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2 **Canine size, condition and health in wild boars**

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21

22

**23 Abstract**

24 Canines in wild boar *Sus scrofa* constitute weapons used in male-male  
25 conflict. We analyzed extensive data for the ecological correlates of canine  
26 size in several study sites in Extremadura, Spain, to determine their degree  
27 of condition-dependence and their relationship with health status. Boars  
28 with relatively large body size had larger canines than small boars. Canine  
29 size was larger in estates without livestock, in estates with low population  
30 density, and in estates with rich holmoak forest. These findings are  
31 consistent with predictions for condition-dependent secondary sexual  
32 characters. Boars with relatively large canines had large spleens for their  
33 body size, higher prevalence of Aujeszky's disease and higher prevalence  
34 of macroscopic lesions compatible with Bovine Tuberculosis than boars  
35 with relatively small canines. Thus, boars with large canines that were  
36 likely to be dominant and have differential access to females were in poorer  
37 health than boars with small canines. Since the virus responsible for  
38 Aujeszky's disease and *Mycobacterium bovis* are readily transmitted  
39 through direct contact during mating, we suggest that there is sexual  
40 conflict over mating. Boars with large canines that are most likely to  
41 copulate with sows are also the boars that are most likely to be a direct  
42 cause of transmission of disease in these sows.

43

**44 Keywords**

45 condition-dependence; disease; sexual conflict; sexual selection; *Sus*  
46 *scrofa*.

47

## 48 **Introduction**

49 Secondary sexual characters have evolved in the context of competition for  
50 mating success, with female choice and male-male competition being the  
51 two major processes resulting in the evolution and the maintenance of such  
52 characters (Andersson, 1994). Many different characters show evidence of  
53 condition-dependence, with individuals in prime condition developing  
54 large secondary sexual characters (Johnstone, 1995). Empirical evidence  
55 consistent with condition-dependence suggests that males with large  
56 secondary sexual characters are in better condition both before and after  
57 developing such characters (Jennions et al., 2001). While most of these  
58 studies are based on traits that appear to be involved in mate choice, only a  
59 few weapons have been investigated in this context (e. g. Badyaev et al.,  
60 1998; Connor, 1988; von Schantz et al., 1989).

61 The information content of secondary sexual signals has elicited  
62 considerable theoretical and empirical attention during the last few  
63 decades. Ideas vary from such traits being arbitrary to secondary sexual  
64 characters reliably reflecting the condition or health status of the signaler  
65 (Andersson, 1994; Hamilton & Zuk, 1982; Zahavi, 1975). Hamilton & Zuk  
66 (1982) proposed that sexual signals might provide reliable information  
67 about the health status of signalers because only healthy individuals in  
68 prime condition would be able to develop and maintain exaggerated  
69 secondary sexual characters without compromising their health status.  
70 Numerous studies have since investigated the relationship between level of  
71 parasitism and expression of secondary sexual characters, showing an  
72 overall weak, but highly significant negative relationship across studies and  
73 different taxa (Møller et al., 1999). An increasing number of studies have  
74 shown that the ability to raise an immune response is positively related to  
75 the expression of secondary sexual characters, with a mean effect size that  
76 is large (Møller et al., 1999). This suggests that females or other receivers

77 may gain reliable information on health status and ability to cope with  
78 parasites from inspection of secondary sexual characters. However,  
79 available studies are strongly biased towards characters that are involved in  
80 mate choice, while weapons rarely have been the targets of such studies (e.  
81 g. von Schantz et al., 1996).

82         Secondary sexual characters involved in male-male competition are  
83 particularly good candidates for signaling of health status because of the  
84 relationship between secondary sexual characters, physical contests and  
85 steroid hormones or other physiological mechanisms underpinning such  
86 fights. Folstad & Karter (1992) suggested that the immuno-suppressive  
87 effects of androgens, combined with their beneficial effects for  
88 development of secondary sexual characters and other kinds of displays,  
89 provided a basis for a trade-off between display and health status. This  
90 immunocompetence handicap hypothesis provided a mechanism for  
91 individual optimization that would cause secondary sexual characters to  
92 reliably signal health status of the individual signaler. Assumptions and  
93 predictions of this hypothesis have met with support (review in Roberts et  
94 al., 2004). However, again, most studies are based on secondary sexual  
95 characters involved in female choice, but not on weapons that are likely to  
96 be particularly influenced by the immuno-suppressive effects of hormones.

97         Canines are used in male-male interactions during competition for  
98 access to females (Hooijer, 1948; Andersson, 1994) in taxa as diverse as  
99 primates (Struhsaker, 1969; Lauer, 1975) and Suidae and Tayassuidae  
100 (Frädriich, 1967; Herring, 1972; Bauerle, 1975). Comparative studies of  
101 weapons, including canines have shown clear relationships between  
102 operational sex ratio and degree of sexual size dimorphism (Alexander et  
103 al., 1979; Jarman, 1983; Andersson, 1994), with males having weapons  
104 that are suitable for winning in male-male fights, while female weapons

105 show characteristics suggesting a role in anti-predator defense (Packer,  
106 1983).

