The effects of captive versus wild rearing environments on long bone articular surfaces in common chimpanzees (*Pan troglodytes*)

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The physical environments of captive and wild animals frequently differ in substrate types and compliance. As a result, there is an assumption that differences in rearing environments between captive and wild individuals produce differences in skeletal morphology. Here, this hypothesis is tested using a sample of 42 captive and wild common chimpanzees (*Pan troglodytes*). Articular surface areas of the humerus, radius, ulna, femur, and tibia were calculated from linear breadth measurements, adjusted for size differences using Mosimann shape variables, and compared across sex and environmental groups using two-way ANOVA. Results indicate that the articular surfaces of the wrist and knee differ between captive and wild chimpanzees; captive individuals have significantly larger distal ulna and tibial plateau articular surfaces. In both captive and wild chimpanzees, males have significantly larger femoral condyles and distal radius surfaces than females. Finally, there is an interaction effect between sex and rearing in the articular surfaces of the femoral condyles and distal radius in which captive males have significantly larger surface areas than all other sex-rearing groups. These data suggest that long bone articular surfaces may be sensitive to differences experienced by captive and wild individuals, such as differences in diet, body mass, positional behaviors, and presumed loading environments. Importantly, these results only find differences due to rearing environment in some long bone articular surfaces. Thus, future work on skeletal morphology could cautiously incorporate data from captive individuals, but should first investigate potential intraspecific differences between captive and wild individuals.

1 **The effects of captive versus wild rearing environments on long bone articular surfaces in**

2 **common chimpanzees (*Pan troglodytes*)**

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20   **Abstract**

21   The physical environments of captive and wild animals frequently differ in substrate types and

22   compliance. As a result, there is an assumption that differences in rearing environments between

23   captive and wild individuals produce differences in skeletal morphology. Here, this hypothesis is

24   tested using a sample of 42 captive and wild common chimpanzees (*Pan troglodytes*). Articular

25   surface areas of the humerus, radius, ulna, femur, and tibia were calculated from linear breadth

26   measurements, adjusted for size differences using Mosimann shape variables, and compared

27   across sex and environmental groups using two-way ANOVA. Results indicate that the articular

28   surfaces of the wrist and knee differ between captive and wild chimpanzees; captive individuals

29   have significantly larger distal ulna and tibial plateau articular surfaces. In both captive and wild

30   chimpanzees, males have significantly larger femoral condyles and distal radius surfaces than

31   females. Finally, there is an interaction effect between sex and rearing in the articular surfaces of

32   the femoral condyles and distal radius in which captive males have significantly larger surface

33   areas than all other sex-rearing groups. These data suggest that long bone articular surfaces may

34   be sensitive to differences experienced by captive and wild individuals, such as differences in

35   diet, body mass, positional behaviors, and presumed loading environments. Importantly, these

36   results only find differences due to rearing environment in some long bone articular surfaces.

37   Thus, future work on skeletal morphology could cautiously incorporate data from captive

38   individuals, but should first investigate potential intraspecific differences between captive and

39   wild individuals.

Introduction

42   Morphological studies on primates tend to focus on osteological samples that derive from

43   wild-caught individuals because of the assumption that the skeletons of individuals raised in

44   captive environments differ from those living in wild or large range sanctuary environments

45   (e.g., Albrecht, 1982). This perception is especially true among studies of great apes given the

46   potentially large differences in wild versus captive ape environments. Chimpanzees in the wild,

47   for example, have large day ranges (e.g., 7.8-14.9 km², Chapman & Wrangham, 1993), use

48   varied, three-dimensionally complex arboreal substrates as well as terrestrial substrates (Doran &

49   Hunt, 1994), and males engage in large territory patrols (Mitani & Watts, 2005) and large-scale

50   hunting (e.g., Stanford et al., 1994). In captive environments, enclosure size is limited and less

51   three-dimensionally complex, and substrate types and compliance can be quite different than

52   those found in the wild (i.e., less variation in heights, inclines, and compliance of simulated

53   arboreal substrates, and increased hard surfaces such as rocks and concrete in captive settings).

54   Because of this, and other issues related to potential differences in nutrition, growth, and

55   physiology, skeletons of wild-caught individuals have been preferred for studies of

56   morphological variation.

57   A handful of studies have investigated whether there are morphological differences

58   between captive and wild osteological specimens (McPhee, 2004; Zuccarelli, 2004; O'Regan &

59   Kitchener, 2005; Bello-Hellegouarch et al., 2013; Hartstone-Rose et al., 2014; Antonelli et al.,

60   2016; Kapoor et al., 2016; Turner et al., 2016). Studies on cranial anatomy have shown

61   differences in both size and shape of the skull in mice and felids (McPhee, 2004; Zuccarelli,

62   2004; Hartstone-Rose et al., 2014). The felid studies in particular have suggested that differences

63   in skull shape between captive and wild individuals are related to differences in masticatory

64   loading resulting from dietary differences. Studies on postcrania, however, have revealed that

65   there are no differences between captive and wild specimens in the scapula of hominoids (Bello-

66   Hellegouarch et al., 2013) nor in the lengths of long bones of vervet monkeys (Turner et al.,

67   2016). The effects of captivity on postcranial joint surfaces, however have not previously been

68   investigated. Given that long bone joint surfaces are responsible for load-bearing, and given that

69   felids exhibit differences in skull shape related to masticatory loading differences, it is

70   reasonable to hypothesize that differences in captive and wild loading environments may affect

71   the articular surfaces of long bones.

72   Although diaphyseal cross-sectional geometry of long bones is phenotypically plastic and

73   can respond to loading regimes (e.g., Goodship, Lanyon & McFie, 1979; Burr et al., 1982; Ruff

74   and Hayes, 1983; Shaffler et al., 1985; Ruff and Runestad, 1992), the effects of altered loading

75   regimes on long bone articular surfaces have been less well studied. Compared to diaphyseal

76   dimensions, long bone epiphyses are more morphologically constrained and less labile (Ruff,

77   1988; Ruff, Scott & Liu, 1991; Lieberman, Devlin, & Pearson, 2001). However, previous work

78   has not compared long-term effects of altered loading environments on long bone articular

79   surfaces.

80   The aim of this study is to test the hypothesis that long bone articular surfaces differ

81   between captive and wild chimpanzees.

82

83   **Materials and Methods**

84   The sample includes 42 *Pan troglodytes* adult individuals (20 captive-raised and 22 wild,

85   Table 1). Adulthood was assessed by long bone epiphyseal fusion. Only captive individuals aged

86   10 years or older that exhibited epiphyseal fusion were included in the study (an exception was

87   made to include a 9-year-old individual that exhibited complete epiphyseal fusion). Individuals

88   categorized as "captive" were captive-raised; most were born in captivity, but some were wild-

89   born and brought to the United States during infancy. Fifteen (10 females, 5 males) of the

90   captive-raised individuals were from the Primate Foundation of Arizona (PFA) skeletal

91   collection, for which age at death, sex, cause of death, and life history information are known.

92   Five additional adult male captive-raised chimpanzee skeletons were measured at the School of

93   Human Evolution and Social Change at Arizona State University. The wild sample includes 22

94   adult (11 males, 11 females) skeletons from the Cleveland Museum of Natural History.

