Brains vs Brawn: Relative brain size is sexually dimorphic amongst weapon bearing ruminants

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6   **Abstract**

7   Here, we investigate the relationship between relative brain size and sexual weapons in

8   ruminants. In most cases, sexual weaponry is heavily male-biased, and costs resulting from

9   growing, maintaining, or wielding weapons will be suffered primarily by males. We used

10   comparative phylogenetic analyses to test whether increased investment in sexual weapon size

11   (tusks, antlers, and horns) across four families (Tragulidae, Moschidae, Cervidae, and Bovidae)

12   was associated with decrease in relative brain size, and whether the difference in weapon

13   investment relative to conspecific females led to sexual differences in relative brain size. We

14   found no relationship between relative brain size and relative weapon size within males or

15   females, but when we compared males directly to conspecific females, we found that as males

16   possessed larger weaponry, they had smaller brain sizes, regardless of weapon type. Our finding

17   suggest male investment in some types of elaborate weapons could be related to male reduction

18   in larger brains.

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27   **Significance Statement:**

28   We took measurements of antlers, horns, and tusks from skulls of both males and females, as

29   well as brain volume and looked at the relationship between relative weapon size and relative

30   brain size. Our work found support that bearing large, exaggerated sexually selected weapons

31   results in a negative relationship with relative brain size: when males invest more in sexual

32   weaponry, they evolve smaller brains relative to females, who typically don't invest in

33   weaponry. Given that most studies largely are focused on tradeoffs solely within one sex, our

34   study provides a novel approach comparing the relationship between sexes to measure sexual

35   dimorphic investment. The evolution of weaponry in ruminants is one of the most widely studied

36   topics of the last 70 years and this study yields new support for the possible presence of sexual

37   dimorphic trade-offs amongst sexually selected traits.

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Introduction

Natural selection favoring greater cognitive ability is hypothesized to explain the evolution of large brain sizes in many bird and mammal species (Eisenberg & Wilson, 1978; Iwaniuk et al., 2001; Jerison, 1973; Lefebvre et al., 2004; Reader & Laland, 2002; Sol et al., 2005a; Tsuboi et al., 2020). The "expensive brain" hypothesis predicts that energy spent to develop and maintain large brains will result in the diminishment of other expensive physiological functions including reproductive rates (Isler & van Schaik, 2006) and morphological structures like gut (Kotrschal et al., 2013) and testes size (Lemaitre et al., 2009). A recent study in mammals showed that significant investments in morphological antipredator defenses (e.g., spines/quills, dermal armor, noxious sprays) were associated with reductions in relative brain size, suggesting that selection favoring costly morphological defenses can overwhelm selection favoring advanced cognitive abilities, especially in dangerously exposed environments (Stankowich & Romero, 2017). Given that intrasexual selection strongly favors elaborate sexual weapons in male ruminant mammals (tusks, horns, antlers) and these can be costly to grow, maintain, and carry around (Festa-Bianchet et al., 2004; Landete-Castillejos et al., 2019; Loe et al., 2019; Moen et al., 1999; Mysterud et al., 2005), we investigated whether investment into such expensive structures might also have resulted in an negative evolutionary relationship with relative brain size between males and females of the same species (i.e., when males evolve to invest more in their weapon, does their brain size decrease relative to females of the same species?).

Males of many species expend tremendous energy growing elaborate, often heavy sexual weapons used to signal fighting strength and to fight with other males for access to reproductive females (Emlen, 2008; Landete-Castillejos et al., 2019). The sexual weapons of ruminant