107         Among wild boars, male canines have traditionally been assumed to  
108 have an important role in male-male fights for access to females (Barrete,  
109 1986). The exclusive development of canines in males, mainly after  
110 reaching sexual maturity (Fernández-Llario & Mateos-Quesada, 2003),  
111 together with the development of hardened tissue on the flanks (Barrete,  
112 1986; Rushen & Pajor, 1987), suggest that canines play a role in  
113 intrasexual selection. Although Fernández-Llario (2004) found no signs of  
114 fights on the skin of males hunted during the rut period, aggressive  
115 interactions over dominance among sexually mature males are often  
116 resolved without physical fights (review in Andersson, 1994). Jarman  
117 (1983, 1989) has provided extensive evidence of a role of hardened tissue  
118 as protective devices during fights among male ungulates and marsupials.

119         The aims of this paper were to analyze (1) whether canine size of  
120 male wild boar is condition-dependent, and (2) whether canine size is a  
121 reliable indicator of health status. To achieve this, we analyzed whether  
122 canine size could be predicted by body condition, interspecific competition  
123 as reflected by presence of livestock in certain estates, intraspecific  
124 competition as reflected by population density, and forest quality. As  
125 concerns the relationship between canine size and health status we  
126 investigated relationships between canine width and relative size of spleen,  
127 titers of antibodies for a herpes virus, which causes Aujeszky's disease ,  
128 and prevalence of macroscopic lesions compatible with Bovine  
129 Tuberculosis.

130

131 **Material and methods**

## 132 Study area

133 The study was carried out in Monfragüe Natural Park and its surroundings  
134 (39°45' N, 6°00' W) and the nearby zone Las Villuercas (39°20' N, 5°30'  
135 W), both in central-west Spain. Monfragüe is an area with a noticeable  
136 Mediterranean character, where well-preserved holm oak *Quercus ilex* and  
137 cork oak *Quercus suber* forest is still present (Pulido, 1999). Kermes oak  
138 *Quercus coccifera*, *Cistus ladanifer* and *Erica arborea* are the most  
139 abundant shrubs. This area is made up of hills reaching no more than 685  
140 m altitude. The climate of the area is Mediterranean, with a dry and hot  
141 summer and mild winters. Precipitation averages 623 mm and is  
142 concentrated in November-April, which therefore is the period with high  
143 primary production and hence abundant availability of food plants for wild  
144 boar. Mean annual temperature averages 17.7°C, with January and July  
145 being the coldest and the warmest months, respectively. Las Villuercas  
146 consists of mountain ranges of high altitude (up to 1601 m). Dominant tree  
147 species are oak *Quercus pyrenaica* and cork oak *Quercus suber*, while  
148 *Erica* ssp and *Arbustus unedo* are the main shrubs. Climate, soil and use  
149 land in these mountain ranges result in high botanical diversity.  
150 Precipitation averages 749 mm and is concentrated in November-May.  
151 Mean annual temperature averages 16.6°C. The summers are milder than in  
152 Monfragüe (Mateos-Quesada, 1998).

153 All wild boars studied were hunted in typical game activities, called  
154 monterías during October-February 2001-2002 and 2002-2003. This  
155 system enabled us to obtain a sample of individuals unbiased with respect  
156 to sex and age (Fernández-Llario et al., 2003).

157 We calculated the relative density of wild boar on the basis of the  
158 number of hunted individuals and the surface area of the different estates  
159 used for hunting. In all cases we selected for this study estates with similar  
160 characteristics in terms of land use and hunting pressure. We assumed that

161 wild boars from estates with higher density suffered more from  
162 intraspecific competition than wild boars from estates with low density.

163 Some of the studied estates were also used for grazing livestock in  
164 particular cattle and Iberian pig, and samples were classified as originating  
165 from estates with or without livestock. We assumed that wild boars  
166 originating from estates with livestock suffered more in terms of  
167 interspecific competition for food than wild boars from estates without  
168 livestock.

169 The wild boars originated from two different forest types: Holmoak  
170 forests and oak forests. Holm oak forests are characterized by a high  
171 abundance of acorns, while oak forests have a lower abundance of acorns  
172 (Herrera et al., 1998; Koenig et al., 1994). Therefore, we assumed that wild  
173 boars originating from holm oak forests had superior access to food  
174 compared to wild boars from oak forests.

