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Effects of Parity on Pelvic Size and Shape Dimorphism in *Mus*

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ABSTRACT The pelvis is a sexually dimorphic structure and although the causes of that dimorphism have long been studied, relatively little is known regarding the effects of partuitive events on the magnitude of that dimorphism. Here, we use a sample of *Mus musculus domesticus* to contrast dimorphism in body length and os coxae size and shape between males and parous and nulliparous females. We also test for correlations between relative litter size (L/M) and relative offspring size (O/M) with body length and os coxae size and shape in parous females. Males had greater body length than nulliparous females but were not different from parous females. Females as a whole had the largest os coxae, with parous females having the largest and males the smallest. Os coxae shape was also significantly different between groups and was most divergent between parous females and males than between nulliparous females and males. Os coxae shape differences between females are associated with differences in body length between females and O/M is correlated with os coxae shape in parous females such that females with the largest offspring have the most divergent shapes along the relative warp one axis. Pelvic shape differences between males and females were consistent with previous findings in other taxa which identify the pubo-ischial complex as the primary region of dimorphism. J. Morphol. 270:834–842, 2009.

KEY WORDS: geometric morphometrics; parturition; pelvis; dimorphism

INTRODUCTION

Pelvic dimorphism, although mostly studied in humans, is present in numerous mammalian species (Schultz, 1949; Dunmire, 1955; Bernstein and Crelin, 1967; Mobb and Wood, 1977; Chapman et al., 1994; Tague, 2003). This dimorphism is genetically determined and continues to develop in response to sex hormones into sexual maturity (Gardner, 1936; Uesugi et al., 1992; Iguchi et al., 1995). Dimorphism in the pelvis consequently emerges along a developmental timeline such that patterns of dimorphism are mostly set by the time an individual is sexually mature (Berdnikovs et al., 2007). However, considerable change also takes place in response to pregnancy and parturition (Todd, 1923; Gardner, 1936; Houghton, 1974; Kelley, 1979; Johnson et al., 1988; Tague, 1988, 1990; Cox and Scott, 1992). Consequently, the pelvic changes experienced by females during pregnancy and parturition are likely to affect pelvic dimorphism between males and females.

One of the important factors responsible for alterations to the female pelvis during parturition is the relationship between maternal size and neonatal size. Neonate size has been correlated with female pelvic dimensions and magnitude of pelvic sexual dimorphism (Schultz, 1949; Leutenegger, 1974; Morrison et al., 1985; Johnson et al., 1988; Ridley, 1995; Cloete et al., 1998; Johanson and Berger, 2003; Tague, 2005). Although many of these studies use various ratios and other transformations of linear data to represent pelvic capacity (volume) (Morrison et al., 1985; Johnson et al., 1988; Cloete et al., 1998) and to assess differences in specific pelvic regions such as the pubis and the regions surrounding the sacro-iliac joint (Leutenegger, 1974; Tague, 1988, 1990; Ridley, 1995), they do not generally examine the overall change in shape of the os coxae. Because of the lack of an examination of pelvic shape changes due to parturition, the relationship between litter/neonate size and holistic changes in maternal pelvic shape with parturition remains unexamined.

This study investigates how shape and size dimorphism of the os coxae vary in association with body size and parturition. To do so, we used laboratory bred mice (*Mus musculus domesticus*). We chose to use this laboratory organism for our study for three specific reasons. First, both sexual size dimorphic and pelvic dimorphism have been documented (Gardner, 1936; Schwarz and Schwarz, 1943; Crelin, 1960; Dewsbury et al., 1980; Uesugi et al., 1992). Second, for parous females, the timing of breeding and weaning were

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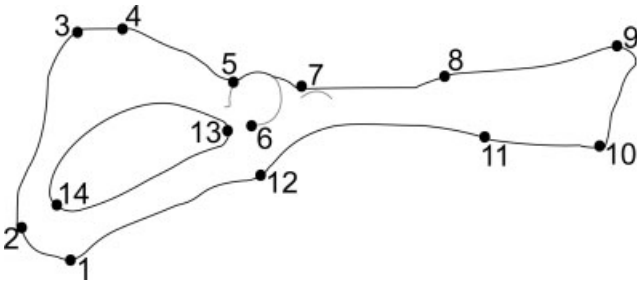

Fig. 1. Lateral view of the os coxae with 14 numbered landmarks corresponding to landmark descriptions in Table 1.

controlled. Third, for all mice, the food availability and age at euthanasia were also controlled ensuring that these did not become confounding factors. The specific goals of this study were to 1) compare body length and the size and shape of the os coxae of male, parous, and nulliparpous female mice, 2) assess the effects of body length, size of the os coxae, and relative offspring size on these shape differences, and 3) describe how patterns of shape variation in the os coxae between males and females change with regard to parturition using a geometric morphometric approach.

