Canine size, condition and health in wild boars

P Fernández-Llario, Anders Pape Møller

► To cite this version:

P Fernández-Llario, Anders Pape Møller. Canine size, condition and health in wild boars. Journal of Zoology, 2019. hal-03024870

HAL Id: hal-03024870

<https://cnrs.hal.science/hal-03024870>

Submitted on 26 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Canine size, condition and health in wild boars

P. Fernández-Llario¹ & A. P. Møller^{2,3}

1 Innovación en Gestión y Conservación de Ungulados S.L.
(INGULADOS), 10001 Cáceres, Spain

2 Ministry of Education Key Laboratory for Biodiversity Science and
Ecological Engineering, College of Life Sciences, Beijing Normal
University, Beijing 100875, China

3 Ecologie Systématique Evolution, Université Paris-Sud, CNRS,
AgroParisTech, Université Paris-Saclay, F-91405 Orsay Cedex, France

Word count: 5835

Correspondence to APM:

Tel: (+33) 1 69 15 56 88

Fax: (+33) 1 69 15 56 96

E-mail: amoller@u-psud.fr, pfernandezllario@gmail.com

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

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

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

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

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

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

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

Characters measured

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

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

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

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

Statistical analyses

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

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

Results

Condition-dependence of canine size

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

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

FIG. 1 ABOUT HERE

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

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

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

Canine size and environmental conditions

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

FIG. 2 ABOUT HERE

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

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

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

Canine size and health

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

FIG. 3 ABOUT HERE

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

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

Discussion

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

Condition-dependence of canines

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

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

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

We found considerable evidence of age predicting canine width. Since body volume also increased with age, the increase in size with age may simply reflect the ability of older individuals with more experience to differentially acquire resources. Old individuals have proven their ability to survive, and females may acquire genes associated with longevity by mating with male boars with the largest canines, as hypothesized by 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

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

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

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

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

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

Acknowledgments

We are most grateful to Pilar Gonçalves, David Risco, Waldo Garcia, Julián Navarro and Rosario Cerrato for help with fieldwork, Alberto Parra for help with some clinical analyses and Prof. Javier Hermoso de Mendoza (Universidad de Extremadura, Spain) for partially funding this work.

Author contribution

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

Data accessibility statement

We will make the data available upon acceptance.

460 References

461

462 Able, D.J. (1996). The contagion indicator hypothesis for parasite-mediated
463 sexual selection. *Proc. Natl. Acad. Sci. USA* 93, 2229-2233.

464 Alexander, R.D., Hoogland, J.L., Howard, R.D., Noonan, K.M. &
465 Sherman, P.W. (1979). Sexual dimorphisms and breeding systems in
466 pinnipeds, ungulates, primates, and humans. In: *Evolutionary*
467 *biology and human social behavior* (Chagnon, N.A. & Irons, W.,
468 eds.). North Scituate, Mass: Duxbury Press, pp. 402-435.

469 Andersson, M. (1994). *Sexual selection*. Princeton: Princeton University
470 Press.

471 Arvy, L. (1965). *Splénologie*. Paris: Gauthiers-Villars.

472 Badyaev, A.V., Etges, W.J., Faust, J.D. & Martin, T.E. (1998). Fitness
473 correlates of spur length and spur asymmetry in male wild turkeys. *J.*
474 *Anim. Ecol.* 67, 845-852.

475 Barrete, C. (1986). Fighting behavior of wild *Sus scrofa*. *J. Mammal.* 67,
476 177-179.

477 Bauerle, W. (1975). Freilanduntersuchungen zum Kampf-Sexualverhalten
478 des europäischen Wildschweines (*Sus scrofa* L.). *Z. Tierpsychol.* 39,
479 211-258.

480 Boitani, L., Mattei, L., Nonis, D. & Corsi, F. (1994). Spatial and activity
481 patterns of wild boars in Tuscany, Italy. *J. Mammal.* 75, 600-612.

