Use of cast antlers to assess antler size variation in red deer populations: effects of mast seeding, climate and population features in Mediterranean environments

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cast antlers; masting; red deer; population density; age structure; Mediterranean; Cervus elaphus; real bioclimatic index.

Abstract

Fundamental understanding of the factors influencing cervid antler size, development and investment has been traditionally drawn from harvest data. However, depending on the hunting tactic, harvest data may not represent a random sample of the population leading to possible inferential biases. Cast antlers may represent an alternative, cost-effective and non-invasive method. We used 4756 red deer (Cervus elaphus L.) cast antlers collected during a 10-year period to evaluate the relationship between annual antler gross score and three key environmental components that determine habitat quality and resource availability in Mediterranean systems: (1) population traits (density and male age structure), (2) acorn yield and (3) a proxy of plant productivity [Real Bioclimatic Index (RBI)]. Population traits and acorn yield were measured before antler formation (autumn/winter) whereas RBI was calculated before (autumn/winter) and during (spring) antler formation. Population traits explained the highest amount of variance in antler score, followed by acorn yield and spring RBI, while no effect was found for autumn/winter RBI. Antler gross score was negatively related to population density but positively associated with acorn yield, spring RBI and male age structure. Interestingly, a significant interaction between population traits and acorn yield suggests a disproportional effect of population traits on antler size during non-mast years (poor acorn crops), whereas no significant population effect was observed during mast years. Similarly, we found a positive effect of spring RBI on antlers when density was medium or low and/or age structure was balanced or older. These findings have important ecological implications in environments with high inter-annual resources variability where high population densities lead to strong intraspecific competition during years of low food availability (e.g. during non-mast years or drier springs), producing large antler size variation. Finally, although cast antlers reflect changes in environmental conditions we do not recommend their use unless reliable data on age structure is available.

Introduction

Multiple factors have been identified as determinant in red deer (Cervus elaphus L.) antler development. Beyond genetic control and individual age, the most relevant factors described are early life conditions and yearly environmental factors (e.g. density and weather parameters; Schmidt et al., 2001; Kruuk et al., 2002; Mysterud et al., 2005; Landete-Castillejos et al., 2012). Antler formation requires partial demineralization of the skeleton (19–24% of the bone mass; Gómez et al., 2012) as the amount of minerals required for antler growth (13.7 g day−1 on average at peak deposition; Muir, Sykes & Barrell, 1987) cannot be supplied exclusively via nutrition in such a short period of time (95% of final antler length is formed in a mean of 112 days; Muir et al., 1987). Hence, poor early life nutrition exerts negative delayed effects on adult body and skeleton size limiting potential allocation to sexual secondary traits (Moore, Littlejohn & Cowie, 1988; Schmidt et al., 2001; Michel et al., 2016). In addition, antler size relative to body size was found to be greater during years with favorable environmental conditions (Mysterud et al., 2005). In particular, weight recovery after the rut (~25% of weight is lost during
the rut; McMahon, 1994; Strickland et al., 2017) and body size/condition at antler casting have been suggested to strongly correlate with allocation to antler growth (Hyvärinen, Kay & Hamilton, 1977; Muir et al., 1987; Gaspar-López et al., 2010; Gómez et al., 2012), although weight gain during antler development is also important (Gaspar-López et al., 2010). An example of high-quality food after the rut is that provided by mast-seeding trees (e.g. acorns, beechnuts and chestnuts) which offer an irregular but highly nutritious food source in many temperate and Mediterranean environments (red deer: Picard, Oleffe & Boisaubert, 1991; San Miguel, Roig & González, 2000; Azorit et al., 2012; white tailed deer Odocoileus virginianus: Wentworth et al., 1992). Most studies on red deer, however, have overlooked the potential influence of mast-seeding trees on antler development (but see Wentworth et al., 1992).