MATERIALS AND METHODS

Animals

This study utilized a sample of mice (*Mus musculus domesticus*) from an ongoing study at the Biology Department of the University of Nevada, Reno (UNR). All the animals used originated from 50 male and 50 female mice, representing 35 families from a random-bred HS/Ibg strain, obtained from the University of Colorado, Boulder. This starting population was randomly bred (sibling breeding pairs were avoided) at UNR for five generations as part of the larger study. Individuals from across all generations were used. Animals were weaned at 3 weeks of age, segregated by sex, and housed five animals per cage. Constant access to water and food was provided. Individual females in the parous group were bred with a random, nonsibling male at ~14 weeks of age. Males were removed from the female's cage 2 weeks after pairing and females gave birth ~21 days after mating. Females were separated from their pups 3 weeks following birth and euthanized 2 days later. Nulliparous females and males were kept in the same cages they were weaned into. University of Nevada IACUC approved all husbandry and procedures (Protocol # A06/07-19).

Samples

Before skeletonizing, we measured total body length of the mouse carcasses from the rostrum to the anus. Body length was used as a measure of body size instead of body mass because carcasses had been frozen for a varying number of months and mass was not measured when they were euthanized. Consequently, we felt that body mass would vary too greatly to be of use. For parous females, we also collected the following data: mass at breeding, live litter mass, and number of pups per litter. Carcasses were skinned and the organs were removed before being introduced into a dermestid colony for cleaning. Carcasses were checked daily and were removed as soon as the pelvic bones were free of muscle tissue. Each pelvis was separated into left and right os coxae and cleaned of any remaining connective tissue.

After skeletonizing, we took high resolution digital images of the ossa coxae of 90 individuals (30 males, 30 nulliparous females, 30 parous females) making sure to use equal numbers of left and right elements in each subset to provide an average value for the whole pelvis and avoid potential problems caused by asymmetry. All imaging and landmarking was performed by one individual to reduce sampling variation. All data were collected from specimens that were between 18.7 and 22.2 weeks old with an average age of 20.2 weeks old for the sample. This age range was chosen because epiphysial fusion and cessation of long-bone growth occurs at 13–18 weeks and fusion of the bones of the os coxae occurs at 12–14 weeks in this species (Johnson, 1933; Zoetis et al., 2003). Thus, we were confident that the specimens sampled for this study were skeletally mature.

Landmarks were recorded as 14 two-dimensional Cartesian coordinates along with scales on the digital images utilizing tpsDIG (Rohlf, 2006). Landmarks are illustrated in Figure 1 and described in Table 1. Because inaccuracies in specimen orientation (due to parallax) and inconsistencies in landmark position (making landmarks difficult to replicate across specimens) can produce measurement error, measurement error is an important issue to address. We took the following steps to reduce measurement error in our sample: 1) chose an element orientation that was highly repeatable, that is, the acetabulum was placed at the center of the focal plane to reduce measurement errors caused by parallax and variation in element position (Cardini and Tongiorgi, 2003), 2) photographed the elements with a lens distance that was at least 10× the length of the element, and 3) chose highly repeatable landmarks that were as coplanar as possible. In addition, we assessed the degree of measurement error in our sample. To do so, we digitized 10 individuals from each of the three specimen groups five times. Within-sample error was quantified following Bailey and Byrnes (1990). A one-way multivariate analyses of variance (MANOVA) of the Relative Warp (RW) scores was conducted with specimen as the independent variable. A significant effect of specimen indicates that replication error does not markedly interfere with measurement of between-individual shape. Percent measurement error (%ME) was calculated as the ratio of within specimen variance to among specimen variance and for the entire sample, ME was 9% and the effect of specimen in the MANOVA was significant.