95   Measurements taken on the humerus, radius, ulna, femur, and tibia of each individual

96   include linear dimensions (anteroposterior, mediolateral, and superoinferior) of the proximal and

97   distal articular surfaces and total bone length. Each linear variable was measured three times and

98   the average recorded for analysis. Articular surface areas were estimated using the linear

99   dimensions following Ruff's (2002, 2003) published equations (Table 2). Bone lengths were

100   measured in standard orientation following Buikstra and Ubelaker (1994). Each surface area

101   variable was size-standardized and converted to a Mosimann shape variable using a

102   dimensionless ratio of the square root of the area variable to the geometric mean (Mosimann,

103   1970; Jungers, Falsetti, & Wall, 1995). The geometric mean consisted of 15 variables: five bone

104   lengths and the square roots of each articular surface area. Means and standard deviations for

105   articular surface areas, bone lengths, and geometric means are listed in Table 3 (raw data are in

106   Supplemental Table 1).

107   Principal component analysis (PCA) was used to explore multivariate variation using

108   shape variables ($\text{area}^{1/2}$/geometric mean). Factor loadings from the PCA were examined to

109   determine which articular surfaces most influenced differences among sex-rearing groups. To

110   test the hypothesis that captive and wild chimpanzees differ in articular surface areas, a

111   multivariate analyses of variance (MANOVA) with sex, rearing, and sex*rearing effects was

112   performed to yield a whole-model F-test for each of the three effects. This test determined that

113   there were statistically significant sex, rearing, and sex*rearing effects within the sample (Table

114   4). This analysis was followed by univariate two-way analyses of variance (ANOVA) on each

115   scaled articular surface area with rearing and sex as factors, each with two levels. Sex was

116   included as a main effect because chimpanzees are sexually dimorphic in body mass (Smith &

117   Jungers, 1997, although they are not particularly dimorphic in skeletal size, Gordon, Green, &

118   Richmond, 2008). Thus, this statistical model allows the examination of the potential interaction

119   effect between sex and rearing. When there was a significant sex*rearing interaction effect, *post*

120   *hoc* pairwise comparisons were performed using Tukey's HSD tests. All analyses were

121   performed in JMP Pro 13 (SAS Institute Inc.). Although ANOVA is relatively robust to

122   violations of assumptions of parametric statistics, the data were examined for violations of

123   normality (using normal probability plots), homogeneity of variances (using Levene's test), and

124   potential outliers (by examining studentized residuals), and were not found to violate these

125   assumptions. One individual (DO) exhibited pathological morphology of the distal radius, and

126   was excluded from the distal radius articular surface area analyses as well as the PCA.

127

128   **Results**

129   *Analyses of variance*

130   The two-way ANOVAs revealed that five of the ten articular surface area shape variables

131   exhibited significant differences in rearing, sex, or the interaction between sex and rearing (these

132   are the humeral head, distal radius and ulna, femoral condyles, and tibial plateau; Table 4). There

133   were significant differences due to rearing in the tibial plateau and distal ulna; captive

134   individuals have relatively larger articular surfaces than wild individuals (Table 4, Figs. 1 & 2).

135   Both the tibial plateau and the distal ulna only exhibited differences between captive and wild

136   individuals without evidence of sex differences or an interaction effect between sex and rearing

137   (Table 4). When scaled by size, the tibial plateau is 4.7% larger in captive females and 5% larger

138   in captive males compared to their wild conspecifics. Similarly, the distal ulna is 7.1% larger in

139   captive females and 8.6% larger in captive males compared to wild individuals (Table 3).

140   There were significant differences due to sex in the femoral condyles and distal radius;

141   males have relatively larger femoral condyles and radiocarpal surfaces than females (Figs. 3 &

142   4). Lastly, there was a significant sex*rearing interaction effect in the femoral condyles, humeral

143   head, and distal radius (Tables 4 & 5). For each of these interaction effects, captive males were

144   significantly different from other sex-rearing groups (Table 5). Specifically, for the femoral

145   condyles and distal radius, captive males have relatively larger articular surface shape variables

146   than all other sex-rearing groups (Figs. 2 & 4). The scaled femoral condyles are 4.6% larger in

147   captive males than in wild females, 5% larger than in wild males, and 6.6% larger than in captive

148   females. The scaled distal radius is 6.6% larger in captive males than in wild males, 9.1% larger

149   than wild females, and 9.4% larger than captive females. The only deviation from this general

150   pattern of captive males having relatively larger articular surfaces is the humeral head, in which

151   captive males have relatively smaller articular surfaces than wild males and captive females (Fig.

152   5).

153   *Principal component analysis*

154   The first four principal components capture 76% of the variation within the sample

155   (eigenvalues listed in Table 6). The plot of PC 1 on PC 2 captures 54.8% of sample variation and

156   shows broad overlap between captive and wild specimens (Fig. 6). The only group that is

157   differentiated in this plot is captive males, which separate from captive females on PC 1, and

158   show only minimal overlap with wild males and females. The three variables that load heavily on

159   PC 1 are those that have a significant sex*rearing interaction effect (humeral head, distal radius,

160   femoral condyles). The variable that loads heavily on PC 2 is femoral head surface area (Table

161   7). The plot of PC 3 on PC 4 captures an additional 21% of sample variation (Fig. 7). Neither PC

162   3 nor PC 4 differentiate groups by sex or rearing.

163

164   **Discussion**

165   This study demonstrates that there are some differences in scaled articular surface areas

166   between captive and wild chimpanzees. Captive chimpanzees have relatively larger articular

167   surfaces of the tibial plateau, distal radius, and distal ulna. The results also demonstrate an

168   interaction effect between sex and rearing in which captive males have larger distal femur and

169   radius articular surfaces than all other sex-rearing groups. Contrary to all other results, captive

170   males have relatively smaller humeral heads than wild males. Although these data suggest that

171   there are some differences in articular surface morphology between captive and wild

172   chimpanzees, the differences are not ubiquitous, since only two out of ten variables differed

173   solely due to rearing. This finding has two important implications: 1) long bone articular

174   surfaces, like diaphyses, *can* differ due to different rearing environments, and 2) because only a

175   few variables studied here differ between captive and wild chimpanzees, it may be appropriate to

176   pool captive and wild specimens in analyses of bones that do not show statistically significant

177   differences between the two groups. This would increase sample sizes, which is important when

178   studying rare species such as great apes that are represented in skeletal collections by relatively

179   few specimens.

180   *Behavioral, physiological, and environmental differences between captive and wild chimpanzee*

181   *populations*

182   Differences between captive and wild chimpanzees in the articular surfaces of the knee

183   and wrist may be related to differences in positional behavior, differences in substrate types and

184   compliance, or to a combination of these factors between these two groups. Schwandt (2002)

185   found slight differences in the ontogeny of positional behavior in the PFA chimpanzees

186   compared to wild chimpanzees from the Taï Forest (Doran, 1989; Doran, 1992). The captive

187   PFA chimpanzees knuckle-walked more often during youth than wild chimpanzees, used more

188   suspensory behaviors during 6-9 years of age, and retained more variety in positional behavior

189   repertoires compared to Taï Forest chimpanzees, whose positional behavior repertoires are static

190   at six years of age (Schwandt, 2002). Given the role of the wrist in achieving knuckle-walking

191   and suspensory behaviors, differences in frequencies of these behaviors, and concomitant effects

192   on loading and/or joint range of motion, may affect the articular surfaces of the distal radius and

193   ulna, as found here.

194   There are also environmental differences between captive and wild chimpanzees that may

195   affect bony morphology. Most of the captive chimpanzee population was housed in enclosures

196   with concrete flooring (as well as simulated arboreal substrates, Schwandt, 2002), which could

197   affect joint surfaces. Previous research has demonstrated that long-term locomotion on concrete

198   substrates affects the articular cartilage and joint congruency of the knee in sheep housed on

199   tarmac compared to sheep housed in pasture (Radin et al., 1982). Perhaps the differences in tibial

200   plateau articular surface area found here could be explained by altered loading regimes resulting

201 from concrete substrates in the captive chimpanzee sample. Concrete surfaces might result in

202 larger joint reaction forces than those that result from the more compliant arboreal and terrestrial

203 substrates found in wild environments. However, some of the captive individuals studied here

204 were not housed for the entirety of their lives at PFA, and the details of the substrates of their

205 rearing environments are uncertain.