175

### 176 **Characters measured**

177 For each culled wild boar, the following parameters were recorded: sex,  
178 age, body length (cm, without tail), height (cm), perimeter (cm), spleen  
179 mass (g), and canine width at base (only males) (cm). We recorded  
180 information on the size of the spleen, because it is an immune defence  
181 organ that comprises part of the peripheral lymphoid tissue (Arvy, 1965;  
182 John, 1994). We assume throughout this paper that a larger spleen can  
183 produce a better immune defence than a smaller organ. The spleen was  
184 dissected out and weighed on a precision balance. We used canine width  
185 rather than canine length because the latter is subject to wear and damage  
186 much more frequently than width. We calculated an estimate of body size  
187 as the squared value of perimeter multiplied with length (hereafter  
188 volume).

189 Age was calculated on the basis of the pattern of tooth eruption,  
190 replacement and dental attrition. We used two different methods to

191 determine the age of wild boar. The first one is based on the pattern of  
192 tooth eruption, which allows us to correctly determine the age of wild boar  
193 during the first 36 months of life (Matschke, 1967). For older animals, the  
194 age was determined by tooth wear pattern (Iff, 1978; Grant, 1982). In order  
195 to check our ageing method in older wild boar we tested our method  
196 against wild boar from Gonçalves et al. (2015) ageing study. There is a  
197 strong positive correlation between the age of known wild boar from  
198 Gonçalves et al.'s study and the results obtained by tooth wear estimation.

199       Blood samples were collected from shot wild boars and analyzed at  
200 Department of Medicine and Animal Health, Universidad de Extremadura  
201 (Spain), where the samples were centrifuged and sera of acceptable quality  
202 selected for serology studies. All sera were stored at -20°C until analyzed.  
203 The sera were analyzed with competitive enzyme-immunoassay  
204 (competitive ELISA) using the commercial kit AUJESKYTEST II  
205 (CHEKIT-Dr BOMMELI AG). We tested for the presence of Aujeszky's  
206 disease because it develops sub-clinical processes with an important  
207 immune response in wild boar (Martin and Wardley 1987). We analyzed  
208 each animal for lesions compatible by Bovine Tuberculosis using the  
209 criteria listed by Gortazar et al. (2003).

210

### 211 **Statistical analyses**

212 We tested for condition-dependence of the size of canines by using  
213 generalized linear models (GLM). We tested for over-dispersion, but found  
214 no evidence. Canine width, body volume, head length, and spleen mass  
215 were log-transformed to meet the requirements for parametric analyses.  
216 Presence of livestock, forest type and presence of Aujeszky's disease and  
217 tuberculosis were used as factors. We started modeling by investigating the  
218 relationship between pairs of variables and subsequently entered potentially  
219 confounding variables that may have biased the simple bivariate

220 relationships. We used a stepwise procedure using Aikaike's information  
221 criterion as an estimate of the improvement in fit (Burnham and Anderson,  
222 1998). The fit of models with or without a given factor was compared using  
223 AIC as a guideline, until the best-fit model had been found.

224

## 225 **Results**

### 226 **Condition-dependence of canine size**

227 We had a total of 99 males and 130 females. Canine width was on average  
228 1.06 cm (range 0.2 to 3.0 cm, SE = 0.06, N = 99, with a coefficient of  
229 variation of 41.9%). In comparison head length was on average 37.54 cm  
230 (SE = 0.64) with a coefficient of variation of 17.2%, while ear length was  
231 on average 11.10 cm (SE = 0.20) with a coefficient of variation of 58.8%.  
232 Thus, canine width was significantly more variable than head or ear length  
233 (head length 16.4%; ear length 17.6%).

234 Canine width increased significantly with body volume (Fig. 1A;  
235 likelihood ratio  $\chi^2$  (LR) = 39.76, d.f. = 1,101,  $P < 0.001$ , slope (SE) = 2.04  
236 (0.29)). The slope of this relationship was significantly larger than the  
237 predicted value of 0.33 given that canine width is linear while body size is  
238 measured in volume ( $t = 5.83$ , d.f. = 101,  $P < 0.001$ ). Thus, there was  
239 evidence of positive allometry for canine size.

240

241 **FIG. 1 ABOUT HERE**

242

243 Next, we investigated whether canine size was related to body  
244 volume after taking body size into account. Therefore, this is a test for  
245 condition-dependence by relating canine size to residual body volume after  
246 controlling for body size. Indeed, canine size was still strongly positively  
247 related to volume after controlling for head length (Fig. 1B; full model LR  
248 = 48.38, d.f. = 2,100,  $P < 0.001$ ; head length: partial LR = 8.62, d.f. =

249 1,100,  $P = 0.0015$ , estimate (SE) = 1.26 (0.42); body volume: partial LR =  
250 10.09, d.f. = 1, 100,  $P = 0.0033$ , estimate (SE) = 1.25 (0.38)).