Morphometric Data

Using the tpsRelw software (Rohlf, 2007), a generalized least squares Procrustes fit was performed on the raw landmark data

TABLE 1. Description of the 14 lateral os coxae landmarks represented by Figure 1

Number	Definition
1	Dorsal pubic tubercle: the rostral-most point of the pubic symphysis in the inferior ramus (or ventral-most on superior pubic ramus)
2	Caudal-most point of the pubic symphysis on the inferior pubic ramus
3	Dorsal-most point of the ventral ramus of ischium
4	Ischial tuberosity
5	Junction of sciatic notch and caudal border of acetabulum
6	Ventral tubercle of acetabular semi-lunar surface
7	Notch at junction of ventro-caudal iliac spine and rostral border of acetabulum
8	Dorso-caudal iliac spine
9	Dorso-cranial iliac spine
10	Ventro-cranial iliac spine
11	Ventro-caudal iliac spine
12	Ilio-pubic eminence/tubercle
13	Obturator groove: On cranial apex of obturator foramen
14	Caudal apex of obturator foramen

and then a relative warps analysis of the shape data was performed with a α set to a value of 0. This procedure is similar to a principal components analysis and allows for the heuristic evaluation of group shape differences in the os coxae. The resulting RW scores were saved and used in the subsequent analyses as the multivariate shape variables.

Using the same software, we extracted centroid size, defined as the square root of the sum of squared distances from the centroid. Centroid size is a geometrically-based measure of size that in the absence of allometry is statistically uncorrelated with shape variables (Bookstein, 1991). Centroid size provides information on the geometric size of the object being studied and is a measure of os coxae size.

Statistical Analyses

To test for significant group (male, parous female, nulliparous female) differences in body length and the size of os coxae, we performed two sets of analyses of variance (ANOVAs) with log centroid size as the dependent variable and group as the independent variable in one set and body length as the dependent variable and group as the independent variable in the other. For each ANOVA, follow-up tests were conducted to evaluate pairwise differences among the means.

To test for significant shape differences between the three groups, we performed a MANOVA using all of the RW scores as the dependent variables and group as the independent variable. This analysis also helped us to determine if RW axis best differentiated between the groups. We then calculated an index of shape difference between pairs of the three groups based on Procrustes distances.

We utilized "shape index 1" introduced by Schutz et al. (in press), which allowed us to quantify the magnitude of shape differences between group means and assess how significant were these pairwise differences. In this index, the Procrustes distances between the means of two groups are divided by the sum of the variances between the groups. Significance was determined by performing 10,000 randomizations where individuals were randomly assigned to either group with subsequent recalculation of the index. The two groups were considered significantly different if the index was larger than 95% (0.05 level of significance) of the randomly generated indices (Manly, 2006). All index calculations, including generation of Procrustes distances, calculation of the index and the necessary realignment of specimens after each randomization, were performed in Mathematica 6.0 (Wolfram Research, 2005).

To test for differences in shape between the groups while holding centroid size and body length constant, we performed two sets of multivariate analyses of covariance (MANCOVAs) using the RW scores as the dependent variables, group as the independent variable, and centroid size and body length as covariates. The first set of analyses contained two MANCOVAs, both of them using centroid size as a covariate, but one included all three groups and the other included only the two female groups. The second set also contained two MANCOVAs, one including all three groups and the other only the two female groups, but this time body length was the covariate. In all the cases, before interpreting the main effects of group, centroid size, or body length, we performed an analysis including the interaction term (group * centroid size or group * body length). A significant interaction between group and one of these covariates would suggest a difference in allometry between groups and prevent us from directly interpreting the main (group) effects. If the interaction term was not significant it was removed and the MANCOVA was rerun with just the main effects.

To understand the effects of parturition on female body length and pelvic size and shape, we also calculated two ratios to represent the relationship between maternal mass and offspring and litter mass. The first ratio (O/M) is the ratio of mean pup mass to maternal mass at mating. Pup mass was calculated by dividing live litter mass by the number of pups in the litter. The second ratio (L/M) is the ratio of the mass of the litter to the maternal mass at mating. We then performed three multiple regressions using the two ratios as independent variables. The dependent variables for the three regressions were 1) body length, 2) pelvic centroid size, and 3) the RW axis which best differentiated between groups.

Finally, to describe the patterns of variation between the sexes, we used the tpsRelw software (Rohlf, 2007) to generate deformation grids representing shape changes associated with the RW axes. These deformation grids along with the RW axes allowed us to visualize ox coxae shape differences between groups.

RESULTS

Size Differences Among Groups

The two ANOVAS revealed significant differences between groups in both body length ($F_{2,87} = 14.2$, $P < 0.001$) and centroid size of the os coxae ($F_{2,87} = 50.0$, $P < 0.001$). In both the cases, the variances among the three groups spanned a limited range. Consequently, we chose to assume homogenous variances and conducted post hoc comparisons using Tukey's honestly significant difference (HSD). Comparisons were considered significant when $P < 0.05$.