mammals are particularly well studied and vary considerably in size, shape, weight, growth patterns, and use in battle (Caro et al., 2003; Davis et al., 2011). For example, large upper canines, tusks, are only used in sexual combat (Barrette, 1977; Dubost & Terrade, 1970; Wilson & Mittermeier, 2011) and are found exclusively on males in three extant deer families: Tragulidae (mouse deer; Cabrera & Stankowich, 2018; Wilson & Mittermeier, 2011), Moschidae (musk deer; Fennessy, 1984; Wilson & Mittermeier, 2011), and some Cervidae (Chinese water deer (*Hydropotes inermis*), muntjacs (*Muntiacus* spp.), and tufted deer (Elaphodus; Wilson & Mittermeier, 2011). Antlers are found almost exclusively in the males of all cervids (true deer) except the Chinese water deer, and both male and female caribou (*Rangifer tarandus*) bear antlers. Muntjacs and tufted deer possess both tusks and antlers, where antlers are used in dominance displays before combat with tusks (Barrette, 1977). Finally, true horns are the sole sexual weapons in the Bovidae (e.g., antelope, goats, bovines) and have evolved into many different shapes and sizes based on fighting style and are also used both in combat and/or visual intrasexual male contests (Caro et al., 2003); many female bovids also grow horns, although they are usually shorter and weaker than the males' horns of their species (Stankowich & Caro, 2009).

While antlers are deciduous (i.e., shed and regrown annually), tusks and horns are permanent. For most cervid and bovid species, antler and horn sizes increase quickly during the first few years until males reach full adult size; from that point weapons increase in size gradually with age (Fennessy, 1984). Within species, static samples of adult antlers, horns, and tusks scale disproportionately steeply (i.e., hyperallometrically) with body size (Lopez & Stankowich, 2023), resulting in some cases of extreme weapon sizes in the largest individual males. This pattern of weapon expression is predicted when costs of weapon production outweigh the benefits of large weapons for poor condition or relatively small individuals (Emlen,

93   2008; Emlen et al., 2012; Kodric-Brown et al., 2006; Nur & Hasson, 1984), which suggests that

94   investment in sexual weapons in these species could limit relative investment in other growing

95   structures.

96   Because sexual weapons in the majority of ungulates are male biased, we hypothesized a

97   negative relationship between weapons and brains, where increased investment in weaponry

98   leads to decreased investment in brain size. We predicted this effect within each sex, but we also

99   predicted that as sexual dimorphism in relative weapon investment increases in a species (i.e., as

100   males evolve larger weapons relative to females of their species), male brain size will decrease

101   relative to females of the same species. We tested for relationships between sexual weaponry and

102   relative brain size in ruminant artiodactyls by measuring weapon length (canine, antler, or horn),

103   skull length, and endocranial volume from male and female skulls of 8 tusk-bearing species

104   across three families (Tragulidae, Moschidae, and Cervidae), 13 antler-bearing cervid species,

105   and 11 horn-bearing bovid species (Fig. 1A). We calculated sex-specific measures of relative

106   brain and weapon size and used comparative phylogenetic analyses to test our predictions.

107   **Methods**

108   *Data Collection*

109   In this study, we tested the effects of sexual weaponry on relative brain size in ungulates

110   bearing three different weapon types: horns, antlers and tusks. Four hundred and thirteen

111   specimens (N_{horn} = *113*, N_{antler} = *171*, N_{tusk} = *131*) from 29 species were measured at the

112   following museums: National Museum of Natural History (NMNH), Natural History Museum of

113   Los Angeles County (LACM), CSULB Collections (CSULB), American Museum of Natural

114   History (AMNH), California Academy of Sciences (CAS), and the Field Museum of Natural

115   History (FMNH). We took measurements on both adult male and female specimens, and only

116   included species in our analyses where we had complete measurements from at least three

117   individuals of each sex (one exception, *Rangifer tarandus*, only 2 females measured). While our

118   final sample was 29 species, we want to note how difficult it is to find at least 3-5 fully intact

119   male and 3-5 fully intact female skulls (that include at least one weapon and a cranium that isn't

120   broken to measure volume) of ungulate species in natural history museums, and the time it takes

121   to take these measurements. We feel that the fact that we were able to detect a significant effect

122   despite having only 29 species (and fewer in the separate weapon tests) suggests a strong

123   negative relationship and a more conservative approach.

