant differences at both the sex and sub-species levels (sex: $F_{1,70} = 33.97$, $P < 0.01$; sub-species: $F_{5,70} = 3.88$, $P < 0.01$). Also, the interaction between sex × sub-species was almost significant at the 0.05 level (sex × sub-species: $F_{5,70} = 2.27$, $P = 0.056$). Thus, there may be small but significant size dimorphism at the population level, but the sex differences in size are smaller than inter-population size differences (Fig. 6).

Size and shape dimorphism in the os coxae

Unlike the cranium, the os coxae was dimorphic in both size and shape albeit in just one species, *U. littoralis*. The os coxae size was significantly size dimorphic in *U. littoralis*, which also had considerably higher shape index magnitudes (Table 1). Our results also indicate that the two species differ in the magnitude of pelvic size dimorphism with the smaller

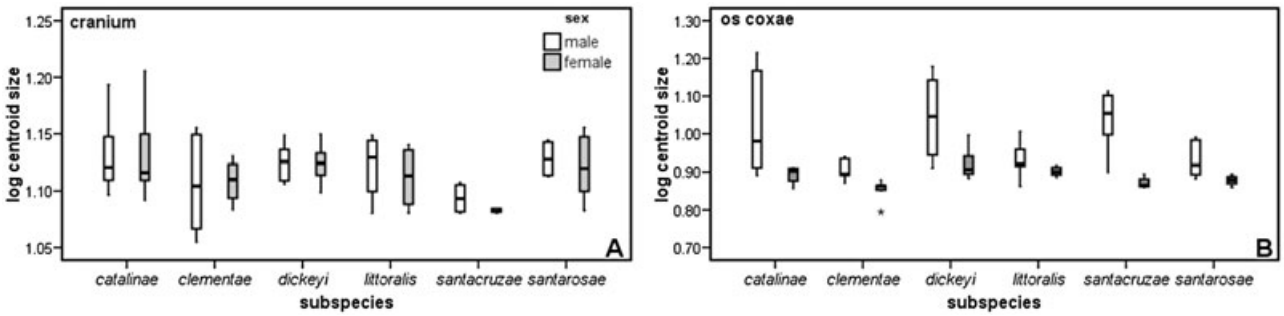

Figure 6. Box plots of mean log centroid size for the cranium (A) and ossa coxae (B) of the six *Urocyon littoralis* sub-species. Each sub-species in represented as follows: *U. l. catalinae* (crania: six males, six females, ossa coxae: five males, five females), *U. l. clementae* (crania: five males, four females, ossa coxae: five males, five females), *U. l. dickeyi* (crania: seven males, seven females, ossa coxae: eight males eleven females), *U. l. littoralis* (crania: four males, four females, ossa coxae: eight males, eight females), *U. l. santacruzae* (crania: six males, five females, ossa coxae: seven males, nine females), *U. l. santarosae* (crania: four males, six females, ossa coxae: eight males, four females).

species having a greater magnitude of dimorphism than the larger species (Table 2).

Although the MANOVAs indicated that os coxae shape dimorphism was significant in both species, only in *U. littoralis* was there a significant shape dimorphism index (Table 2) and significant allometry between the sexes (Table 3). This significant allometric effect indicates that pelvic size differences between the sexes are closely associated with pelvic shape differences between the sexes.

In terms of shape dimorphism patterns, the os coxae of *Urocyon* males had a wider and longer obturator foramen and a wider acetabulum than females. These two differences are likely associated with the larger body size and greater muscle mass of males. By contrast, the female os coxae had a longer and wider iliopubic ramus and a shorter pubic symphysis and these differences are likely associated with the partuitive function of the female structure. These shape differences (along with the associated size differences mentioned above) in the os coxae of male and female foxes potentially encompass both differences in body size and reproductive function of the two sexes.

Links between os coxae shape and size

In many mammalian species, pelvic dimorphism has been associated with the size of offspring relative to the mother. In particular, females of numerous species tend to have longer pubic bones than males (Schultz, 1949; Dunmire, 1955; Mobb & Wood, 1977; Arsuaga & Carretero, 1994; Berdnikovs *et al.*, 2007). This dimorphism in the pubis has been previously associated with the magnitude of the maternal size to offspring size ratio such that increased offspring size relative to maternal size requires an enlargement of the birth canal leading to a lengthening of the pubis (Schultz, 1949; Leutenegger, 1974; Mobb & Wood, 1977; Ridley, 1995; Berdnikovs, 2005).