For body length, there was a significant difference in mean body length between males and nulliparous females and between nulliparous females and parous females. However, body length did not differ significantly between males and parous females (Fig. 2B).

For centroid size of the os coxae, there was a significant difference in mean centroid size between males and both groups of females as well as between parous and nulliparous females. Parous females had the largest os coxae, whereas males had the smallest (Fig. 2A).

Shape Differences Among Groups

The MANOVA results indicated that significant shape differences were present between the groups (Wilk's $\lambda = 0.016$, $F_{48,128} = 18.4$, $P < 0.001$) and that the RW1 axis differentiated between the three groups most effectively ($F_{2,87} = 277$, $P < 0.001$). Subsequent calculations of shape difference indices between pairs of groups showed that all pairs were significantly different in shape from one another. Males and parous females demonstrated the greatest shape disparity (index 1 = 1.88, 100%), males and nulliparous females were in the middle (index 1 = 1.21, 100%), whereas parous and nulliparous females demonstrated the least shape disparity (index 1 = 0.32, 100%). Percentage values refer to the percentage of the randomizations that generated a smaller index value than the calculated index for each pairwise comparison as described in the methods.

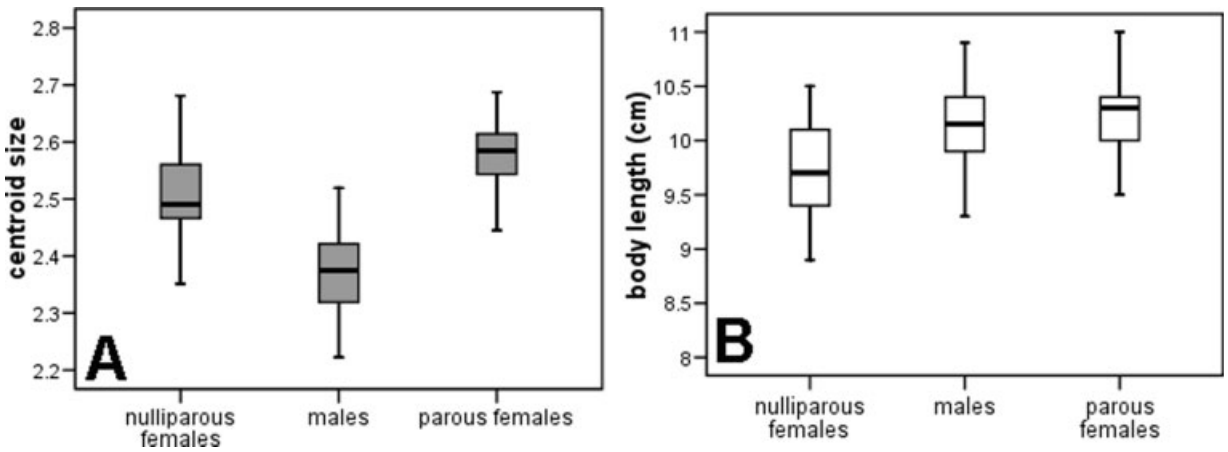

Fig. 2. Size differences in the os coxae and body size between groups. (**A**) Box plot of os coxae centroid size for each group. (**B**) Box plot of body length for each group.

Effects of Size on Shape

The MANCOVA of all three groups with centroid size as a covariate demonstrated homogenous slopes (no significant interaction between group and centroid size), and pelvic shape was significantly different at different centroid sizes when controlling for group and between groups when controlling for centroid size (Table 2). When the same analysis was run on just females, the result was the same with no significant interaction between group and centroid size, and pelvic shape was again significantly different at different centroid sizes when group was controlled for and between groups when controlling for the centroid size (Table 2).

The MANCOVA on all three groups with body length as a covariate resulted in a nearly significant interaction between group and body length, suggesting that differences in pelvic shape between groups are potentially associated with body length differences between groups. The main effect of group was significant when body length was controlled for. When the same analysis was run on just females, the interaction between group and body size was significant. Consequently, any further results could not be interpreted because pelvic shape differences between parous and nulliparous females were associated with the body length differences between them (Table 2).