206   There may be other differences between captive and wild chimpanzees besides positional

207 behaviors and physical environments that could affect long bone articular surfaces. In baboons,

208 for example, it has been suggested that dietary differences between captive and wild individuals

209 could be responsible for observed differences in somatic maturation rates, where captive animals

210 may be "overfed," resulting in more energy that can be allocated to growth than in their wild

211 counterparts (Phillips-Conroy and Jolly, 1988). Similar scenarios have been suggested for

212 chimpanzees. Wild chimpanzees in Gombe National Park spend just over 50% of their time

213 foraging and feeding (Wrangham, 1977). Their diets consist mostly of fruit, but they eat a variety

214 of other items including other aspects of plant material (nuts, seeds, leaves, flower blossoms, and

215 piths) as well as honey, insects, and meat (Boesch and Boesch-Achermann, 2000). Captive

216 chimpanzees, on the other hand, tend to eat a less varied diet that is higher in caloric content, and

217 they tend to spend less time foraging and feeding than wild chimpanzees (Pruetz and McGrew,

218 2001). Perhaps the combined effects of reduced activity levels and higher-calorie diets in captive

219 chimpanzees could result in the observed accelerated skeletal growth rates in which captive

220 chimpanzees reach skeletal maturity from six months to up to three years before wild

221 chimpanzees (Zihlman et al., 2007). However, if nutritional differences were responsible for the

222 articular surface area differences found in this study, then one might expect to observe uniform

223 differences between captive and wild specimens across all measured long bone epiphyses. That

224   this study only found rearing differences in two out of ten measured articular surfaces (proximal

225   tibia and distal ulna) suggests that the likely cause of skeletal differences is multifactorial and

226   more complex than diet alone.

227   The differences in skeletal maturation rates between captive and wild chimpanzees

228   demonstrated by Zihlman and colleagues (2007) suggests that exploring the effects of allometry

229   on differences in skeletal size between captive and wild chimpanzees could provide additional

230   explanatory power. Although a full allometric analysis is beyond the scope of this paper, a test of

231   homogeneity of slopes of the regressions of the square root of each articular surface area on the

232   geometric mean between the captive and wild samples demonstrates that most variables do not

233   differ in their allometric coefficients of long bone articular surface areas (Table 8). The

234   exception is the distal tibia, for which the slope test was significant. However, this variable does

235   not differ by sex or rearing, so any allometric differences are likely not meaningful. Thus, there

236   are likely additional hormonal, nutritional, size, or gestational differences that could affect the

237   epiphyses of long bones. Future work investigating the likely multifactorial causes of increased

238   somatic growth rates in captive chimpanzees would be valuable for understanding the biology of

239   the genus as a whole.

240   *Environmental effects on long bone articular surfaces*

241   In addition to providing more information about the potential differences between captive

242   and wild osteological specimens, this study provides some broader information about how

243   articular surfaces may respond to loading regimes. Some previous work has found that cartilage

244   and subchondral bone thickness and hardness respond to loading (e.g., Bouvier and Zimny,

245   1987; Murray et al., 2001; Plochocki, Riscigno & Garcia, 2006, but see Hammond et al., 2010),

246   and dimensions of joint surfaces can respond to loading by increasing in overall size (Bouvier

247   and Zimny, 1987; Plochocki, Riscigno & Garcia, 2006, but see Lieberman, Devlin & Pearson,

248   2001). This study finds that captive chimpanzees exhibit relatively larger articular surface areas

249   of parts of the knee and wrist joints compared to wild chimpanzees, which could potentially

250   result from long-term housing on stiff, relatively noncompliant substrates. If larger articular

251   surfaces in captive animals are related to different loading regimes, then one might expect that

252   distal postcranial joints would be more susceptible to increases in peak substrate reaction forces.

253   The wrist data from this study support this hypothesis, but the ankle data do not. Additionally, it

254   is unclear why the knee joint would show articular changes while the elbow joint does not.

255   Kinetic data on the effects of compliant versus noncompliant substrates on postcranial joint

256   reaction forces are necessary to address these complex questions. Like other primates (e.g.,

257   Kimura, Okada & Ishida, 1979), chimpanzees experience larger hindlimb peak vertical forces

258   during quadrupedalism than forelimb forces (Reynolds, 1985; Demes et al., 1994). Given this

259   phenomenon, one might also expect that hindlimb joints would respond more readily to

260   increasing loading regimes in captive animals.

261

262   **Conclusions**

263   Skeletal collections of primates are rare and encompass endangered species for which

264   data are dwindling (e.g., Gordon, Marcus & Wood, 2013). Therefore, using captive-reared

265   specimens that are curated within existing skeletal collections, as well as imaging data (e.g.,

266   computed tomographic scans) of sanctuary or zoological specimens, may be important ways to

267   increase sample sizes. Previous work on the effects of captivity on long bones did not find

268   differences between captive and wild specimens in long bone lengths (Turner et al., 2016) or

269   scapular shape (Bello-Hellegouarch et al., 2013), and the present study only found differences in

270   some long bone articular surfaces (i.e., aspects of the knee and wrist). Taken together, this body

271   of work suggests that there is no *a priori* reason to exclude captive individuals from

272   morphological analyses. However, if one chooses to combine captive and wild specimens in a

273   study of morphological variation, it would be prudent to first examine the data to determine

274   whether significant differences exist between captive and wild specimens, or whether captive

275   specimens are statistical outliers.

276

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283   (IACUC).

284

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401

402 **Figure legends**

403 **Figure 1.** Boxplot of the tibial plateau shape variable by sex and rearing. Captive specimens

404 have significantly greater tibial plateau scaled surfaces areas than wild specimens (p=0.0002).

405 There are no sex differences in tibial plateau area.

406

407 **Figure 2.** Boxplot of the distal ulna shape variable by sex and rearing. Captive specimens have

408 significantly greater distal ulna scaled surface areas than wild specimens (p=0.0002). There are

409 no sex differences in the distal ulna shape variable.

410

411 **Figure 3.** Boxplot of the femoral condyles shape variable by sex and rearing. There are

412 significant sex and sex*rearing effects; males have greater femoral condyle scaled surfaces than

413 females (p=0.01) and captive males have greater femoral condyle areas than all other groups

414 (p=0.004).

415

416 **Figure 4.** Boxplot of the distal radius shape variable by sex and rearing. This plot shows

417 significant sex and sex*rearing interaction effects. Males have relatively greater distal radius

418 scaled surface areas than females (p=0.0006), and captive males have relatively greater areas

419 than all other groups (p=0.04).

420

421 **Figure 5.** Boxplot of the humeral head shape variable by sex and rearing. There is a significant

422 sex*rearing interaction effect; captive males have smaller humeral head scaled surface areas than

423 wild males (p=0.01) and captive females (p=0.02).

424

425 **Figure 6. Bivariate plot of principal component scores 1 and 2.** The plot of PC 1 on PC 2

426 demonstrates overlap among captive and wild individuals. PC 1 differentiates captive males from

427 the other sex-rearing groups. PC 2 does not differentiate among the four sex-rearing groups.

428 Circles are captive specimens, triangles are wild specimens. Filled symbols are females, open

429 symbols are males. Convex hull polygons enclose each group.

430

431 **Figure 7. Bivariate plot of principal component scores 3 and 4.** The plot of PC 3 on PC 4

432 does not differentiate the sample by either sex or rearing. Circles are captive specimens, triangles

433 are wild specimens. Filled symbols are females, open symbols are males. Convex hull polygons

434 enclose each group.

435

Sample.

Table 1. Sample.

Wild, N=22			Captive, N=20				
ID	Sex	Collection	ID	Sex	Environment	Age	Collection
HTB 1056	M	CMNH	AP	F	Zoo	30	PFA
HTB 1708	M	CMNH	CQ	F	PFA	19	PFA
HTB 1720	F	CMNH	JE	F	PFA	18	PFA
HTB 1713	F	CMNH	KI	F	PFA	14	PFA
HTB 1718	M	CMNH	PR	F	PFA	20	PFA
HTB 1722	M	CMNH	TR	F	PFA	17	PFA
HTB 1759	F	CMNH	DO	F	PFA	25	PFA
HTB 1739	M	CMNH	JU	F	Zoo	22	PFA
HTB 1723	F	CMNH	LO	F	Pet	Ad.	PFA
HTB 1748	F	CMNH	SA	F	Pet	Ad.	PFA
HTB 1758	M	CMNH	BB	M	PFA	16	PFA
HTB 1770	F	CMNH	PD	M	PFA	18	PFA
HTB 1775	F	CMNH	LI	M	Other	11	PFA
HTB 1843	F	CMNH	CC	M	Zoo	27	PFA
HTB 1853	F	CMNH	CH	M	Zoo	Ad.	ASU
HTB 2071	F	CMNH	PN	M	Zoo	15	ASU
HTB 2771	F	CMNH	DA	M	Zoo	21	ASU
HTB 3552	M	CMNH	TO	M	Zoo	10	ASU
HTB 2072	M	CMNH	ED	M	Other	17	ASU
HTB 1882	M	CMNH	SM	M	PFA	9	PFA
HTB 2026	M	CMNH					
HTB 2746	M	CMNH					

CMNH: Cleveland Museum of Natural History, PFA: Primate Foundation of Arizona, ASU: Arizona State University

List of linear measures and equations used to calculate articular surface areas (from Ruff, 2002).