124   We collected the following cranial measurements. Skull length (mm) was measured from

125   the anterior tip of the premaxilla to the most posterior point of the skull (typically the occipital

126   crest or occipital condyles) (Fig. S1a, Online Resource). Skull width (mm) was measured

127   transversely from one zygomatic arch to the other (Fig. S1a, Online Resource) at the greatest

128   width of the skull. Skull height (mm) was measured from the lowest point on the squamosal at

129   the back of the skull to the highest point on the dorsal midline of the cranium (Fig. S1b, Online

130   Resource), not including the antlers/horns or pedicels. Endocranial volume was measured by

131   filling the skull with 3mm glass beads (smaller skulls) or 6x9mm plastic beads (larger skulls)

132   through the foramen magnum, and then measuring the volume of beads (mL) in a graduated

133   cylinder. Due to the curved nature of tusks, we collected two measurements: (1) from the most

134   mesial point on the buccal surface where the tooth emerges from the skull to the tooth tip, and

135   (2) from the most distal point on the buccal surface where the tooth emerges from the skull (Fig

136   S1b, Online Resource). Then we took an average of both values from each complete, unbroken

137   tusk and used the value from the longest tusk as our weapon length (mm). The cranial weaponry

138   data were collected by measuring the curl of the antler or horn using a flexible measuring tape

139   (mm). Antler curl was measured as the greatest length from the posterior lateral base, along the

140   outer curved surface, to the tip of the antler (Fig. S2, Online Resource). Horn curl was measured

141   as the average of the lengths of the maximum and minimum curvature ridges of the largest horn

142   on each skull (Fig. S3a; S3b, Online Resource). We then used the average of the two lengths of

143   the largest horn on each skull for horn length.

144   All skull and tusk measurements were collected using digital calipers to the nearest

145   0.01mm then converted into centimeters (cm), and all antler and horn measurements were

146   collected using a flexible measuring tape to the nearest 1cm. As both weapon length and

147   endocranial volume were required on all skulls, only intact skulls were used, and any broken

148   skull dimensions or teeth were not measured. From these raw measurements, we calculated skull

149   volume (SkV) (mm^3) as the product of Skull Length x Skull Width x Skull Height and brain

150   mass (BM) (g) as the product of Brain Volume (mL) x1.036 (g/mL; Stephan et al., 1981).

151   From these baseline measurements, we used traditional methods of calculating relative

152   brain size to generate two variables, Weapon Quotient (WQ), a new measure, and traditional

153   Encephalization Quotient (EQ) (Boddy et al., 2012; Jerison, 1973). Skull length (cm) was used

154   as a representation of body size over body mass since it was individually measured for each

155   specimen and body mass would be a less accurate species average. First, we ran separate linear

156   regressions of log_{10}-transformed male average weapon lengths (WL) for all species averages

157   (tusks, antlers, and horns combined): WL (cm) vs Skull Length (cm) (Skl). Next, we ran linear

158   regressions of log_{10}-transformed species average brain mass (BrM) versus body size for all

159   species: BrM (g) vs SkL (cm^3). Lastly, we phylogenetically corrected our results by using the

160   function 'pgls' (Orme, 2013) resulting in a different set of parameters and only these corrected

161   values were used in the following calculations (Table 1)

162   Next, we used the resulting corrected ß (slope) and b (intercept) estimates to calculate

163   the predicted brain masses and weapon lengths for each individual specimen based on their

164   individual skull lengths: $BrM_{i(predicted)} = 10^{b(BrMvsSkL)} \times SkL_i^{ß(BrMvsSkL)}$; $WL_{i(predicted)} = 10^{b(WLvsSkV)}$

165     $\times SkV_i^{ß(WLvsSkV)}$. EQ_i for each individual skull was calculated as $BrM_{i(measured)}/BrM_{i(predicted)}$,

166   where an EQ above 1.0 would represent a relatively large brain and an EQ below 1.0 would be a

167   relatively small brain. Similarly, WQ_i for each individual skull would be calculated as

168     $WL_{i(measured)}/WL_{i(predicted)}$ and be interpreted the same way relative to a value of 1.0. Antler WQ

169   was automatically set to zero for almost all female cervids, with the exception for antlered

170   female caribou (*Rangifer tarandus*).