Effects of Parturition on Shape

To understand how body length and the size and shape of the os coxae are affected by the relationship between maternal size and offspring size, the two ratios (O/M and L/M) were regressed on body length, os coxae centroid size, and RW1 in three multiple linear regressions. Before performing these analyses, we computed a Pearson correlation coefficient between the two indices (0.212). Because this value was so low, we felt confident in using both indices in the analyses. For the body length, the linear combination of the two indices was not significantly related to the body length, $F_{2,27} = 1.33$, $P = 0.28$, $R^2_{adj} = 0.022$. The partial correlations between the indices and body length were positive for L/M (0.295, $P = 0.12$) and negative for O/M (-0.118, $P = 0.541$) and neither was statistically significant. The linear combination of the two indices also was not significantly related to the centroid size, $F_{2,27} = 1.67$, $P = 0.207$, $R^2_{adj} = 0.044$. The partial correlations between the indices

TABLE 2. MANCOVA results with centroid size as a covariate or with body length (BL) as a covariate for all groups and for just females

Model	Wilks λ	*F*	d*f*	*P*
Group (NP, P, M)	0.621	0.683	48,122	0.933
Centroid size	0.586	1.79	2,461	0.035[a]
Group X centroid size	0.655	0.60	48,122	0.978
Main effects				
Group	0.033	11.740	48,126	<0.001[a]
Centroid size	0.575	1.94	2,463	0.019[a]
Group (NP and P)	0.730	0.51	2,433	0.956
Centroid size	0.405	2.02	2,433	0.031[a]
Group X centroid size	0.738	0.49	2,433	0.964
Main effects				
Group	0.256	4.13	2,434	<0.001
Centroid size	0.404	2.08	2,434	0.024[a]
Group (NP, P, M)	0.412	1.420	48,122	0.065
Body length	0.680	1.20	2,461	0.280
Group X body length	0.406	1.45	48,122	0.055
Main effects				
Group	0.017	17.731	48,128	<0.001[a]
Body length	0.725	0.998	2,463	0.482
Group (NP and P)	0.393	2.124	2,433	0.023[a]
Body length	0.404	2.03	2,433	0.030[a]
Group X body length	0.395	2.10	2,433	0.024[a]

NP, nulliparous females; P, parous females; M, males. Results for the MANCOVA including just the main effects are shown separately when the interaction was not significant.
[a]Significance at the 0.05 level.

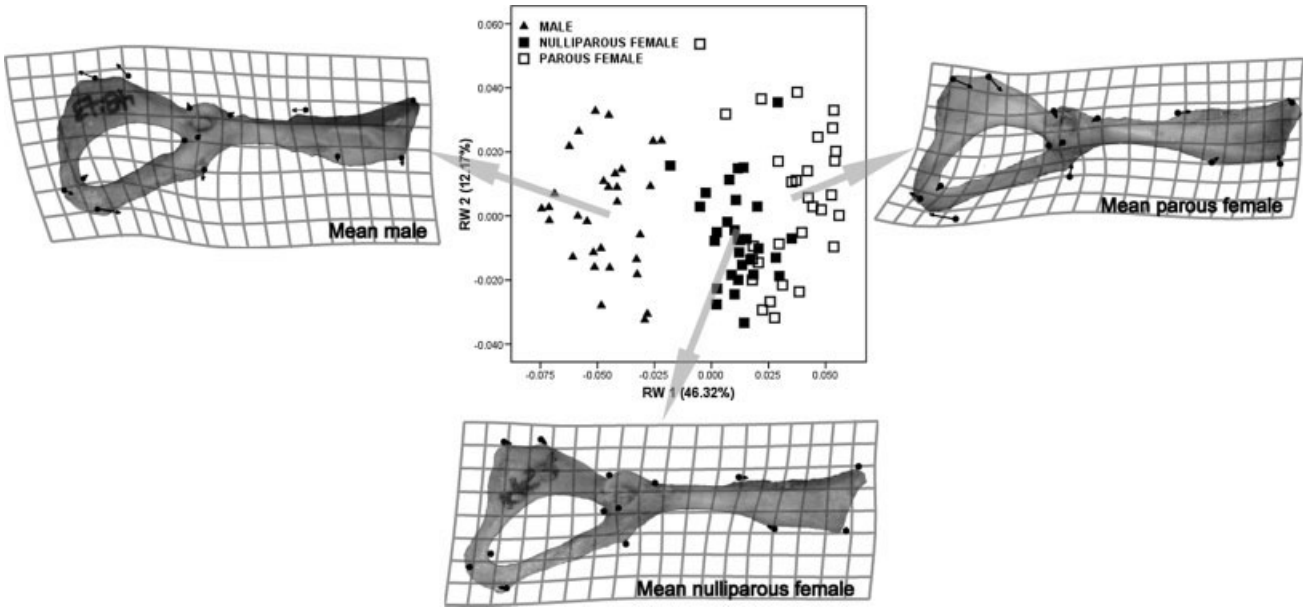

Fig. 3. Scatterplot of relative warp axes 1 and 2 for a RW analysis of the os coxae. Triangles represent males; solid squares represent nulliparous females and open squares represent parous females. Light gray arrows lead from each the group means to the corresponding deformations of the os coxae for each of these group means from the grand mean. Element images representing individuals with the shortest procrustes distances to each of the group means are included with deformation grids for orientation only and do not precisely match landmark configurations because these axes do not encompass all of the shape variation present.