Although those studies found a relationship between the maternal size and offspring size, the direction of that relationship varies across taxonomic groups. At one end of the spectrum are the majority of carnivores, in which larger species have fewer and relatively large offspring (with the exclusion of canids) (Gittleman & Van Valkenburgh, 1997; Webster, Gittleman & Purvis, 2004; Berdnikovs, 2005). However, canids appear to follow a primate pattern where, smaller species have fewer and relatively large offspring (Leutenegger, 1974; Mobb & Wood, 1977; Geffen & McDonald, 1992; Geffen *et al.*, 1996).

Data on litter size are available from the literature for *U. littoralis*, but only anecdotal information on neonatal birth weights exists. This species has an average litter number of 2.2 (Ferguson & Larivière, 2002). The available data for two pups born in captivity at the Santa Barbara Zoo (A. Varsik, pers comm.) show a recorded birth weight in the range 61.4–90 g. Data are better for *U. cinereoargenteus*, which has a litter size of 3.8 and a mean birth weight of 86 g (Ferguson & Larivière, 2002). These limited data suggest that the general canid pattern holds for *Urocyon*, with the smaller species having relatively fewer and larger offspring than the larger.

Our results suggest that pelvic morphology and reproductive life-history characteristics such as the interaction between offspring size and female size covary, but we argue that the reason that such life-history differences exist in carnivores may also be associated with differing modes of locomotion. Canids are cursors with the capacity to run for long distances (Gregory, 1912; Jenkins, 1971; Jenkins & Camazine, 1977; Van Valkenburgh, 1987; Carrano, 1999); as such, they have a limited range of motion at the hip joint, largely restricted to parasagittal rotation (Jenkins & Camazine, 1977). Thus, the locomotor requirements for the canid style of cursoriality likely include a relatively narrow pelvic breadth. Recent work on quantitative trait loci in the skeleton of domestic dogs shows that pelvic morphology is associated with biomechanical performance (Carrier *et al.*, 2005). Highly cursorial breeds such as greyhounds have pelves that are larger, longer, and narrower than stocky, short-legged breeds such as pit bulls, which have smaller, wider, shorter pelves. This biomechanical requirement potentially conflicts with increases in offspring size. In order to give birth to proportionately larger offspring, females require broader pelves, whereas efficient running requires narrow ones. Therefore, females will experience increased morphological differentiation relative to males and this scales with overall size; the smaller the overall body size, the greater the difference.

Thus, in canids, as in primates, locomotor mode may play a critical role in determining the degree of sexual dimorphism present due to conflicting pelvic functions. Other carnivores on the other hand, may have locomotor modes that do not conflict with reproductive function and, in these cases, allometric relationships, and therefore the mating system, may play a greater role in pelvic morphology. Although, the relationship between pelvic morphology and locomotor mode has been examined (Maynard Smith & Savage, 1955; Jenkins & Camazine, 1977; Berdnikovs *et al.*, 2007) and the allometric relationships between maternal size and offspring size are known (Schultz, 1949; Leutenegger, 1974; Mobb & Wood, 1977; Ridley, 1995), the covariation between these factors and the degree of pelvic sexual dimorphism present remain untested. Future work spanning major carnivore groups should shed further light on how competing functional forces have shaped pelvic shape and size differentially in males and females.

CONCLUSIONS

Our examination of cranial and pelvic size and shape in this study revealed that cranial and pelvic size and shape dimorphism differ in magnitude within these two species. Our data showed no significant dimorphism in either size or shape of the cranium and no concrete indication that the level of dimorphism differed between the two species, a pattern consistent with the results obtained in previous studies. By comparison, our data on os coxae size and shape dimorphism showed greater size and shape dimorphism than in the cranium, particularly in the smaller versus the larger species. These results indicate that a potentially different and complicated suite of interactions is at play in the pelvis than in the cranium; one that is likely associated with parturition and locomotion.