251 Finally, we tested whether canine width was related to body volume  
252 after controlling for age. A GLM was statistically significant (LR = 105.36,  
253 d.f. = 2,100,  $P < 0.001$ ), with a highly significant effect of age (LR = 65.59,  
254 d.f. = 1,100,  $P < 0.001$ , slope (SE) = 0.17 (0.02)), but also a significant  
255 effect of body volume (LR = 2.85, d.f. = 1,100,  $P = 0.09$ , slope (SE) = 0.46  
256 (0.27)). This implies that body volume still accounts for variation in canine  
257 width, even after controlling statistically for age.

258

259

## 260 **Canine size and environmental conditions**

261 Wild boar occurred on estates with or without livestock. We found a highly  
262 significant difference in residual canine width, after controlling statistically  
263 for body volume in a multiple regression analysis (Fig. 2A). Canines were  
264 predicted to be smaller on estates with forest than on estates without  
265 livestock (LR = 10.21, d.f. = 1,101,  $P = 0.00014$ , estimate (SE) = -0.143  
266 (0.044)). A similar conclusion was reached after adding head length and  
267 age as additional independent variables (partial LR = 4.63, d.f. = 1,99,  $P =$   
268 0.031, slope (SE) = 0.060 (0.028)).

269

270

FIG. 2 ABOUT HERE

271

272 We predicted that relative canine size decreased with increasing  
273 population density. Indeed, a GLM revealed a significant negative  
274 relationship between relative canine width and density (Fig. 2B; LR =  
275 143.09, d.f. = 1,101,  $P = 0.0002$ , slope (SE) = -0.085 (0.022)). That was  
276 also the case after entering head length and age as additional independent  
277 variables (LR = 5.30, d.f. = 1,98,  $P = 0.021$ , slope (SE) = -0.033 (0.014)).

278 This effect was independent of livestock since a model with body volume,  
279 head length, age, livestock and density as predictor variables still revealed a  
280 significant effect of density (LR = 3.96, d.f. = 1,98, P = 0.047, slope (SE) =  
281 -0.027 (0.013)).

282 Finally, we predicted that relative canine size would be larger on  
283 holmoak estates than on oak estates. That was also the case for the partial  
284 effect of holmoak after controlling for body volume, livestock and density  
285 (Fig. 2C; LR = 10.21, d.f. = 1,101, P = 0.0014, estimate (SE) = 0.143  
286 (0.044)). A model that included head length and age as additional predictor  
287 variables provided a similar conclusion (LR = 4.63, d.f. = 1,98, P = 0.031,  
288 slope (SE) = 0.060 (0.028)). However, entering livestock and density as  
289 additional factors rendered the effect of forest type non-significant (LR =  
290 0.07, d.f. = 1,96, P = 0.79).

291

### 292 **Canine size and health**

293 Spleen mass was on average 143 g (SE = 5), with no significant difference  
294 between sexes (LR = 0.71, d.f. = 1,101, P = 0.40). There was a significant  
295 positive relationship between spleen mass and canine width (Fig. 3A; linear  
296 model based on log-transformed data: LR = 1.71, d.f. = 1,48, P = 0.19).  
297 Entering body volume as an additional independent variable only caused  
298 canine width to enter as a significant predictor of spleen mass.

299

300

FIG. 3 ABOUT HERE

301

302 The prevalence of Aujeszky's disease was 0.38 among 228 wild  
303 boars, and among 103 males the prevalence was very similar at 0.40.  
304 Residual canine width after controlling for body volume was significantly  
305 larger among males infected with Aujeszky's disease than among  
306 uninfected individuals (Fig 3B; LR = 22.79, d.f. = 1,101, P < 0.001,

307 estimate (SE) = 0.0012 (0.0002)). A similar conclusion was reached when  
308 controlling canine width for both body volume and age (LR = 5.78, d.f. =  
309 1,101, P = 0.016; mean (SE) 0.00046 (0.00019)). Finally, there was a  
310 significant relationship between canine width and tuberculosis (LR = 6.60,  
311 d.f. = 1,101, P = 0.010; mean (SE) 3.76 (1.73)).

312

### 313 **Discussion**

314 Male wild boar had condition-dependent canines. Larger males and males  
315 in better body condition (as reflected by relatively larger body volume for  
316 their body size) had larger canines. Canines showed positive allometry,  
317 with large males having disproportionately large canines. Relative canine  
318 size, after controlling for the effects of body size, was suppressed by the  
319 presence of livestock, high population density of wild boars and poor forest  
320 quality. These effects of environmental conditions were statistically  
321 independent for livestock and conspecific population density. Relative  
322 canine size was indicative of a larger spleen size and higher prevalence of  
323 Aujeszky's disease and tuberculosis. This indicates that male wild boars  
324 with large canines were in poor health status. We will briefly discuss these  
325 results and their implications.