Table 2. List of linear measures and equations used to calculate articular surface areas (from Ruff, 2002).

Measurement	Abbreviation/Equation
Humerus length	HL
Humeral head breadth	
Anteroposterior	HHAP
Superoinferior	HHSI
Humeral head depth	HHDP
Humeral trochlea breadth	
Mediolateral	TRML
Superoinferior	TRSI
Anteroposterior	TRAP
Distal articular surface total breadth	HDML
Humeral capitulum breadth	
Mediolateral	CPML
Superoinferior	CPSI
Humeral capitulum depth	CPDP
Humeral head surface area	$HHSA = 3.14*((0.0625*(HHSI+HHAP)^2)+HHDP^2)$
Trochlea surface area	$TRSA = TRAP*TRML*ACOS(1-((2*TRSI)/TRAP))$
Capitulum surface area	$CPSA = CPSI*CPML*ACOS(1-((2*CPDP/CPSI))$
Total humeral distal surface area	$HDSA = TRSA+CPSA$
Radius length	RL
Radial head breadth	
Anteroposterior	RHAP
Mediolateral	RHML
Radiocarpal surface breadth	
Anteroposterior	RCAP
Mediolateral	RCML
Radial head surface area	$RHSA = 0.785*(RHML*RHAP)$
Radiocarpal surface area	$RCSA = RCML*RCAP$
Ulna length	UL
Trochlear notch breadth	
Mediolateral	UTML
Superoinferior	UTSI
Trochlear notch depth	UTDP
Ulnar distal articular surface breadth	
Anteroposterior	UCAP
Mediolateral	UCML
Trochlear notch surface area	$UTSA = UTSI*UTML*ACOS(1-((2*UTDP)/UTSI))$
Ulnar distal articular surface area	$UCSA = 0.785*(UCML*UCAP)$

Femur length		FL
Femoral head breadth		
	Anteroposterior	FHAP
	Superoinferior	FHSI
Femoral head depth		FHDP
Femoral condyle breadth		
	Medial condyle anteroposterior	MCAP
	Lateral condyle anteroposterior	LCAP
	Total mediolateral breadth	FCML
	Medial condyle superoinferior	MCSI
	Lateral condyle superoinferior	LCSI
Femoral condyle depth		
	Medial	MCDP
	Lateral	LCDP
Femoral head surface area		FHSA=1.57*FHDP*(FHSI+FHAP)
Femoral condyle surface area		
	Medial	MCSA=MCSI*MCML*ACOS(1-((2*MCDP)/MCSI))
	Lateral	LCSA=LCSI*LCML*ACOS(1-((2*LCDP)/LCSI))
	Total	FCSA=MCSA+LCSA
Tibia length		TL
Tibial plateau breadth		
	Medial surface ML	MPML
	Lateral surface ML	LPML
	Total tibial plateau ML breadth	TPML
	Medial surface AP	MPAP
	Lateral surface AP	LPAP
Tibiotalar surface breadth		
	Anteroposterior	TTAP
	Mediolateral	TTML
Tibial plateau surface area		
	Medial	MPSA=0.785*(MPML*MPAP)
	Lateral	LPSA=0.785*(LPML*LPAP)
	Total	TPSA=MPSA+LPSA
Tibiotalar surface area		TTSA=TTML*TTAP

Bold denotes the articular surface areas on which all analyses were performed.

Means and standard deviations of absolute articular surface areas (mm^2), the square root of articular surfaces scaled by geometric mean, bone lengths (mm), and geometric mean (mm).

Table 3. Means and standard deviations of absolute articular surface areas (mm²), the square root of articular surfaces scaled by geometric mean, bone lengths (mm), and geometric mean (mm) for each sex-rearing group. Percentage differences between captive and wild sex-specific groups are also shown.

	Captive				Wild				Percentage difference (captive - wild)	
	Female		Male		Female		Male		Female	Male
	Mean (mm²)	SD	Mean (mm²)	SD	Mean (mm²)	SD	Mean (mm²)	SD		
Femoral head (FHSA)	2223.1	352.6	2451.5	333.5	2408.8	467.1	2649.3	255.1	-8.4%	-8.1%
FHSA$^{1/2}$/GM	0.775	0.05	0.775	0.04	0.801	0.04	0.794	0.04	-3.3%	-2.4%
Femoral condyles (FCSA)	1991.0	259.5	2511.1	316.7	2106.9	288.3	2347.9	215.3	-5.8%	6.5%
FCSA$^{1/2}$/GM	0.734	0.03	0.786	0.04	0.750	0.1	0.746	0.02	-2.2%	5.0%
Femur length	285.4	24.8	289.2	15.8	292.1	15.7	302.9	14.5	-2.4%	-4.8%
Tibial plateau (TPSA)	1138.6	165.9	1218.0	99.4	1043.8	120.3	1149.1	166.4	8.3%	5.7%
TPSA$^{1/2}$/GM	0.553	0.02	0.549	0.01	0.527	0.02	0.522	0.03	4.7%	5.0%
Distal tibia (TTSA)	467.5	70.1	495.8	53.1	463.3	76.1	549.7	61.8	0.9%	-10.9%
TTSA$^{1/2}$/GM	0.356	0.03	0.349	0.02	0.353	0.02	0.361	0.02	0.9%	-3.4%
Tibia length	245.9	21.3	246.9	17.2	246.0	17.3	257.5	12.3	-0.1%	-4.3%
Humeral head (HHSA)	2062.8	268.3	1927.2	225.8	1990.0	252.5	2368.3	301.0	3.5%	-22.9%
HHSA$^{1/2}$/GM	0.747	0.03	0.689	0.03	0.731	0.03	0.750	0.1	2.2%	-8.9%
Distal humerus (HDSA)	1517.2	251.2	1713.0	133.4	1482.2	148.5	1734.6	200.0	2.3%	-1.3%
HDSA$^{1/2}$/GM	0.637	0.03	0.649	0.03	0.629	0.02	0.642	0.03	1.2%	1.1%
Humerus length	291.1	24.7	288.1	18.6	297.5	18.0	309.0	13.7	-2.2%	-7.3%
Radial head (RHSA)	427.9	49.7	494.4	45.1	457.9	65.7	500.2	42.5	-7.0%	-1.2%
RHSA$^{1/2}$/GM	0.342	0.01	0.349	0.01	0.351	0.01	0.345	0.01	-2.6%	1.0%
Distal radius (RCSA)	407.6[a]	51.1	553.4	58.8	420.6	44.5	499.5	59.2	-3.2%	9.7%
RCSA$^{1/2}$/GM	0.326	0.03	0.369	0.02	0.335	0.02	0.345	0.02	-2.9%	6.6%
Radius length	268.5	18.5	271.0	17.8	269.5	14.9	287.0	14.2	-0.4%	-5.9%

Proximal ulna (UTSA)	952.9	146.8	1115.3	151.5	952.4	125.1	1088.3	132.2	0.1%	2.4%
UTSA$^{1/2}$/GM	0.506	0.02	0.523	0.03	0.505	0.04	0.509	0.03	0.1%	2.7%
Distal ulna (UCSA)	125.9	19.5	143.5	25.9	107.3	13.7	122.4	15.3	14.7%	14.7%
UCSA$^{1/2}$/GM	0.184	0.01	0.186	0.01	0.171	0.02	0.170	0.01	7.1%	8.6%
Ulna length	280.5	18.7	287.7	17.9	283.6	13.5	301.6	13.8	-1.1%	-4.9%
Geometric mean (GM)	60.7[a]	3.6	63.692	2.77	61.0	2.8	64.8	2.2	-0.4%	-1.7%

[a]Excludes DO due to pathology

Results of analyses of variance on scaled articular surfaces. MANOVA (with sex, rearing, and sex-rearing interaction effects) results are followed by univariate two-way ANOVA results.