and centroid size was positive for L/M (0.023, P = 0.90) and negative for O/M (−0.33, P = 0.082) and neither was statistically significant. Finally, for pelvic shape as represented by the RW1 axis, the linear combination of the two indices was significantly related (at the 0.05 level) to scores on the RW1 axis, $F_{2,27}$ = 3.59, P = 0.042, R^2_{adj} = 0.151. The partial correlations between the indices and RW were negative for L/M (−0.114, P = 0.557) and positive for O/M (0.458, P = 0.012) and only O/M was statistically significant at the 0.05 level.

Shape Differentiation Among Groups

The RW analyses and the associated thin-plate splines showed marked differentiation between the three groups in the shape space and helped us to identify the anatomical regions where those differentiations were most pronounced. RW axes 1 and 2 explained 46.32% and 12.17% of the total shape variation, respectively, and all three groups differentiated along RW1 (see Fig. 3). In terms of overall shape trends, males had negative scores on RW1 whereas females as a whole had positive scores on RW1. Within females, parous females had larger positive scores along RW1 than nulliparous females. Females as a group had longer narrower, more gracile ilia, narrower acetabula (dorso–ventrally), and a longer and narrower, less robust puboischial complex than males. Specifically, the superior pubic ramus (landmarks 1 and 12) was longer, the inferior pubic ramus was narrower, and the ischium, particularly the ischial tuberosity (landmarks 3 and 4), was more gracile than that of males. Within females, ossa coxae of parous females were generally more gracile and elongated than those of nulliparous females. The ilium was more elongated antero–posteriorly, the superior pubic ramus was longer and narrower, and the inferior pubic ramus was slightly longer and markedly narrower, particularly between landmarks 2 and 14.

DISCUSSION

Size Dimorphism

We found significant dimorphism in both the body length and the size of the os coxae, but the magnitude of that dimorphism varied greatly between males and nulliparous females and between males and parous females in both the measures.

For the body length, we found that males were longer than nulliparous females, but shorter than parous females. In terms of body mass, males have generally been found to be heavier and longer than females (Dewsbury et al., 1980). However, sexual dimorphism in body length has been shown to vary in wild populations. Sometimes, males are longer than females and sometimes females are longer than males and these variations in length dimorphism have been attributed to population effects (Schwarz and Schwarz, 1943). Our results suggest, however, that parturition may be an

alternative or additional source of variation in body length dimorphism, particularly in situations where there is unequal sampling of parous and nulliparous females.

Existing evidence suggests that parity events affect the size of various skeletal elements including the pelvis (Bowman and Miller, 1999, 2001; Johanson and Berger, 2003; Specker and Binkley, 2005). Those results, coupled with results presented herein, show that parity events greatly influence the skeletal architecture of females and produce potentially significant increases in their skeletal size regardless of potential losses in bone density.

For the os coxae, we found that females have larger os coxae than males overall, and parous females have the largest os coxae. Thus, along with a potential increase in skeletal size as indicated by our body length results, parity events also significantly affect the size of the os coxae. These findings parallel those of a study that showed increased pelvic area in multiparous versus primiparous cows (Johanson and Berger, 2003). In addition, other studies in rats have shown that mass and endochondral bone growth becomes elevated during pregnancy and remains so during lactation relative to nulliparous animals even though overall bone density is lost (Bowman and Miller, 1999, 2001). Finally in humans, total body bone area is greater in parous versus nulliparous females (Specker and Binkley, 2005). Although none of these studies directly measured changes in skeletal size in individuals pre- and postreproduction, the results presented here as well as in the studies cited above indicate that such changes merit further direct study to asses how parity affect both the skeletal size in individuals and which specific regions or elements (such as the os coxae) are most heavily affected. This effect may be particularly important for studies focusing on sexual size dimorphism and it illustrates the importance of knowing the reproductive history of the female samples in any data set.