326

### 327 **Condition-dependence of canines**

328 Canines showed enormous variation in width among individuals, with the  
329 coefficient of variation exceeding 40%. In contrast, head length and ear  
330 length showed more moderate phenotypic variation with coefficients of  
331 variation in the range of 17-18%, which is large for ordinary morphological  
332 characters, but not when compared with secondary sexual characters  
333 (Andersson, 1994; Pomiankowski & Møller, 1995). Secondary sexual  
334 characters are notorious for their variation, which was on average 22%  
335 across previously studied species (Pomiankowski & Møller, 1995; see also

336 Cuervo & Møller, 1999). Canine width showed positive allometry (Fig.  
337 1A). Weapons often show positive allometry with large individuals having  
338 disproportionately large weapons for their body size (Huxley, 1932;  
339 Andersson, 1994).

340 Condition-dependence of secondary sexual characters implies that  
341 individuals in prime condition have larger secondary sexual characters than  
342 individuals in poor condition. Many studies have addressed this question  
343 using a number of observational and experimental approaches (Andersson,  
344 1994; Johnstone, 1995). However, very few studies have investigated these  
345 patterns for characters involved in male-male competition (see Kotiaho et  
346 al. (2001) for an exception in a horned beetle). Here we used a correlational  
347 approach to test a number of predictions for effects of condition on canine  
348 size. We found considerable evidence consistent with predictions derived  
349 from theory. While the correlational nature of these results does not allow  
350 firm conclusions about causation, we believe that the combined body of  
351 evidence presented here cannot readily be explained by alternative  
352 hypotheses, such as larger canines causing an increase in condition. We  
353 find this alternative unlikely because wild boar does not defend feeding  
354 territories (Boitani et al., 1994; Mauget, 1979). Furthermore, since males  
355 with relatively large canines for their body size more often suffered from  
356 disease, this should everything else being equal suppress rather than  
357 promote condition.

358 We found considerable evidence of age predicting canine width.  
359 Since body volume also increased with age, the increase in size with age  
360 may simply reflect the ability of older individuals with more experience to  
361 differentially acquire resources. Old individuals have proven their ability to  
362 survive, and females may acquire genes associated with longevity by  
363 mating with male boars with the largest canines, as hypothesized by  
364 Manning (1985). However, although age was a confounding variable in

365 several of the analyses, the main effects investigated generally remained  
366 after statistically controlling for male age. In general, these relationships  
367 were weak after removing the effects of age, only explaining a small  
368 amount of the variance. This suggests that the major information content of  
369 relative canine size is age (and correlates thereof). The exact nature of such  
370 age effects remains to be determined.  
371

**372 Canine size, disease status and mating**

373 We found evidence of male wild boars with relatively large canines for  
374 their body size being in poor health. Although the size of their spleen  
375 increased with body volume (Fig. 3A), that was not the case when  
376 controlling statistically for body size. Hence, males with relatively large  
377 canines did not have relatively large spleens. Both Aujeszky's disease and  
378 tuberculosis was more prevalent among male wild boars with large canines  
379 (Fig. 3B). For Aujeszky's disease, this was even the case when controlling  
380 statistically for body size. This implies that male wild boars with relatively  
381 large weapons were of poorer health status than males with small weapons.  
382 Since both Aujeszky's disease and tuberculosis have severe fitness  
383 consequences in terms of reduced viability and fecundity for wild boar (for  
384 Aujeszky's disease: Gueguen & Aynaud, 1980; Medveczky & Szabó,  
385 1981; for Tuberculosis), we can infer that male wild boars with relatively  
386 large canines have higher viability. However, given the overall body size  
387 and the relative and absolute size of the canines of male wild boars, we  
388 may expect that they have differential access to fertile females. The  
389 benefits of large canines in male wild boars could still more than balance  
390 the costs in terms of elevated prevalence of disease. These findings merit  
391 discussion in terms of the mechanisms resulting in elevated prevalence of  
392 disease, but also in terms of the consequences of such prevalence of disease  
393 in males for females.

394 Male wild boars in this study were hunted during fall and winter,  
395 when rut in this population takes place (Fernández-Llario, 2004;  
396 Fernández-Llario et al., 2004). Therefore, it is likely that circulating  
397 testosterone levels were high, although this needs testing. It is likely that  
398 testosterone levels are higher in males with relatively large canines. This  
399 could form the basis for immuno-suppression in such males (Folstad &  
400 Karter, 1992; Saino & Møller, 1996; Peters, 2000). This could partially

401 explain the higher prevalence of disease among males with relatively large  
402 canines, although a larger rate of contact between such males and other  
403 conspecifics may have contributed to this elevated prevalence.