171   We then calculated the average EQ and WQ for the male and female specimens for each

172   species, resulting in average $EQ_\male$, $WQ_\male$, $EQ_\female$, and $WQ_\female$ for each species based on either skull

173   length or body mass (8 total measures for each species). Next, we calculated the difference

174   between $EQ_\male$ and $EQ_\female$ (ΔEQ) and the difference between $WQ_\male$ and $WQ_\female$ (ΔWQ) for each

175   species. A result of ΔEQ below 0 indicates that females have relatively larger brains than males

176   in those species. Since females of antlered species almost exclusively had $WQ_\female=0$, $ΔWQ = WQ_\male$

177   with the exception for antlered female caribou (*Rangifer tarandus*). We used these species

178   averages to determine whether there is a sexually dimorphic relationship between males and

179   females in relative brain investment, and whether males suffer a physiological trade-off between

180   weapon length and relative brain investment.

181   For the following species only*: Elaphodus cephalophus, Muntiacus reevesi, Muntiacus*

182   *muntjak*; WQ is a sum value of WQ for tusk and antler measurements ($WQ = WQ_{tusk} + WQ_{antler}$)

183   because these species bear both weapons and invest differently in each type respectively. This

184   method allows us to generate a total 'weapon' investment. These species are categorized and

185   represented as antler bearing species in our final analyses since previous work supports antlers

186   scale positively allometrically while tusks scale isometrically suggesting greater in investment in

187   antlers over tusks (Lopez & Stankowich, 2023). In addition, we ran separate analyses amongst

188   each weapon type individually (*Horns=11, Antlers=13, Tusks=8*). WQ was weapon specific

189   (tusk WQ or antler WQ) for *Elaphodus cephalophus, Muntiacus reevesi, Muntiacus muntjak*. All

190   additional analyses can be found in our supplemental data (Table S2; Figure S6; S7).

191   *Statistical Analysis*

192   We ran a phylogenetic generalized least squares (Martins & Hansen, 1997), 'pgls'

193   tests using the 'ape' (Paradis 2019) the 'caper' package (Orme, 2013) in R (Team, 2020) across a

194   consensus tree pruned from the Upham et al. (2019) DNA-based consensus mammal-wide tree

195   (N_{tree}= 29; Fig. 1A). We tested the relationship between EQ and WQ amongst males solely,

196   female solely, and for the sexually dimorphic relationship (M-F ΔEQ vs ΔWQ) and included

197   weapon type as a factor (Table 3). In addition, we ran phylogenetically corrected tests for

198   interaction effects on WQ or ΔWQ. All additional results can be found in our Online

199   Supplement. We set our significance level at α = 0.05 and calculated phylogenetic signal for

200   each test using maximum-likelihood estimations of lambda (λ) derived from the PGLS tests.

201   All additional supplemental analyses (each weapon type tested individually) were ran

202   using 'pgls' using the 'ape' (Paradis, 2019) and 'caper' package (Orme, 2013) in R (Team, 2020)

203   across a *weapon specific* consensus trees pruned from the Upham et al. (2019) DNA-based

204   consensus mammal-wide tree (i.e., Horn Tree, Antler Tree, Tusks Tree).

Results

206   Overall, weapon size scales hyperallometrically with body size (as estimated by skull

207   size) suggesting that as individuals (male biased) grow larger, they grow disproportionately

208   larger weapons (Table 2; Fig. S3), similar to findings in other studies (Gould, 1974; Lopez &

209   Stankowich, 2023; Plard et al., 2010). Similarly, brain mass (g) scaled hypoallometrically with

210   body size (as estimated by skull size; Table 2; Fig. S4), similar to findings in other studies

211   (Boddy et al., 2012; Heldstab et al., 2016; Huang et al., 2020). While our results provided further

212   support for these previously established relationships, we next examined the relationship

213   between relative investment in brain size and relative investment in weapon size.

214   We calculated sex-specific measures of relative investments in brain size

215   (encephalization quotient: EQ) and weapon size (weapons quotient: WQ) by correcting for body

216   size (as estimated by skull size): EQ and WQ scores above 1 indicate greater than expected

217   investment in these structures and scores below 1 indicate smaller investments relative to body

218   size. For males, we did not find any effect of investment in weaponry on brain size (Table 3; Fig.

219   1B), although male antlered species had significantly greater investment in their brains than

220   tusked and horned species ($p < 0.05$; Figure 1B; Table 3). We did not find any effect of

221   investment in weaponry on brain size in females (Table 3; Fig. 1C), although, again, female

222   antlered species had significantly greater investment in their brains than tusked species ($p <$

223   0.001).