Table 4. Results of analyses of variance on scaled articular surfaces. MANOVA (with sex, rearing, and sex-rearing interaction effects) results are followed by univariate two-way ANOVA results.

		F	p
Whole model MANOVA (Wilk's lambda)		2.83	**<0.0001**
	Sex	2.95	**0.01**
	Rearing	4.08	**0.001**
	Sex*Rearing	2.59	**0.02**
FHSA$^{1/2}$/GM		0.97	0.42
	Sex	0.07	0.79
	Rearing	2.75	0.11
	Sex*Rearing	0.07	0.79
FCSA$^{1/2}$/GM		5.83	**0.002**
	Sex	7.11	**0.01**
	Rearing	1.70	0.20
	Sex*Rearing	9.41	**0.004**
TPSA$^{1/2}$/GM		5.75	**0.002**
	Sex	0.53	0.47
	Rearing	16.70	**0.0002**
	Sex*Rearing	0.01	0.91
TTSA$^{1/2}$/GM		0.63	0.60
	Sex	0.01	0.93
	Rearing	0.46	0.50
	Sex*Rearing	1.41	0.24
HHSA$^{1/2}$/GM		4.34	**0.01**
	Sex	2.14	0.15
	Rearing	2.85	0.10
	Sex*Rearing	8.40	**0.006**
HDSA$^{1/2}$/GM		1.06	0.38
	Sex	2.31	0.14
	Rearing	0.86	0.36
	Sex*Rearing	0.00	0.96
RHSA$^{1/2}$/GM		1.13	0.35
	Sex	0.04	0.84
	Rearing	0.53	0.47
	Sex*Rearing	2.85	0.10

RCSA$^{1/2}$/GM		7.42	**0.0005**
	Sex	13.95	**0.0006**
	Rearing	4.03	0.05
	Sex*Rearing	4.75	**0.04**
UTSA$^{1/2}$/GM		1.02	0.39
	Sex	1.65	0.21
	Rearing	0.81	0.37
	Sex*Rearing	0.69	0.41
UCSA$^{1/2}$/GM		5.71	**0.003**
	Sex	0.02	0.88
	Rearing	16.94	**0.0002**
	Sex*Rearing	0.17	0.68

p-values in bold are significant at alpha=0.05

Results of Tukey's HSD *post hoc* pairwise comparisons for significant sex-rearing interaction effects.

Table 5. Results of Tukey's HSD post hoc pairwise comparisons for significant sex-rearing interaction effects.

FCSA$^{1/2}$/GM	CF	CM	WF	WM
CF				
CM	**0.002**			
WF	0.60	**0.04**		
WM	0.77	**0.02**	0.99	

HHSA$^{1/2}$/GM	CF	CM	WF	WM
CF				
CM	**0.02**			
WF	0.83	0.13		
WM	1.00	**0.01**	0.73	

RCSA$^{1/2}$/GM	CF	CM	WF	WM
CF				
CM	**0.001**			
WF	1.00	**0.001**		
WM	0.63	**0.02**	0.67	

p-values in bold are significant at alpha=0.05

CF: captive female, CM: captive male, WF: wild female, WM: wild male

Eigenvalues of principal components.

Table 6. Eigenvalues of principal components.

PC	Eigenvalue	Cumulative %
1	0.0027	32.1
2	0.0019	54.8
3	0.0011	67.4
4	0.0007	75.8
5	0.0006	83.3
6	0.0005	89.2
7	0.0004	93.6
8	0.0003	97.1
9	0.0002	99.0
10	0.0001	100

Variable loading matrix for the ten principal components.

Table 7. Variable loading matrix for the ten principal components.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10
HHSA$^{1/2}$/GM	**0.961**	-0.029	0.253	-0.004	0.033	0.078	0.034	0.058	0.002	-0.012
FHSA$^{1/2}$/GM	0.055	**0.970**	-0.141	0.112	0.115	0.099	0.032	0.014	0.001	-0.013
FCSA$^{1/2}$/GM	**-0.411**	0.380	**0.785**	-0.155	-0.147	-0.100	-0.119	-0.021	-0.030	-0.018
HDSA$^{1/2}$/GM	-0.134	-0.238	0.317	**0.647**	**0.593**	-0.169	-0.054	-0.136	-0.066	0.002
UTSA$^{1/2}$/GM	-0.360	-0.085	0.148	**-0.587**	**0.636**	0.106	0.266	0.079	0.065	0.012
TPSA$^{1/2}$/GM	-0.394	-0.241	0.247	0.203	-0.138	**0.756**	0.143	-0.264	0.048	-0.029
TTSA$^{1/2}$/GM	0.291	0.204	0.050	-0.036	-0.232	-0.404	**0.657**	**-0.466**	-0.053	0.043
RCSA$^{1/2}$/GM	**-0.502**	-0.111	0.214	0.433	-0.202	-0.063	**0.448**	**0.493**	0.091	-0.079
RHSA$^{1/2}$/GM	0.066	0.223	0.304	0.277	-0.077	-0.048	-0.082	0.021	**0.668**	**0.561**
UCSA$^{1/2}$/GM	-0.221	0.008	0.087	0.027	-0.079	0.331	0.178	0.327	-0.714	**0.422**

Bold indicates variables that load heavily (absolute value greater than 0.4) on each principal component.

Tests of homogeneity of slopes between captive and wild samples for regressions of the square root of each articular surface area on the geometric mean demonstrate no statistical differences.

Table 8. Tests of homogeneity of slopes between captive and wild samples for regressions of the square root of each articular surface area on the geometric mean demonstrate no statistical differences.

Square root of:		Captive			Wild				
	N	Slope	SE	N	Slope	SE	t	df	p
Femoral head (FHSA)	20	0.72	0.19	22	0.90	0.18	0.68	38	0.50
Femoral condyles (FCSA)	20	0.96	0.18	22	0.81	0.11	0.75	38	0.46
Tibial plateau (TPSA)	20	0.51	0.07	22	0.57	0.10	0.44	38	0.66
Distal tibia (TTSA)	20	0.21	0.09	22	0.46	0.08	2.11	38	**0.04**
Humeral head (HHSA)	20	0.45	0.16	22	0.53	0.22	0.28	38	0.78
Distal humerus (HDSA)	20	0.69	0.11	22	0.71	0.11	0.08	38	0.94
Radial head (RHSA)	20	0.36	0.04	22	0.32	0.06	0.58	38	0.56
Distal radius (RCSA)	19	0.31	0.13	22	0.41	0.06	0.75	37	0.46
Proximal ulna (UTSA)	20	0.65	0.10	22	0.48	0.12	1.09	38	0.28
Distal ulna (UCSA)	20	0.18	0.06	22	0.17	0.04	0.14	38	0.89

p-values in bold are significant at alpha=0.05

Figure 1

Boxplot of the tibial plateau shape variable by sex and rearing.