404         The different immune response in males and females would not only  
405 produce different pathology, but also influence the ways in which the virus  
406 is transmitted. In rodents, although the two sexes are equally susceptible to  
407 infection with Seoul virus, males produce a stronger Th1 response against  
408 Seoul virus than females (Klein et al., 2000, 2002). In addition, males shed  
409 virus in saliva and feces for longer than females, potentially explaining  
410 why males are more likely to acquire natural Seoul virus infection  
411 following aggressive encounters (Klein et al., 2000, 2002). If similar  
412 mechanisms were at work in wild boar, we would expect sex differences in  
413 immune response and shedding of virus, and perhaps bacteria of the Bovine  
414 Tuberculosis, with higher levels in urine and saliva of males. The route of  
415 infection for wild boars is likely to be nasal contact, which is very frequent  
416 during social interactions, as during mating (Puente et al., 2001). Wild boar  
417 males contact the tinkle of other males by wallowing, therefore  
418 encountering the virus, since wallowing reaches a peak during rutting  
419 (Fernández-Llario, 2004).

420         The other source of infection is saliva that is a key element of  
421 contact between males and females during the rut. During copulation, a  
422 large part of sexual stimulation of females is by liberation of pheromones  
423 in male saliva. Males produce large amounts of saliva that comes into  
424 contact with the body of the female (Melrose et al., 1971; Estes et al.,  
425 1982), thereby facilitating transmission of virus from males to females.

426         Wild boars are polygynous with each male potentially copulating  
427 with several females. This opens up the possibility for efficient  
428 transmission of infectious disease (Hamilton, 1990). While comparative  
429 studies and meta-analyses have found mixed evidence consistent with this

430 hypothesis (Able, 1996; Møller et al., 1999), currently available evidence  
431 almost exclusively concerns secondary sexual characters involved in  
432 female choice. An exception to this generalization is spur length and  
433 immunity in pheasants *Phasianus colchicus* (von Schantz et al., 1996).  
434 Since the immuno-suppressive effects of testosterone and other hormones  
435 (Folstad & Karter, 1992 Roberts et al., 2004) will significantly add to the  
436 importance of males as agents of disease transmission in species with  
437 weapons, we can infer that sexual conflict over mating will have an  
438 important impact on the evolution of weapons. Sexual conflict arises from  
439 differences in the evolutionary interests of males and females, causing  
440 males and females to differ with respect to their interest in mating latency,  
441 frequency, duration and other aspects of copulation (Trivers, 1972;  
442 Chapman et al., 2003). Such conflicts should increase in importance when  
443 individuals of one sex have a disproportionate probability of acquiring and  
444 subsequently transmitting disease during copulation, as is the case in wild  
445 boars.

446

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452

#### 453 **Author contribution**

454 APM and PLF designed the study, PLF collected the data, APM performed  
455 the analyses, and all authors drafted the paper.

456

#### 457 **Data accessibility statement**

458 We will make the data available upon acceptance.



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- 624

625 **Legends to figures**

626

627 **Figure 1** Width of canines (cm) in relation to (a) body volume (cm<sup>3</sup>), (b)  
628 residual body volume after controlling statistically for head length, and (c)  
629 age (years). Sample size is 103

630

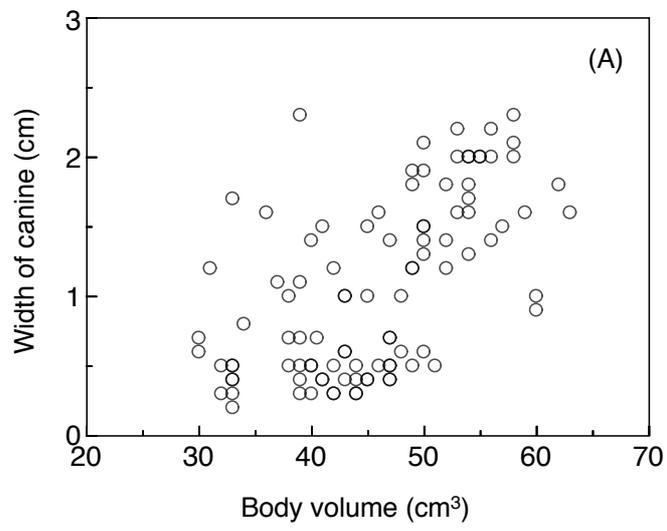
631 **Figure 2** Residual width of canines (after controlling for body volume) in  
632 relation to (a) presence of livestock (no – N = 75, yes – N = 51), (b)  
633 relative population density, and (c) forest quality (holm oak N = 92, oak N  
634 = 11)