Currently, sexual dimorphism studies primarily focus on body size. Although some studies that include other body parts exist (Fairbairn, 2005), they use linear measures and body size is necessarily embedded in these types of data. Our results suggest that, although allometric relationships are present in dimorphism patterns of individual body structures, the effect of overall body size may vary in magnitude from region to region and fluctuate in association with other factors. Given these results, it may not be appropriate to expect that dimorphism patterns are uniform throughout an organism and parallel those that we see for body size.

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REFERENCES

Abouheif E, Fairbairn DJ. 1997. A comparative analysis of allometry for sexual size dimorphism: Assessing Rensch's Rule. *American Naturalist* **149:** 540–562.

Arsuaga JL, Carretero JM. 1994. Multivariate analysis of the sexual dimorphism of the hip bone in a modern human population and in early hominids. *American Journal of Physical Anthropology* **93:** 241–257.

Bailey RC, Byrnes J. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. *Systematic Zoology* **39:** 124–130.

Berdnikovs S. 2005. Evolution of sexual dimorphism in mustelids. DPhil Thesis, University of Cincinnati.

Berdnikovs S, Bernstein M, Metzler A, German RZ. 2007. Pelvic growth: ontogeny of size and shape sexual dimorphism in rat pelves. *Journal of Morphology* **268:** 12–22.

Bookstein FL. 1991. *Morphometric tools for landmark data: geometry and biology*. New York, NY: Cambridge University Press.

Cardini A, O'Higgins P. 2004. Patterns of morphological evolution in *Marmota* (Rodentia, Sciuridae): geometric morphometrics of the cranium in the context of marmot phylogeny, ecology and conservation. *Biological Journal of the Linnean Society* **82:** 385–407.

Cardini A, Thorington RW. 2006. Postnatal ontogeny of marmot (Rodentia, Sciuridae) crania: allometric trajectories and species divergence. *Journal of Mammalogy* **87:** 201–215.

Cardini A, Tongiorgi P. 2003. Yellow-bellied marmots (*Marmota flaviventris*) 'in the shape space' (Rodentia, Sciuridae): sexual dimorphism, growth and allometry of the mandible. *Zoomorphology* **122:** 11–23.

Carrano MT. 1999. What, if anything, is a cursor? Categories versus continua for determining locomotor habit in mammals and dinosaurs. *Journal of Zoology, London* **247:** 29–47.

Carrier DR, Chase K, Lark KG. 2005. Genetics of canid skeletal variation: size and shape of the pelvis. *Genome Research* **15:** 1825–1830.

Collins PW. 1982. Origin and differentiation of the Island Fox: a study of evolution in insular populations. MA Thesis, University of California Santa Barbara.

Collins PW. 1993. Taxonomic and biogeographic relationships of the Island Fox (*Urocyon littoralis*) and Gray Fox (*Urocyon cinereoargenteus*) from Western North America. In Hochberg FG, ed. *Proceedings of the Third California Islands Symposium: Recent Advances in Research on the California Islands*. Santa Barbara, CA: Santa Barbara Museum of Natural History, 351–390.

Crooks KR, van Vuren D. 1996. Spatial organization of the Island Fox (*Urocyon littoralis*) on Santa Cruz Island, California. *Journal of Mammalogy* **77:** 801–806.

Dryden IL, Mardia KV. 1998. *Statistical shape analysis: Wiley series in probability and statistics*. New York, NY: John Wiley & Sons, Ltd.

Dunmire WW. 1955. Sex dimorphism in the pelvis of rodents. *Journal of Mammalogy* **36:** 356–361.

Fairbairn DJ. 2005. Allometry for sexual size dimorphism: testing two hypotheses for Rensch's Rule in the water strider Aquarius remigis. *American Naturalist* **166:** S69–S84.

Fairbairn DJ, Preziosi RF. 1994. Sexual selection and the evolution of allometry for sexual size dimorphism in the Water Strider, *Aquarius remigis*. *American Naturalist* **144:** 101–118.

Ferguson SH, Larivière S. 2002. Can comparing life histories help conserve carnivores? *Animal Conservation* **5:** 1–12.

Fritzell EK, Haroldson KJ. 1982. Urocyon cinereoargenteus. *Mammalian Species* 1–8.

Geffen E, Gompper ME, Gittleman JL, Luh H-K, MacDonald DW, Wayne RK. 1996. Size, life-history traits, and social organization in the Canidae: a reevaluation. *American Naturalist* **147:** 140–160.