Captive specimens have significantly greater tibial plateau scaled surfaces areas than wild specimens (p=0.0002). There are no sex differences in tibial plateau area.
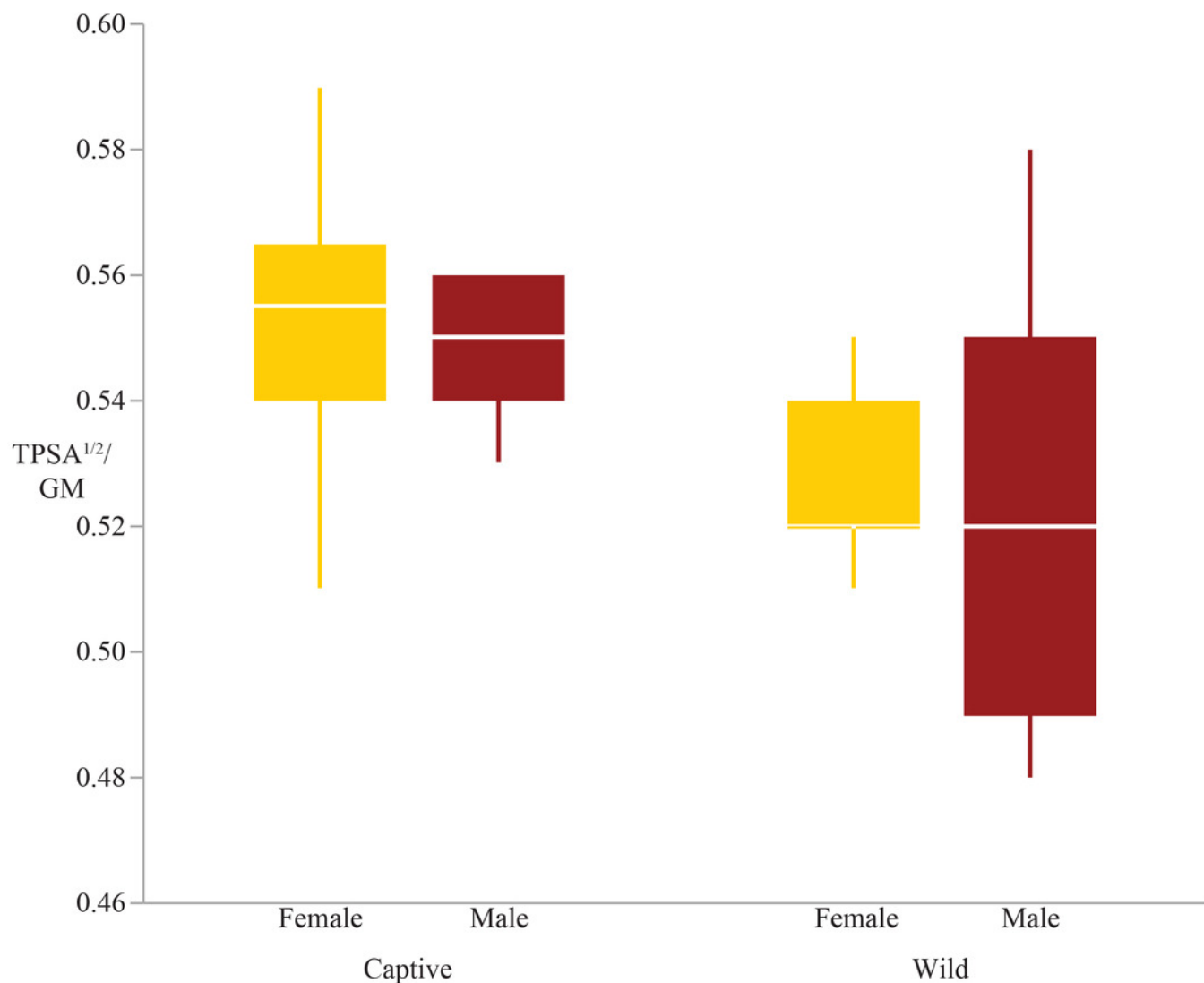
Figure 2

Boxplot of the distal ulna shape variable by sex and rearing.

Captive specimens have significantly greater distal ulna scaled surface areas than wild specimens (p=0.0002). There are no sex differences in the distal ulna shape variable.
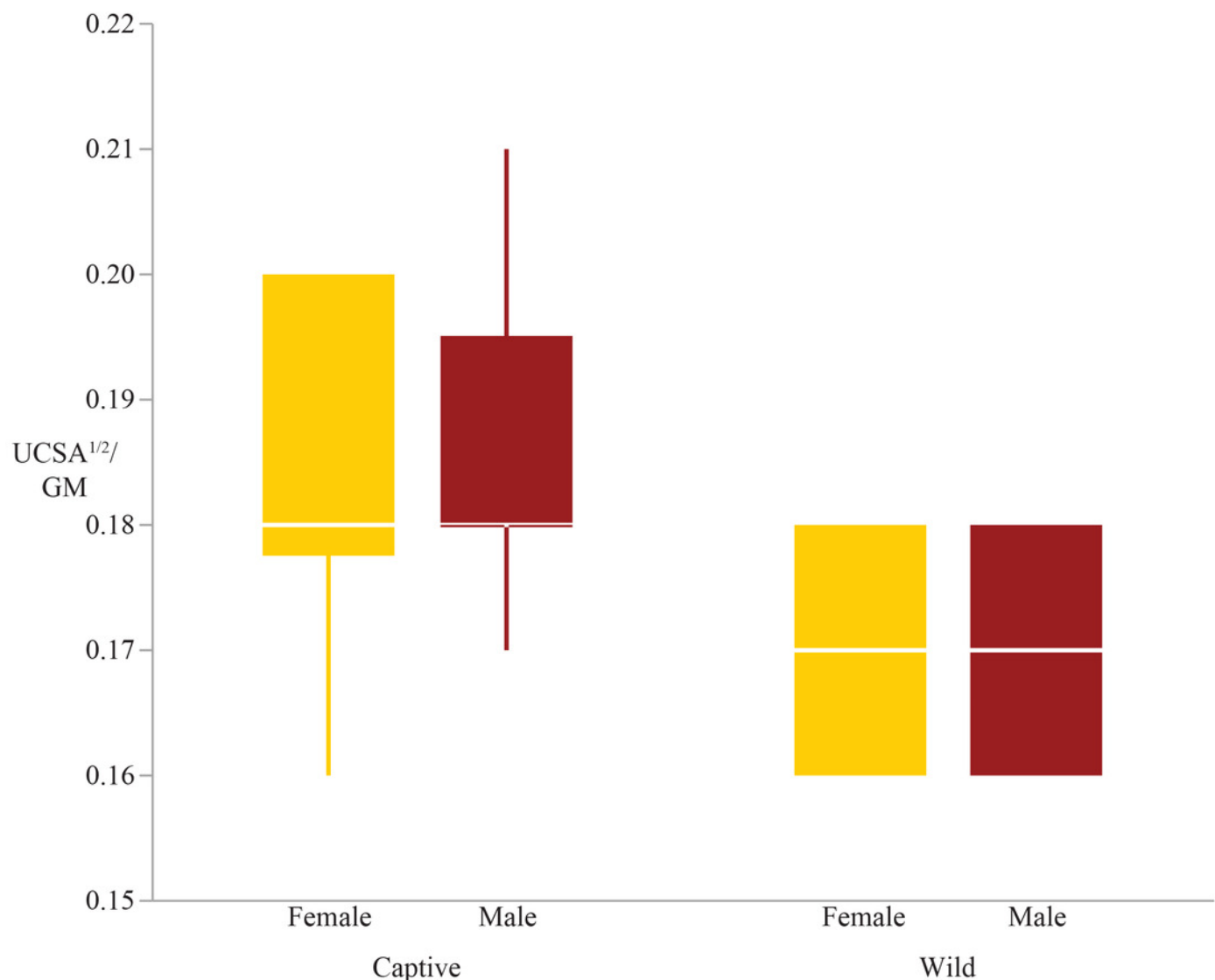
Figure 3

Boxplot of the femoral condyles shape variable by sex and rearing.