635

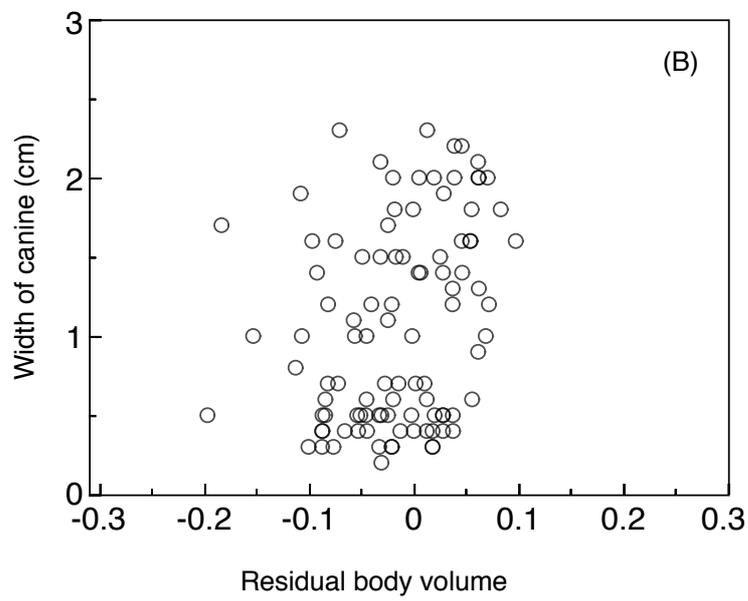
636 **Figure 3** Health parameters in relation to canine width (cm). (a) Spleen  
637 mass (g), (b) Aujeszky's disease (no – N = 62, yes – N = 51), and (c)  
638 tuberculosis (no – N = 94, yes – N = 9)

639

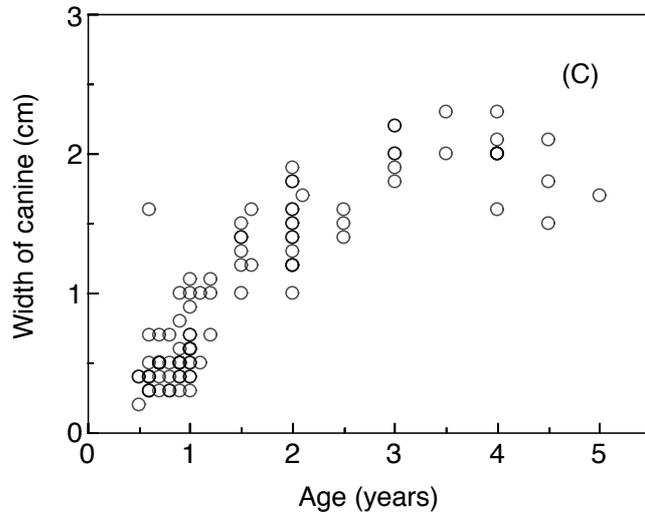
640 Fig. 1



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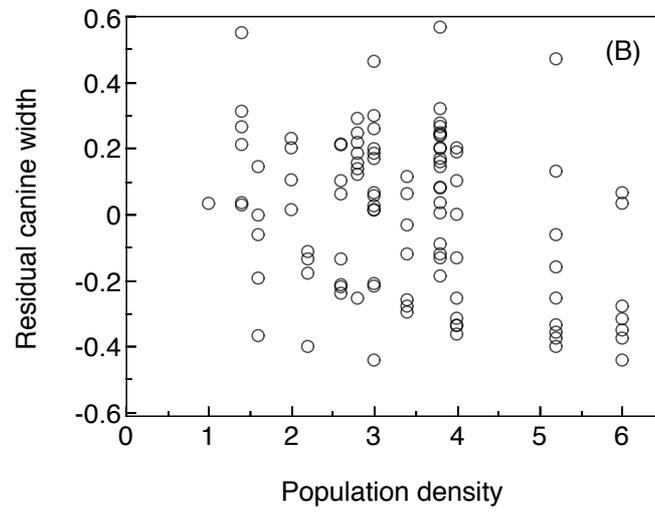
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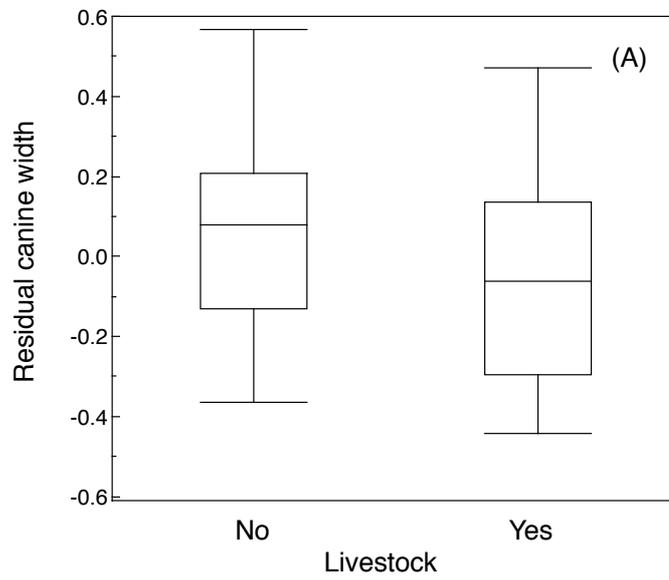
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647 Fig. 2