Geffen E, McDonald DW. 1992. Small size and monogamy: spatial organization of Blanford's foxes, *Vulpes cana*. *Animal Behaviour* **44:** 1123–1130.

Gilbert DA, Lehman N, O'Brien SJ, Wayne RK. 1990. Genetic fingerprinting reflects population differentiation in the California Channel Island fox. *Nature* **344:** 764–767.

Gittleman JL, Van Valkenburgh B. 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny and behavioral ecology. *Journal of Zoology* **242:** 97–119.

Goldstein DB, Roemer GW, Smith DA, Reich DE, Bergman A, Wayne RK. 1999. The use of microsatellite variation to infer population structure and demographic history in a natural model system. *Genetics* **151:** 797–801.

Gregory WK. 1912. Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed mammals. *Annals of the New York Academy of Sciences* **22:** 267–294.

Grinnell J, Dixon J, Lindsdale JM. 1937. *Fur-bearing mammals of California: their natural history, systematic status and relations to man*. Berkeley, CA: University of California Press.

Hager LD. 1989. The evolution of sex differences in the hominid bony pelvis. DPhil Thesis, University of California, Berkeley.

Hall ER. 1981. *The mammals of North America*. New York, NY: John Wiley and Sons.

Hildebrand M, Goslow GE. 2001. *The analysis of vertebrate structure*. New York, NY: John Wiley and Sons.

Hood CS. 2000. Geometric morphometric approaches to the study of sexual size dimorphism in mammals. *Hystrix* **11:** 77–90.

Iguchi T, Irisawa S, Fukazawa Y, Uesugi Y, Takasugi N. 1989. Morphometric analysis of the development of sexual dimorphism of the mouse pelvis. *Anatomical Record* **224:** 490–494.

Jenkins FA. 1971. Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *Journal of Zoology, London* **165:** 303–315.

Jenkins FA, Camazine SM. 1977. Hip structure and locomotion in ambulatory and cursorial carnivores. *Journal of Zoology, London* **181:** 351–370.

Kachigan SK. 1991. *Multivariate statistical analysis*. New York, NY: Radius Press.

Leutenegger W. 1974. Functional aspects of pelvic morphology in simian primates. *Journal of Human Evolution* **3:** 207–222.

Leutenegger W. 1978. Scaling of sexual dimorphism in body size and breeding system in primates. *Nature* **272:** 610–611.

Leutenegger W, Larson S. 1985. Sexual dimorphism in the postcranial skeleton of New World primates. *Folia primatologica; International Journal of Primatology* **44:** 82–95.

Loison A, Gaillard J-M, Pelabon C, Yoccoz NG. 1999. What factors shape sexual size dimorphism in ungulates? *Evolutionary Ecology Research* **1:** 611–633.

Lovich JE, Gibbons JW. 1992. A review of techniques for quantifying sexual size dimorphism. *Growth, Development and Aging* **56:** 269–281.

Lynch JM. 1996. Sexual dimorphism in cranial size and shape among red foxes (*Vulpes vulpes*) from north east Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* **96B:** 21–26.

Lynch JM, Conroy JWH, Kitchener AC, Jefferies DJ, Hayden TH. 1996. Variation in cranial form and sexual dimorphism among five European populations of the otter (*Lutra lutra*). *Journal of Zoology, London* **238:** 81–96.

Lynch JM, O' Sullivan WM. 1993. Cranial form and sexual dimorphism in the Irish otter (*Lutra lutra*). *Proceedings of the Royal Irish Academy* **93:** 97–105.

Manly BFJ. 2006. *Randomization, bootstrap and Monte Carlo methods in biology,* 3rd edn. Texts in Statistical Science Series. Boca Raton, FL: Chapman & Hall.

Maynard Smith J, Savage RJG. 1955. Some locomotory adaptations in mammals. *Zoological Journal of the Linnean Society* **42:** 603–622.

Mobb GE, Wood BA. 1977. Allometry and sexual dimorphism in the primate innominate bone. *American Journal of Anatomy* **150:** 531–537.

Nolte A, Sheets HD. 2005. Shape based assignment tests suggest transgressive phenotypes in natural sculpin hybrids (Teleostei, Scorpaeniformes, Cottidae). *Frontiers in Zoology* **2:** 11.