482 Burnham, K.P. & Anderson, D.R. (1998). *Model selection and inference*.
483 New York: Springer.

484 Chapman, T., Arnqvist, G., Bangham, J. & Rowe, L. (2003). Sexual
485 conflict. *Trends Ecol. Evol.* 18, 41-47.

486 Coetsier, C., Vannuffel, P., Blondeel, N., Deneb, J.-F., Cocito, C. & Gala,
487 J.-L. (2000). Duplex PCR for Differential Identification of
488 *Mycobacterium bovis*, *M. avium*, and *M. avium* subsp.

- 489 *paratuberculosis* in Formalin-Fixed Paraffin-Embedded Tissues
 490 from Cattle. *J. Clin. Microbiol.* 38, 3048-3054.
- 491 Connor, J. (1988). Field measurements of natural and sexual selection in
 492 the fungus beetle *Bolitotherus cornutus*. *Evolution* 42, 735-749.
- 493 Cuervo, J.J. & Møller, A.P. (2001). Components of phenotypic variation in
 494 avian ornamental and non-ornamental feathers. *Evol. Ecol.* 15, 53-
 495 72.
- 496 Estes, R.D., Cumming, D.H.M. & Hearn, G.W. (1982). New facial glands
 497 in domestic pig and warthog. *J. Mammal.* 63, 618-624.
- 498 Fernández-Llario, P. (2004). The sexual function of wallowing in male
 499 wild boar (*Sus scrofa*). *J. Ethol.* 23, 9-14.
- 500 Fernández-Llario, P. & Mateos-Quesada, P. (2003). Afectan las
 501 características morfológicas y los factores ambientales al desarrollo
 502 del canino en el jabalí? *Galemys* 15, 37-46.
- 503 Fernández-Llario, P., Mateos-Quesada, P., Silverio, A. & Santos, P. (2003).
 504 Shooting techniques and habitat effects on wild boar (*Sus scrofa*)
 505 populations in Spain and Portugal. *Z. Jagdwiss.* 49, 120-129.
- 506 Fernández-Llario, P., Parra, A., Cerrato, R. & Hermoso de Mendoza, J.
 507 (2004). Spleen size variations and reproduction in a Mediterranean
 508 population of wild boar (*Sus scrofa*). *Eur. J. Wildl. Res.* 50, 13-17.
- 509 Frädrich, H. (1967). Das Verhalten der Schweine (Suidae, Tayassuidae)
 510 und Flusspferde (Hippopotamidae). *Handb. Zool.* 19, 1-44.
- 511 Folstad, I. & Karter, A.J. (1992). Parasites, bright males, and the
 512 immunocompetence handicap. *Am. Nat.* 139, 603-622.
- 513 Gonçalves, P., Risco, D., Fernández-Llario, P., Barquero-Pérez, O.,
 514 Serrano, E., Hermoso-de-Mendoza, J. & Mateos, C. (2016). A new
 515 method for ageing wild boar using dental measures. *Ecol. Indicat.*
 516 62, 328-332.