Shape Dimorphism and the Effects of Size

In addition to the changes in skeletal and os coxae size, the shape of the pelvis is also affected by parturition. Our shape indices and MANOVA results showed that male and female pelves have significantly different shapes from one another, and these differences are further exacerbated by a reproductive event, such that pelvic shape dimorphism between parous females and males is greater than between nulliparous females and males. Our subsequent MANCOVA results (Table 2) also show that os coxae shape differences between parous and nulliparous females are significantly affected by body length but not pelvic size (centroid size). These results combined with the results on the size differences of the os coxae between the two groups suggest that parity events significantly affect the size and shape of the female os coxae and produce differences in the magnitude of pelvic shape dimorphism.

Relationships Among Parturition, Size, and Pelvic Shape

Although parous females have larger bodies and larger os coxae than nulliparous females, and although those body size differences affect os coxae shape, the results of the multiple regression analysis show that neither of these two size components is correlated to either of the two offspring size ratios (L/M or O/M). Thus, body length changes and os coxae size changes are not associated with either relative litter size (L/M) or relative neonate size (O/M).

Os coxae shape on the other hand was significantly correlated to relative neonate size (O/M ratio), such that females with the largest average individual neonates relative to their prebreeding mass, had the largest score along RW1, that is, their pelvic shape was the most disparate from the mean.

Consequently, it appears that two different patterns of change occur in females following a single reproductive event. First, females likely experience a significant increase in both body length and os coxae size, and these increases are independent of litter size and relative offspring size. Second, a separate suite of changes occur in the shape of the os coxae following a female's first reproductive event, and these changes are significantly correlated with the relative size of individual offspring.

The relationship between offspring size and maternal size and its correlation with indicators of pelvic shape and size are well studied in primates but only marginally so in other mammalian taxa (Leutenegger, 1974; Morrison et al., 1985; Ridley, 1995; Cloete et al., 1998; Berdnikovs, 2005; Tague, 2005; St. Clair, 2007). The primate studies in particular, have become the centerpiece of two hypotheses regarding pelvic dimorphism. The first is that female pelvic morphology is selected upon for obstetric function such that neonatal cranial size (Schultz, 1949; Leutenegger, 1974; Wood and Chamberlain, 1986; Ridley, 1995) or mass (St. Clair, 2007) relative to the size of the maternal birth canal affect female pelvic morphology resulting in an ample aperture for successful parturition. The second is that pelvic size and shape differences are mediated by different allometric growth trajectories between males and females caused by androgens during puberty, with the differences becoming more exacerbated in species that exhibit body size dimorphism than in species that do not exhibit body size dimorphism (Schultz, 1949; Tague, 2005). Studies in laboratory animals

examining the ontogeny of pelvic dimorphism and hormonal effects during pelvic growth show that the pelvic components respond differently to sex hormones and the growth trajectories of the different components differ between the sexes (Gardner, 1936; Uesugi et al., 1992; Berdnikovs et al., 2007).

However, the two hypotheses are difficult to test for various reasons. First, they are not mutually exclusive and both sets of mechanisms are likely in effect (Schultz, 1949; Tague, 2005; St. Clair, 2007). Second, the comparative nature of many studies dictates that they be performed on museum collections and as such, the exact age of individuals is largely unknown. Therefore, data on offspring size are often unavailable, forcing the use of species averages.

Our study differs from previous studies in two fundamental ways. First, we do not examine size changes between males and females as a result of normal development, but rather size differences between adult females due to pregnancy. Thus, we test the obstetric function hypothesis, but not the allometry hypothesis as it relates to ontogenetic differences between males and females. Our results show that both parity and size have a significant effect on female pelvic morphology. Thus, it appears that it is both the size changes in the females due to pregnancy and the relative size of their offspring which affect pelvic shape. Second, our study was also able to overcome some of the data limitations that have hampered other studies. We utilized a sample of laboratory bred animals and allowed us to control a variety of potentially confounding factors. The number of reproductive events for parous females was limited to one and breeding took place at the same age, the offspring of specific individuals were measured for our ratios and the age of all individuals was consistent. Consequently, we were able to more closely measure the effects of parturition. Finally, we also studied the potential effects of parturition within a single species, rather than across multiple species as done in other studies. This narrower focus allowed us to look at the effects of parturition without the need to account for the confounding effect of phylogeny.