224   We found a significant negative relationship between the degrees of sexual dimorphism

225   in relative brain size (ΔEQ) and relative weapon size (ΔWQ; Table 3, Fig. 1D), whereas males

226   evolve to invest proportionally more in weapons than females of their species, they evolve to

227   invest proportionally less in brain size ($p = 0.014$). This result supports that investment in

228   relative brain size is sexually dimorphic and likely influenced by the presence of exaggerated

229   sexual weapons in these male ungulates. We also found that the difference between male and

230   female relative brain size investment was greater in antlered species than horned species ($p =$

231   0.049; Figure 1D; Table 3)

232   Phylogenetic signal in the analyses was either completely absent ($\lambda = 0.000$) or very

233   strong (λ near or equal to 1; Tables 2 & 3, S1), suggesting great variation in the degree to which

234   shared ancestry explains variation in relative brain and weapon size. We did not find any

235   evidence of an interaction effect of WQ on EQ in any analyses, so the interaction term was

236   dropped from all final models (Table S1). In addition, we ran separate analyses amongst each

237   weapon type individually (*Horns=11, Antlers=13, Tusks=8*). For all groups, we found similar

238   insignificant results between male WQ and male EQ, except amongst tusked species, we found a

239   significant negative relationship between male WQ and EQ and female WQ and EQ. Lastly, for

240   our sexual dimorphic analysis, we found similar results in our tusked and horned groups, with

241   significant negative relationships between M-F EQ and M-F WQ. However, we did not find any

242   relationship amongst our antlered group. All additional analyses can be found in our

243   supplemental data (Table S2; Figure S6; S7).

244   **Discussion**

245   Our data support the hypothesis that increased investment into male weapon size is

246   associated with a sexual dimorphic investment in relative brain size. Across twenty-nine species

247   and three weapon types (horns, tusks, antlers), as males evolved to invest relatively more than

248   conspecific females in building larger weapons, they invested relatively less than conspecific

249   females in building larger brains. Past studies support physiological and behavioral tradeoffs

250 when males possess large, exaggerated weapons (e.g., reduced limbs (Emlen, 2001; Simmons &

251 Tomkins, 1996), reduced efforts in nuptial gift giving (Liu et al., 2015), survival rate (Douhard et

252 al., 2020; Garratt et al., 2015) or increased grooming time (Allen & Levinton, 2007; McCullough

253 et al., 2020)) but this is the first study to show that males may suffer reductions in relative brain

254 size for the development and maintenance of elaborate sexual weapons.

255 Artiodactyl species experiencing more intense sexual selection have greater sexual

256 dimorphism in body size suggesting sexual contests may be the leading force driving differences

257 between male and female morphology (Cassini, 2020). Sexual selection apparently acts so

258 strongly on males to invest in progressively larger weapons that it creates inequity in the brain

259 sizes of males and females, with brain size of males decreasing relative to conspecific females in

260 species with the largest weapons (Fig. 1C). Since EQ has sometimes been used as a rough

261 estimate of cognitive ability in animals (Kotrschal et al., 2015; but see also van Schaik et al.

262 2021, Roth and Dicke 2017; Reader & Laland, 2002; Sol et al., 2005b; Stankowich & Romero,

263 2017), this suggests that males investing relatively less in brain size compared to females may

264 suffer detrimental effects on cognitive and innovative ability.

265 Mammalian teeth scale isometrically with body size (Creighton, 1980), and, within tragulids,

266 the cranium and mandible scale at similar rates among males and females, but males have higher

267 upper canine growth rates than females (Terai et al., 1998). Tusks – enlarged male canines –

268 appear to be the first sexual weapon to evolve in artiodactyls (Cabrera & Stankowich, 2018); and

269 female canines are relatively smaller than those of their conspecific males. Our results further

270 support the positive scaling relationship between weapon size and body size in male tusked deer,

271 but when compared to females, who lack sexual weapons, relative brain size is larger in

272 conspecific females suggesting a potential reduction in expensive structures within these tusk

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273   bearing species. Bovids are unusual among ungulates because females of many species also

274   develop sizeable horns. Bovid females use their horns either for defense against predators or to

275   guard territories against conspecifics (Stankowich & Caro, 2009), so females that invest heavily

276   in horns may also face tradeoffs with relative brain size. We found patterns of sexual

277   dimorphism in relative brain size consistent with this tradeoff, as species with strong sexual

278   dimorphism in weapon size also had the largest difference between male and female brain sizes.