Polly PD. 2001. On morphological clocks and paleophylogeography: towards a timescale for Sorex hybrid zones. *Genetica* **112–113:** 339–357.

Ralls K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *American Naturalist* **111:** 917–938.

Rensch B. 1960. *Evolution above the species level*. New York, NY: Columbia University Press.

Ridley M. 1995. Pelvic sexual dimorphism and relative neonatal brain size really are related. *American Journal of Physical Anthropology* **97:** 197–200.

Roemer GW, Smith DA, Garcelon DK, Wayne RK. 2001. The behavioural ecology of the Island Fox (*Urocyon littoralis*). *Journal of Zoology* **255:** 1–14.

Rohde TD. 1966. Skeletal variation in Gray Fox from southern Illinois. MS Thesis, University of Illinois.

Rohlf FJ. 2006. *tpsDIG2*. 2.10 edn. New York, NY: Department of Ecology and Evolution, State University of New York.

Rohlf FJ. 2007. *tpsRelw*. 1.45 edn. New York, NY: Department of Ecology and Evolution, State University of New York.

Rohlf FJ, Loy A, Corti M. 1996. Morphometric analysis of Old World Talpidae (Mammalia, Insectivora) using partial-warp scores. *Systematic Biology* **45:** 344–362.

Rohlf FJ, Slice D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* **39:** 40–59.

Rosenberg KR, Trevathan W. 2002. Birth, obstetrics and human evolution. *BJOG: An International Journal of Obstetrics and Gynaecology* **109:** 1199–1206.

Rosenberg KR, Trevathan W. 2005. Bipedalism and human birth: the obstetrical dilemma revisited. *Evolutionary Anthropology: Issues, News, and Reviews* **4:** 161–168.

Schultz AH. 1949. Sex differences in the pelves of primates. *American Journal of Physical Anthropology* **7:** 401–424.

Sheets HD. 2006. *CVAGen6L*. Buffalo, NY: Department of Physics. Canisius College.

Smith RJ. 1999. Statistics of sexual size dimorphism. *Journal of Human Evolution* **36:** 423–459.

Sokal RR, Rohlf FJ. 1981. *Biometry*. San Francisco, CA: W.H. Freeman and Company.

Tabachnick BG, Fidell LS. 1996. *Using multivariate statistics*. New York, NY: HarperCollins College Publishers.

Tague RG. 2003. Pelvic sexual dimorphism in a metatherian, *Didelphis virginiana*: implications for eutherians. *Journal of Mammalogy* **84:** 1464–1473.

Uesugi Y, Ohta Y, Asashima M, Iguchi T. 1992. Comparative study of sexual dimorphism of the innominate bone in rodents and amphibians. *Anatomical Record* **234:** 432–437.

Van Valkenburgh B. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. *Journal of Vertebrate Paleontology* **7:** 162–182.

Van Valkenburgh B, Sacco T. 2002. Sexual dimorphism, social behavior and intrasexual competition in large Pleistocene carnivorans. *Journal of Vertebrate Paleontology* **22:** 164–169.

Van Valkenburgh B, Wayne RK. 1994. Shape divergence associated with size convergence in sympatric east African jackals. *Ecology* **75:** 1567–1581.

Washburn SL. 1948. Sex differences in the pubic bone. *American Journal of Physical Anthropology* **6:** 199–208.

Wayne RK, George SB, Gilbert D, Collins PW, Kovach SD, Girman D, Lehman N. 1991. A morphologic and genetic study of the Island Fox, *Urocyon littoralis*. *Evolution* **45:** 1849–1868.

Webster AJ, Gittleman JL, Purvis A. 2004. The life history legacy of evolutionary body size change in carnivores. *Journal of Evolutionary Biology* **17:** 396–407.

Weckerly FW. 1998. Sexual-size dimorphism: Influence of mass and mating Systems in the most dimorphic mammals. *Journal of Mammalogy* **79:** 33–52.

Wolfram Research I. 2005. *Mathematica edition*. Version 5.2 edn. Champaign, IL: Wolfram Research, Inc.

Zelditch ML, Swiderski DL, Sheets HD, Fink WL. 2004. *Geometric morphometrics for biologists: a primer*. London: Elsevier Academic Press.