In addition to the body size changes due to pregnancy, the composition of the litter has a specific effect on the pelvis. As our results show, the average size of individual offspring is correlated to the degree of pelvic shape change. So which factors affect offspring size? In primates and other species, neonates can be moderately sexually size dimorphic (Smith and Leigh, 1998). It has been suggested that this dimorphism, however slight, can have significant effects on the mother such that a female whose litter has a greater number of offspring of the larger sex, will have a heavier litter and relatively larger individual offspring than a female whose litter has a greater number of offspring of the smaller sex (Smith and Leigh, 1998). In *Mus*, females are known to produce litters with variable sex ratios under various conditions (Krackow and Gruber, 1990; Clark et al., 1991; Krackow, 1992; Rosenfeld et al., 2003) and neonate size dimorphism of varying levels occurs in lines selected for low and high adult size dimorphism (Krackow et al., 2003). Thus shifts in neonate sex ratio, and as a result, in average pup mass could potentially occur in *Mus* and could subsequently affect female pelvic morphology.

Unfortunately, our data were too limited to test this hypothesis directly. As described in the methods, we derived mean pup mass by dividing litter mass by the number of pups in the litter. The individual pups were never actually weighed and as such the masses of each individual offspring were not recorded and we could not ascertain if sexual size dimorphism was present at birth in our sample. In addition, sex ratios for offspring were not recorded at birth, but rather at weaning, thus we could not use them to examine the effects of litter composition at birth on body length or os coxae centroid size and shape.

Functional Significance of Pelvic Shape Changes

Although *M. m. domesticus* females have larger os coxae in terms of centroid size, they are generally more gracile than males. In addition, the pubic and ischial regions show the greatest shape disparity between the sexes particularly at or near the midplane, one of the three obstetric planes of the birth canal (Rosenberg and Trevathan, 1995; Walrath, 2003). Finally, these differences were clearly exacerbated by a reproductive event such that parous females were most different from males and nulliparous females were the closest group to the "mean shape" of males and females.

The os coxae shape patterns we observed were consistent with studies of several other mammalian species including primates (Washburn, 1948; Schultz, 1949; Leutenegger, 1974; Mobb and Wood, 1977; Steudel, 1981; Leutenegger and Larson, 1985; MacLaughlin and Bruce, 1986; Hager, 1989; Arsuaga and Carretero, 1994; Ridley, 1995; Correia et al., 2005; Tague, 2005; Helen, 2007), mustelid carnivores (Berdnikovs, 2005), cervids (Edwards et al., 1982), chiropterans (Crelin and Newton, 1969; Chapman et al., 1994), metatherians (Tague, 2003), and rodents (Chapman, 1919; Gardner, 1936; Guilday et al., 1951; Dunmire, 1955; Bernstein and Crelin, 1967; Iguchi et al., 1989; Uesugi et al., 1992). In all of these groups, the most extreme regions of dimorphism are at the pubis and ischium, particularly near the midplane. However, few of these studies compared the overall morphological differences between the os coxae of

parous and nulliparous females with the exception of Gardner (1936) who studied differences in *Mus*.

Gardner (1936) specifically observed that females overall had an elongated, thin, and gracile pubis versus males and this characteristic was more exaggerated in parous females. In addition, he observed that males had a more robust ischial region and the contrast was greatest with parous females. We not only document the same types of differences described by Gardner (1936) but we also able to identify other differences in the os coxae of parous versus nulliparous females. These differences include: an exaggeration of the elongation of the ilia and narrowing of the acetabulum and a marked elongation of the entire element.

The similarity in regions of change across multiple taxa suggests that even though great variation exists in the locomotor modes of all these mammals, there is a consistent pattern of pelvic "adjustment" localized at the pelvic midplane (the most constricted pelvic region). Further laboratory studies should also be performed to shed light on the effects of subsequent parity events beyond the first. It has been shown that recovery after a first parity event in terms of bone mineral density and bone calcium content is different and perhaps more intense than in subsequent parity events (Bowman and Miller, 2001). This may indicate that additional bone remodeling and associated shape changes may occur, but at a different magnitude than after first parity and the cumulative effects on pelvic shape are worth investigating. However, from these data, we unfortunately have little basis for generating predictions regarding pelvic shape and repeated parity events due to the fact that many additional factors can contribute to bone remodeling (e.g., age, time lapse between parity events, nutritional status, time since weaning, etc.). We also suggest that comparative studies that examine pelvic shape dimorphism across species with different locomotor modes and which include data on offspring size may shed light on significant interactions between these two functional components of the pelvis and the evolution of pelvic sexual dimorphism in mammals, rather than just particular groups of mammals.

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