279   The potential difference in energy investment when developing weapons (permanent vs.

280   deciduous) may explain why cervids suffer a reduction with relative brain size. Cervids may

281   invest more in antler production during their early years resulting in a stronger trade-off with

282   other developing organs like the brain. Further analyses are recommended to make stronger

283   inferences about trends during ontogenetic development as our study only focused on adult

284   measurements.

285   Initially, we hypothesized that, within males, as relative investment in sexual weapons

286   increased, the relative investment in brain size would drop, we found no relationship between

287   relative brain and weapon size in females or males. Although many other studies found little to

288   no support for male costs at larger weapon sizes (Dinh, 2022; McCullough & Emlen, 2013;

289   Somjee, 2021; Somjee et al., 2018) suggesting some weapons might be costly to grow, but not

290   maintain or weapons are not equally costly across every stage of development. We suggest two

291   *post hoc* hypotheses that may explain why males do not appear to pay for their relatively longer

292   weapons with reductions in relative brain size.

293   First, previous research found horned rhino beetles (*Trypoxylus dichotomus*) suffered no

294   direct fitness tradeoff with immune system, growth of other structures, and overall survival,

295   which may be due to support through neighboring structures (i.e., legs/wings) (McCullough &

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296 Emlen, 2013). Biomechanically, horns and antlers are large, weight-bearing cranial weapons

297 which likely require larger, more domed platforms to support the size and weight of these sexual

298 weapons and to withstand the physical stresses of aggressive combat (e.g., torque and impact),

299 possibly imposing strong positive selection for larger cranium size. If large, robust crania are

300 required to support large horns and antlers and if cranium size scales isometrically with weapon

301 size, it is likely that endocranial volume may also scale isometrically, which could explain why

302 our measure of relative brain size (estimated from endocranial volume) did not decline with

303 weapon lengths.

304 Second, the evolution of larger weapons allows for more extensive pre-combat signaling of

305 fighting ability, especially in cervids and bovids that have large bodies, large weapons, and live

306 in more open habitats where assessment of rivals from a distance is greater (Cabrera &

307 Stankowich, 2018; Emlen, 2008; Geist, 1998; Lopez & Stankowich, 2023). Increased signaling

308 and assessment may require greater cognitive and decision-making abilities in these species,

309 strengthening selection for larger brains. In contrast, tusked species tend to be "slinkers" that

310 tend to be smaller in size, live in more closed habitats, and engage in quick slashing and stabbing

311 combat in close quarters when they meet, without much signaling. In support of this, we found

312 that tusked species, had lower EQ values in both males and females.

313 While some argue that EQ is a suboptimal measure of cognitive ability (Deaner et al., 2007;

314 van Schaik et al., 2021), it commonly used in large studies of comparative cognition (Boddy et

315 al., 2012; Jerison, 1973; Marino, 1998; Stankowich & Romero, 2017; Tsuboi et al., 2018)

316 because endocranial volume is quickly measured from skulls in museum collections, allowing

317 for a larger sample size and broader taxonomic sampling. Here, we use EQs to examine the

318 relationship between relative brain size and sexual weapon size, rather than as a measure of

319 higher cognition; though the declines in relative brain sizes we found with greater weapon sizes

320 in males relative to females may extend to cognitive effects as well. Future studies should further

321 question if males with larger sexual weapons may energetically compensate with reductions in

322 cranial thickness, musculature, fecundity, or longevity, or with significant increases in energetic

323 intake relative to females of the same species.

340 *Availability of data and material:* The datasets supporting this article have been uploaded as part

341 of the supplementary material.

342 *Code availability:* The statistical coding scripts supporting this article have been uploaded as part

343 of the supplementary material.