There are significant sex and sex*rearing effects; males have greater femoral condyle scaled surfaces than females (p=0.01) and captive males have greater femoral condyle areas than all other groups (p=0.004).
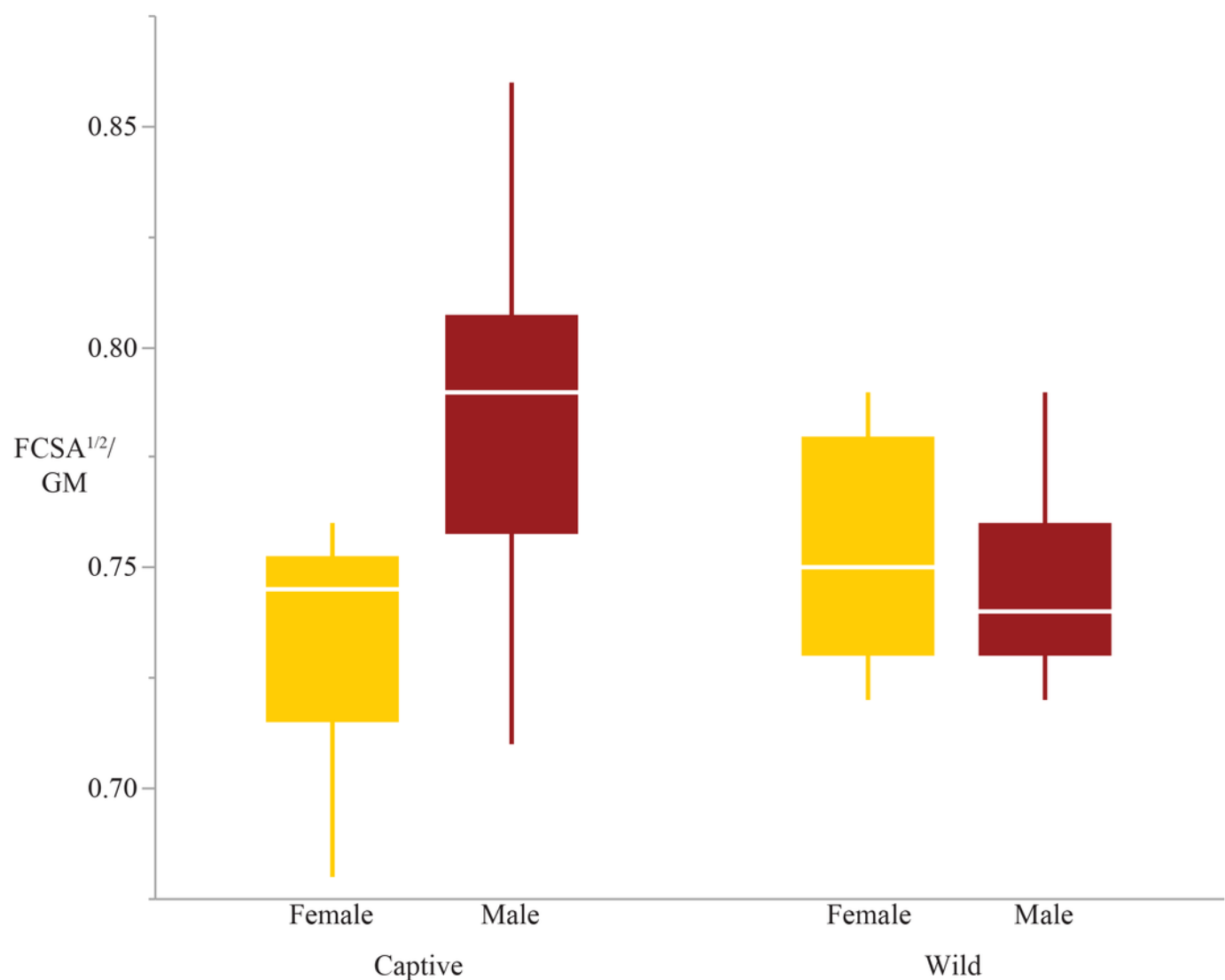
Figure 4

Boxplot of the distal radius shape variable by sex and rearing.

This plot shows significant sex and sex*rearing interaction effects. Males have relatively greater distal radius scaled surface areas than females (p=0.0006), and captive males have relatively greater areas than all other groups (p=0.04).
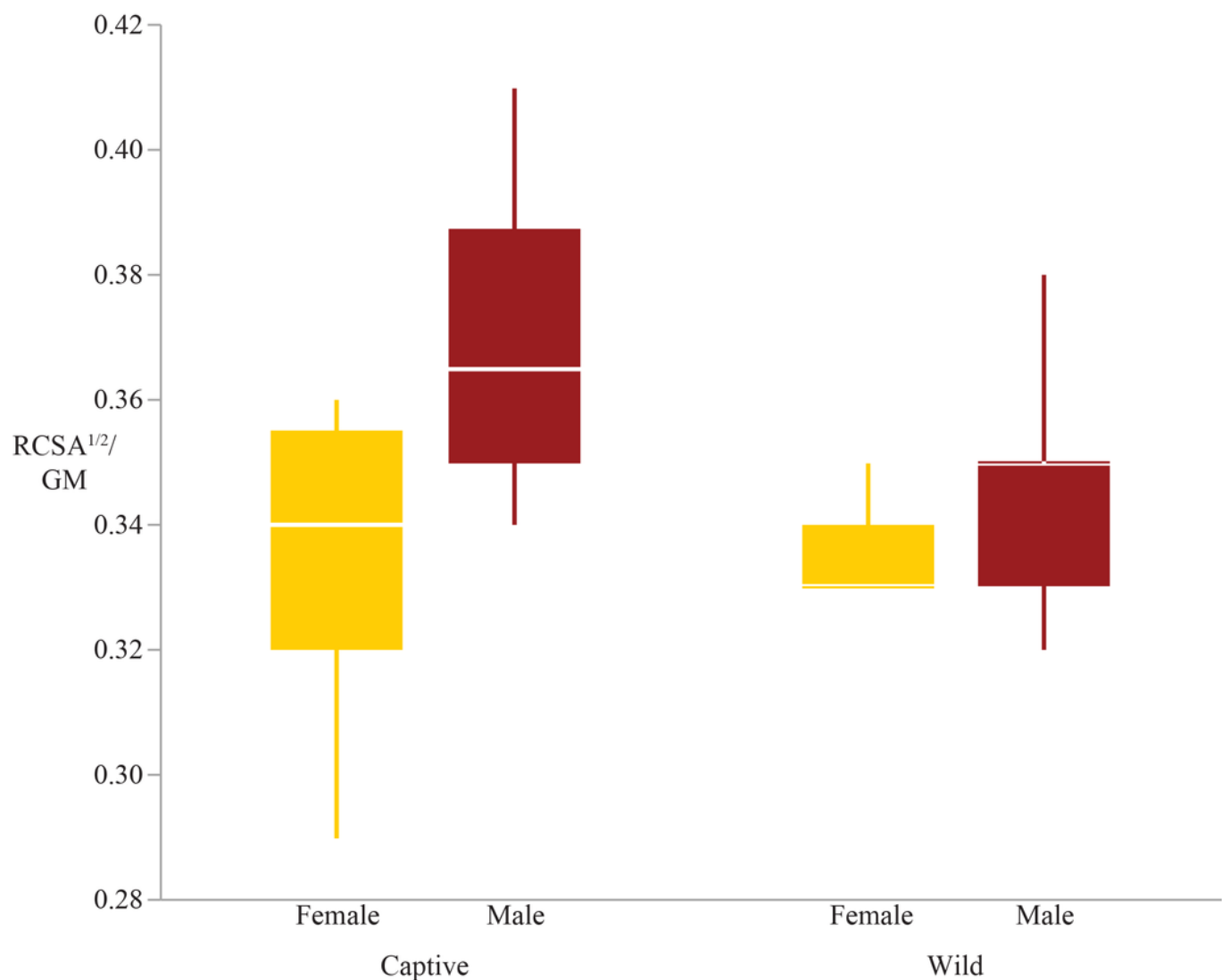
Figure 5

Boxplot of the humeral head shape variable by sex and rearing.