- 517 Gortazar, C., Vicente, J. & Gavier-Widen, D. (2003). Pathology of bovine
518 tuberculosis in the European wild boar. *Vet. Rec.* 152, 779-780.
- 519 Grant, A. (1982). The use of tooth wear as a guide to the age of domestic
520 ungulates. In: Wilson, B., Grigson, C. & Payne, S. (eds) *Aging and*
521 *sexing animal bones from archaeological sites*. BAR British Series,
522 pp. 91-109.
- 523 Gueguen, B. & Aynaud, J.M. (1980). Étude de l'excretion du virus de la
524 maladie d'Aujeszky par les voiles genitales du porc. *Rec. Med. Vet.*
525 156, 307-312.
- 526 Hamilton, W.D. (1990). Mate choice near and far. *Am. Zool.* 30, 341-352.
- 527 Hamilton, W.D. & Zuk, M. (1982). Heritable true fitness and bright birds: a
528 role for parasites? *Science*, 218, 384-387.
- 529 Herrera, C.M., Jordano, P., Guitán, J. & Traveset, A. (1998). Annual
530 variability in seed production by woody plants and the masting
531 concept: reassessment of principles and relationships to pollination
532 and seed dispersal. *Am. Nat.* 152, 576-594.
- 533 Herring, S.W. (1972). The role of canine morphology in the evolutionary
534 divergence of pigs and peccaries. *J. Mammal.* 53, 500-512.
- 535 Hooijer, D.A. (1948). Evolution of the dentition of the orang-utan. *Nature*
536 162, 306-307.
- 537 Huxley, J.S. (1932). *Problems of relative growth*. London: Methuen.
- 538 Jarman, P.J. (1983). Mating system and sexual dimorphism in large,
539 terrestrial mammalian herbivores. *Biol. Rev.* 58, 485-520.
- 540 Jarman, P.J. (1989). On being thick-skinned: Dermal shields in large
541 mammalian herbivores. *Biol. J. Linn. Soc.* 36, 169-191.
- 542 Jennions, M.D., Møller, A.P. & Petrie M. (2001). Sexually selected traits
543 and adult survival: A meta-analysis of the phenotypic relationship.
544 *Q. Rev. Biol.* 76, 3-36.

- 545 John, J. (1994). The avian spleen: a neglected organ. *Q. Rev. Biol.* **69**, 327–
546 351.
- 547 Johnstone, R.A. (1995). Sexual selection, honest advertising and the
548 handicap principle: reviewing the evidence. *Biol. Rev.* 70, 1-65.
- 549 Klein, S.L., Bird, B.H. & Glass, G.E. (2000). Sex differences in Seoul virus
550 infection are not related to adult sex steroid concentrations in
551 Norway rats. *J. Virol.* 74, 8213-8217.
- 552 Klein, S.L., Bird, B.H., Nelson, R.J. & Glass, G.E. (2002). Environmental
553 and physiological factors associated with Seoul virus infection
554 among urban populations of Norway rats. *J. Mammal.* 83, 478-488.
- 555 Koenig, W.D., Mumme, R.L., Carmen, W.J. & Stanback, M.T. (1994).
556 Acorn production by oaks in central coastal California: variation
557 within and among years. *Ecology* 75, 99-109.
- 558 Kotiaho, J., Simmons, L.W. & Tomkins, J.L. (2001). Towards a resolution
559 of the lek paradox. *Nature* 410, 684-686.
- 560 Lauer, C. (1975). A comparison of sexual dimorphism and range of
561 variation in *Papio cynocephalus* and *Gorilla gorilla* dentition.
562 *Primates* 16, 1-7.
- 563 Manning, J.T. (1985). Choosy females and correlates of male age. *J theor*
564 *Biol* 116:349-354.
- 565 Martin, S., & Wardley, R.C. (1987). Local humoral and cellular responses
566 in Aujeszky's disease virus infection in pigs. *Res. Vet. Sci.* 42, 170-
567 174.
- 568 Mateos-Quesada, P. (1998). *Parámetros poblacionales y sistema de*
569 *apareamiento del corzo en Las Villuercas*. PhD dissertation.
570 Cáceres: University of Extremadura.
- 571 Matschke, G.H. (1967). Ageing European wild hogs by dentition. *J. Wildl.*
572 *Manage.* 31, 109–113.