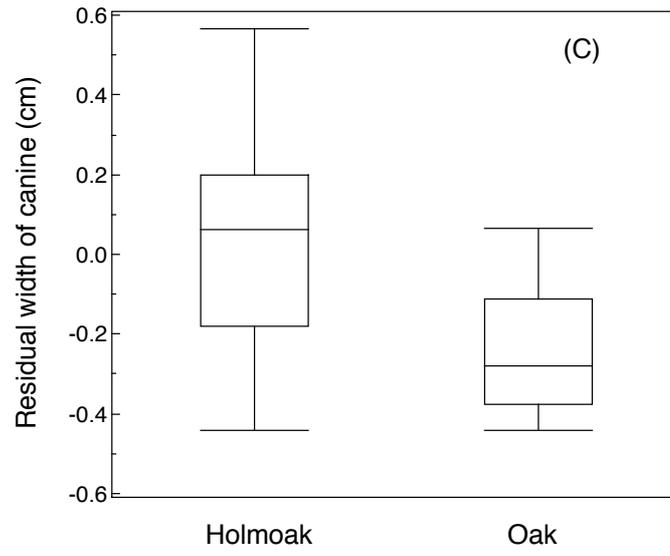


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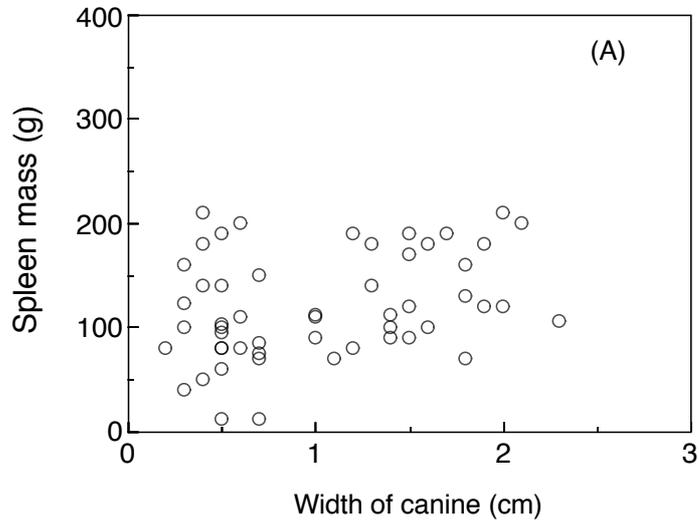
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654 Fig. 3

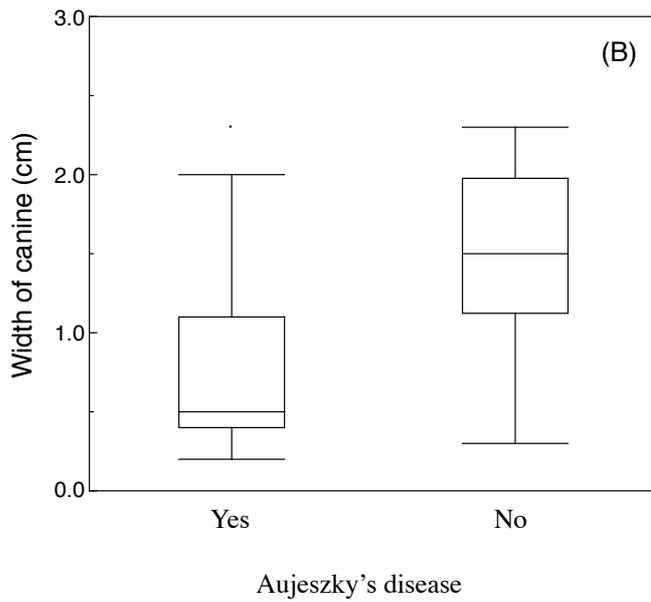
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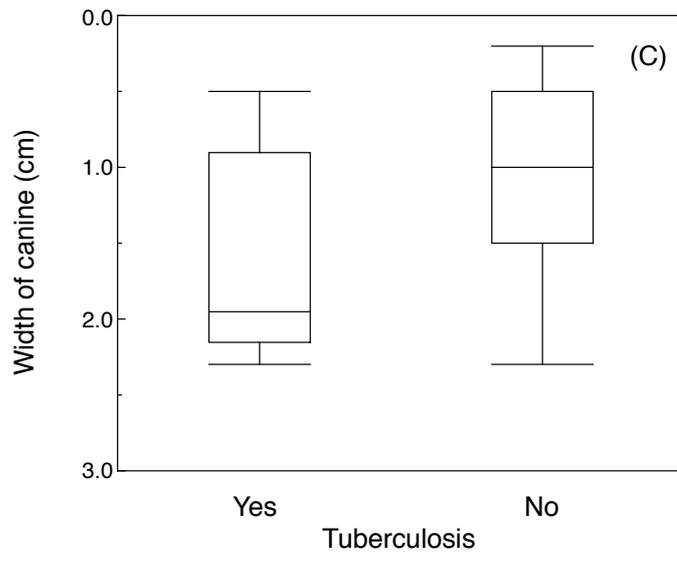
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