There is a significant sex*rearing interaction effect; captive males have smaller humeral head scaled surface areas than wild males (p=0.01) and captive females (p=0.02).
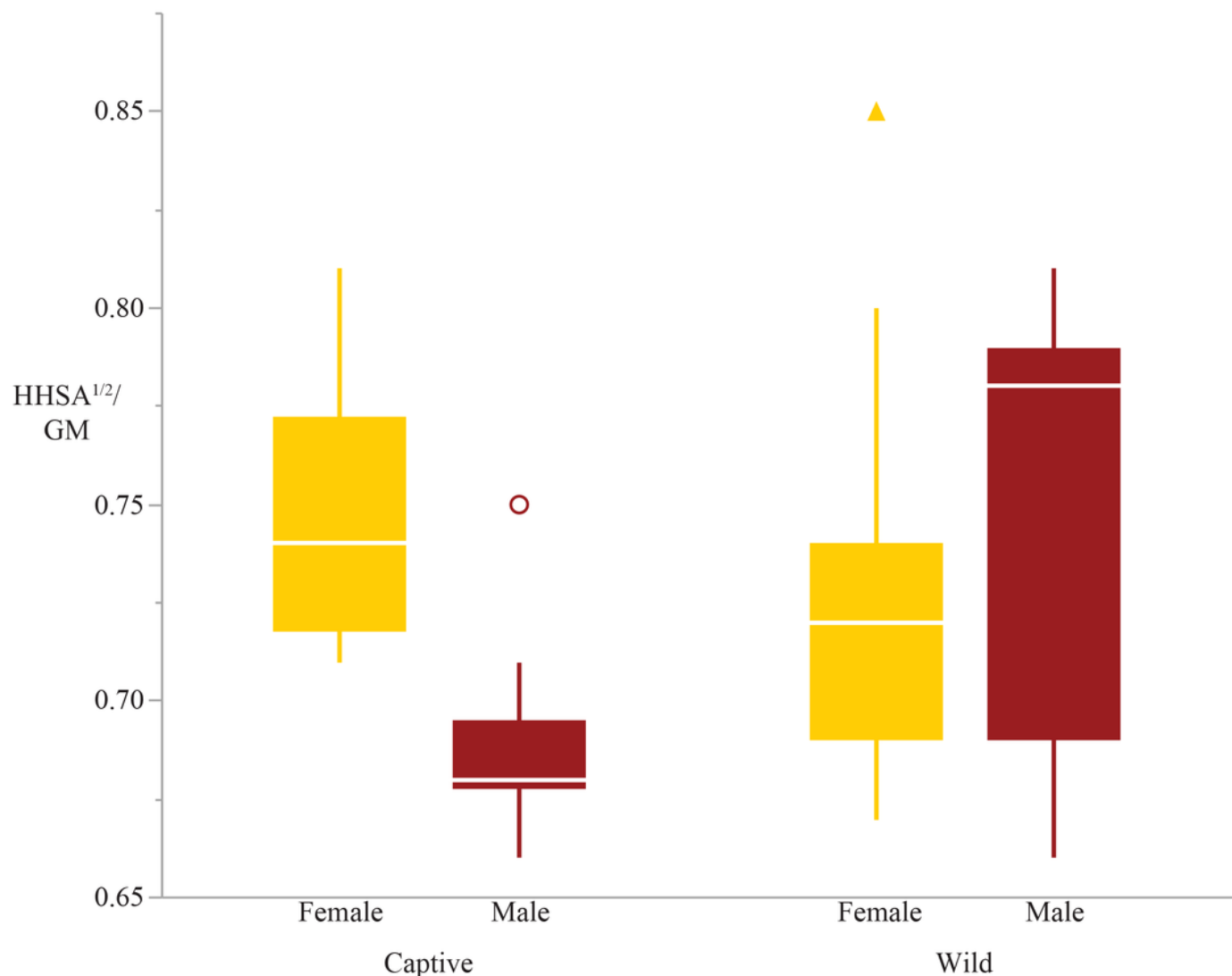
Figure 6

Bivariate plot of principal components 1 and 2.

The plot of PC 1 on PC 2 demonstrates overlap among captive and wild individuals. PC 1 differentiates captive males from the other sex-rearing groups. PC 2 does not differentiate among the four sex-rearing groups. Circles are captive specimens, triangles are wild specimens. Filled symbols are females, open symbols are males. Convex hull polygons enclose each group.
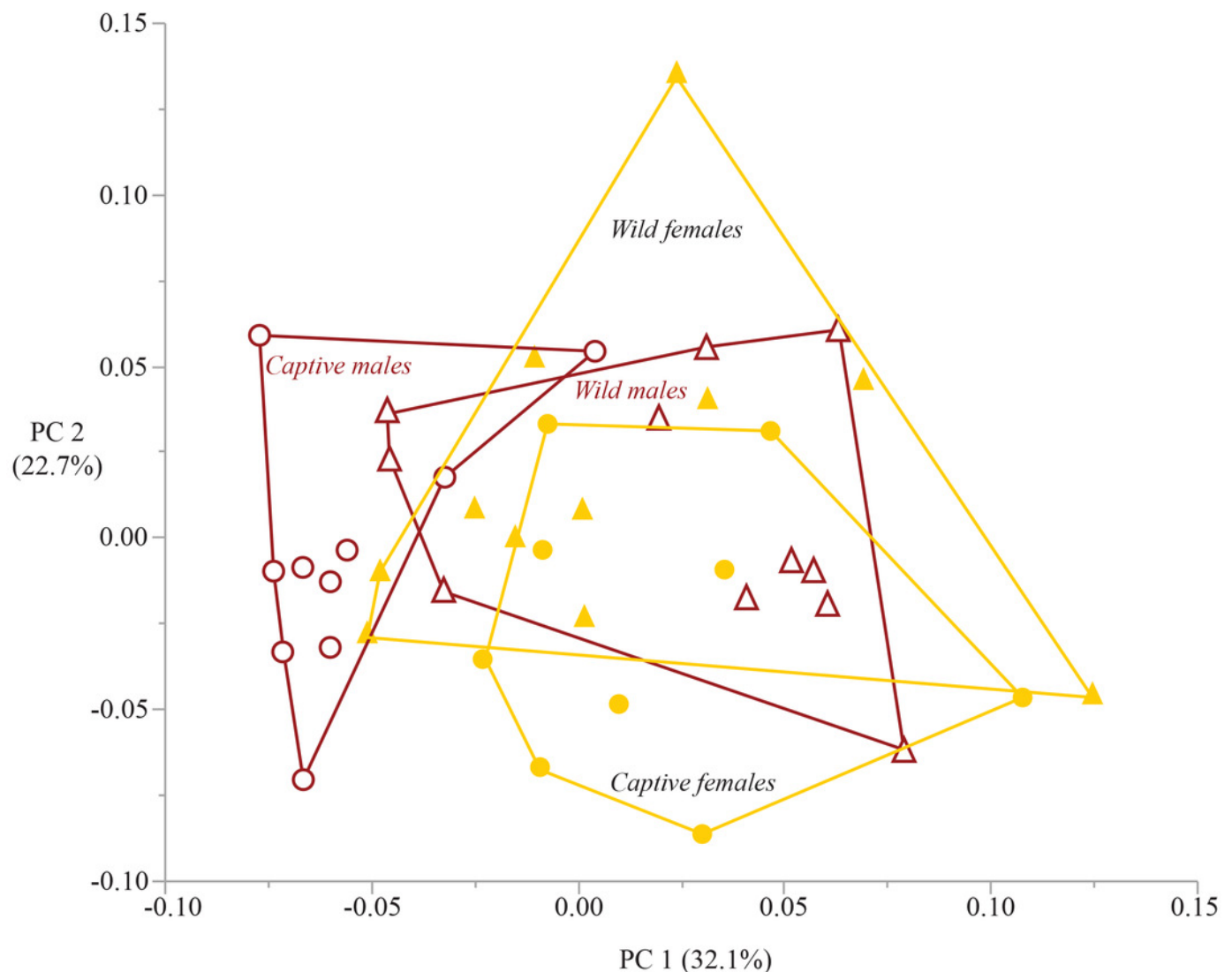
Figure 7

Bivariate plot of principal components 3 and 4.

The plot of PC 3 on PC 4 does not differentiate the sample by either sex or rearing. Circles are captive specimens, triangles are wild specimens. Filled symbols are females, open symbols are males. Convex hull polygons enclose each group.