- 573 Mauget, R. (1979). Mise en évidence, par captures-recaptures et
 574 radiotracking, du domaine vital chez le sanglier (*Sus scrofa* L.) en
 575 forêt de Chizé. *Biol. Behav.* 1, 25-41.
- 576 Medveczky, I. & Szabó, I. (1981). Isolation of Aujeszky's disease virus
 577 from boar's semen. *Acta Vet. Acad. Sci. Hung.* 29, 29-35.
- 578 Melrose, D.R., Reed, H.C.B. & Patterson, R.L.S. (1971). Androgen
 579 steroids associated with odour as an aid to the detection of oestrus in
 580 pig artificial insemination. *Br. Vet. J.* 127, 497-501.
- 581 Møller, A.P., Christe, P. & Lux, E. (1999). Parasitism, host immune
 582 function, and sexual selection. *Q. Rev. Biol.* 74, 3-20.
- 583 Packer, C. (1983). Sexual dimorphism: The horns of African antelopes.
 584 *Science* 221, 1191-1193.
- 585 Parra, A. (2003). *Epidemiología de la Tuberculosis en Artiodáctilos*
 586 *salvajes de Extremadura*. PhD dissertation. Cáceres: University of
 587 Extremadura.
- 588 Peters, A. (2000). Testosterone treatment is immunosuppressive in superb
 589 fairy-wrens, yet free-living males with high testosterone are more
 590 immunocompetent. *Proc. R. Soc. Lond. B* 267, 883-889.
- 591 Pomiankowski, A. & Møller, A.P. (1995). A resolution of the lek paradox.
 592 *Proc. R. Soc. Lond. B* 260, 21-29.
- 593 Puente, E., Cancio, E. & Seoane, R. (2001). La enfermedad de Aujeszky:
 594 latencia. *Porci*, 63, 57-67.
- 595 Pulido, F.J. (1999). *Herbivorismo y regeneración de la encina (Quercus*
 596 *ilex* L.) *en bosques y dehesas* (PhD dissertation). Cáceres: University
 597 of Extremadura.
- 598 Risco, D., Gonçalves, P., Mentaberre, G., Navarro-González, N., Casas-
 599 Díaz, E., Gassó, D., Colom-Cadena, A., Fernández-Aguilar, X.,
 600 Castillo-Contreras, R., Velarde, R., Barquero-Pérez, O., Fernández-
 601 Llario, P., Lavín, S., Fonseca, C. & Serrano, E. (2018). Biometrical

- 602 measurements as efficient indicators to assess wild boar body
 603 condition. *Ecol. Indicat.* 88, 43-50.
- 604 Roberts, M.L., Buchanan, K.L. & Evans, M.R. (2004). Testing the
 605 immunocompetence handicap hypothesis: a review of the evidence.
 606 *Anim. Behav.* 68, 227-239.
- 607 Rushen, J. & Pajor, E. (1987). Offence and defence in flights between
 608 young pigs (*Sus scrofa*). *Aggress. Behav.* 13, 329-346.
- 609 Saino, N. & Møller, A.P. (1996). Sexual ornamentation and
 610 immunocompetence in the barn swallow. *Behav. Ecol.* 7, 227-232.
- 611 Struhsaker, T.T. (1969). Correlates of ecology and social organization
 612 among African cercopithecines. *Folia Primatol.* 11, 80-118.
- 613 Trivers, R.L. (1972). Parental investment and sexual selection. In: *Sexual*
 614 *selection and the descent of man* (Campbell, B., ed.). London:
 615 Heinemann, pp. 136-179.
- 616 von Schantz, T., Göransson, G., Andersson, I., Fröberg, M., Grahm, M.,
 617 Helgée, A. & Wittzell, H. (1989). Female choice selects for a
 618 viability-based male trait in pheasants. *Nature* 337, 166-169.
- 619 von Schantz, T., Wittzell, H., Göransson, G., Grahm, M. & Persson, K.
 620 (1996). MHC genotype and male ornamentation: genetic evidence
 621 for the Hamilton-Zuk model. *Proc. R. Soc. Lond. B* 263, 265-271.
- 622 Zahavi, A. (1975). Mate selection – a selection for a handicap. *J. theor.*
 623 *Biol.* 53, 205-214.
- 624

Legends to figures

626

Figure 1 Width of canines (cm) in relation to (a) body volume (cm³), (b) residual body volume after controlling statistically for head length, and (c) age (years). Sample size is 103

630

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

635

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

639

640 Fig. 1

641

642

643

644

645

646

647 Fig. 2

648

649

650

651

652

653

654 Fig. 3
655

656
657
658

659

660

661

662