344 *Authors' contributions:* NL collected primary data ran the statistical analyses, wrote the initial

345 version of the manuscript, and helped edit the manuscript. TS devised the project and protocols,

346 collected primary data, advised on analyses, and helped edit the manuscript. JMT collected

347 primary data and ran preliminary analyses.

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527 **Table 1.** Summary of three weapon groups: Horns, Antlers, and Tusks. *Indicates species that

528 bear both tusks and antlers.

Weapon Type	N	Species
Antlers	13	*Alces alces, Axis porcinus, Capreolus capreolus, Cervus elaphus, Dama dama, Mazama americana, Odocoileus hemionus, Odocoileus virginianus, Pudu mephistophiles, Muntiacus muntjak*, Muntiacus reevesi*, Elaphodus cephalophus*, Rangifer tarandus*
Horns	11	*Antidorcas marsupialis, Capra hircus, Connochaetes taurinus, Damaliscus lunatus, Kobus kob, Litocranius walleri, Nanger granti, Oreotragus oreotragus, Ovis aries, Ovis canadensis, Redunca redunca*
Tusks	8	*Elaphodus cephalophus*, Hydropotes inermis, Moschiola meminna, Moschus moschiferus, Muntiacus muntjak*, Muntiacus reevesi*,Tragulus kanchil, Tragulus napu*

529

530 **Table 2:** This table summarizes results from the uncorrected ('lm') and phylogenetically
531 corrected ('pgls') log-based regressions. Subsequential calculations to generate EQ and WQ
532 reflect the phylogenetically corrected outputs; **Bold**=significant (p<0.05)

Uncorrected ('lm', N=29)					
Y	X	β (95%CI)	Intercept	*p*	λ
Log_{10} (Brain Mass)	Log_{10} (Skull Length^3)	**0.667 (0.603, 0.731)**	-0.612	**<0.001**	NA
Log_{10} (Weapon Length)	Log_{10} (Skull Length)	**2.520 (1.967, 3.073)**	-2.155	**<0.001**	NA
Corrected ('pgls', N=29)					

Log$_{10}$ (Brain Mass)	Log$_{10}$ (Skull Length^3)	**0.592 (0.517, 0.668)**	-0.419	**<0.001**	0.859
Log$_{10}$ (Weapon Length)	Log$_{10}$ (Skull Length)	**2.091 (1.290, 2.889)**	-1.732	**<0.001**	0.718

Table 3: This table summarizes results from sex specific (M, F) and sexual dimorphic (M-F) PGLS analyses testing the relationship between relative weapon size and relative brain size. **Bold**=significant (p<0.05). Weapon type (Horns, Tusks, or Antlers) was included as a factor in these models; Antlers serve as the reference value in our regression models.

N=29; 'pgls'		β	*p*	λ
M EQ	M WQ	0.016	0.609	0.000
	Horns vs. Antlers	***-0.165***	***0.037***	
	Tusks vs. Antlers	***-0.609***	***0.001***	
F EQ	F WQ	0.057	0.417	0.000
	Horns vs. Antlers	*-0.126*	*0.248*	
	Tusks vs. Antlers	***-0.596***	***0.001***	
M-F EQ	M-F WQ	**-0.073**	**0.014**	0.000
	Horns vs. Antlers	***-0.112***	***0.049***	
	Tusks vs. Antlers	*-0.129*	*0.093^*	

Figure 1: A) phylogenetic tree of the species (N=29) analyzed in our study. Yellow=Tusks; Black: Both Antlers and Tusks; Blue: Antlers; Pink: Horns. Artwork by Tayyab Qureshi. B) PGLS insignificant association between weapon size and body size in males (skull length as a measure of body size). C) PGLS insignificant association between weapon size and body size in females (skull length as a measure of body size). D) PGLS negative association between male-female relative brain investment (ΔEQ) and male-female relative weapon investment (ΔWQ; Yellow=Tusks; Blue: Antlers; Pink: Horns). *Rangifer tarandus* was added postproduction for Fig. 1A, but species is included in Fig. 1B-D.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- AntlersSep.csv
- BEASLopezRawData.xlsx
- BESLopezNicoleSupplemental.pdf
- HornsSep.csv
- LopezNicoleEQCode.r
- PostReviewGlobal3.csv
- TusksSep.csv