Importantly, most research on cervid antler growth has been traditionally drawn from harvest data. However, depending on the hunting tactic, harvest data may not represent a random sample of the population and may incorporate a major source of inferential bias (Strickland et al., 2001; Martínez-Jauregui et al., 2005; Andersen et al., 2007). In deer populations, cast antlers may provide a non-invasive and less biased method for gathering large amount of data as cast antlers’ sample size and representativeness are not limited by hunting quotas or methods (Schoenebeck & Peterson, 2014). However, very few studies have focused on this accessible source of information (red deer: Fiero et al., 2002; Kruuk et al., 2002; Landete-Castillejos et al., 2010; white-tailed deer: Schoenebeck & Peterson, 2014; Ditchkoff, Welch & Lochmiller, 2000). The main limitation of using cast antlers is that the age of deer is unknown. Because deer antler size varies dramatically with age (Kruuk et al., 2002; Mysterud et al., 2005), the absence of control for changes in male age structure could lead to inferential error. Because accurate data on population age structure is difficult to obtain for free ranging wild populations, most studies have dismissed the use of antlers. Here, we aimed to evaluate the association between antler size variation at the population level and different environmental components (population density, age structure, mast seeding and weather conditions) based on a large cast antler database. We hypothesized that (1) inter-annual variation of acorn crop (masting) would influence variations in antler size due to its role in the re-establishment of body condition after the rut and previous to antler casting, (2) weather variation before and during antler formation would also affect antler size due to its influence on plant productivity and hence nutritional status, (3) inter-annual variation in antler size would be influenced by population traits (i.e. population density and/or male age structure). Hence, our study represents the first long term investigation (10 years) based on more than 4700 red deer antlers aimed at identifying the environmental factors influencing antler size at the population level.

**Materials and methods**

**Study area**

Cast antlers from Iberian red deer were collected from Quintos de Mora hunting estate (68.6 km²; south-central Spain) with a Continental Mediterranean climate [more details on the study area in Peláez et al. (2017)]. Peak of rutting activity usually occurs at the end of September with 80% of conceptions concentrated from mid-September to mid-October (Peláez et al., 2017). During spring and autumn, pastures provide high-quality food along with the autumnal highly nutritious acorns, mostly from the abundant Holm oak (Quercus ilex L.), but also from the less prevalent Q. faginea Lam. Throughout periods of nutritional constraints (usually summer and some winters), deer increase their browse intake (Bugalho & Milne, 2003) but also have access to 2.1 km² of rainfed crops (oats, barley, rye, common vetch and clover) which are protected by an electric fence the rest of the year. During the study period (2002-2011) deer management goals were: (1) to reduce deer density to an average of 23–24 deer/km² and (2) to approach a sex ratio structure of 1:1.

**Data collection**

A total of 4756 fresh and unbroken cast antlers were collected during the period 2002–2011, with an annual average of 476 ± 86 (±SD). These antlers belonged to males ≥2 years old because of the difficulty to find yearling antlers due to their later cast date and the high percentage of button-stage yearlings in the population.

The following study variables were collected:

1. **Gross score of antlers** was calculated using the C.I.C. method (International Council for Game and Wildlife Conservation; see Table S1), similar to the North American Boone and Crockett scoring method (Nesbitt & Wright, 1981). Both metrics have been widely used in many studies of antlers (Ditchkoff et al., 2000; Fiero et al., 2002; Gaspar-López et al., 2010; Azorit et al., 2012; Strickland et al., 2013).

2. **Deer density**: Line transect surveys were performed every year at dusk during the rutting period (end of September/beginning of October). Absolute deer density and confidence intervals were estimated by distance sampling (Buckland et al., 2001) using the ‘Distance’ package in R software. More details can be found in Peláez et al. (2017). For analysis purposes we used population density calculated during the rut before antler formation.

3. **Real Bioclimatic Index (RBI)** is a Gaussian derived index developed by Montero de Burgos & González-Rebollar (1974) and used as a proxy of plant productivity in studies on Iberian Red deer (see Appendix S3 Martínez-Jauregui et al., 2009; Peláez et al., 2017). We used: (1) average RBI during autumn and winter (prior to antler formation; from September to February) and (2) RBI during spring (while antlers developed; from March to June). We used March as a threshold because cast antlers start to be found in our study area in late February. Weather parameters were obtained from a weather station located inside the study area.

4. **Acorn yield index** was obtained each year during October (before antler formation). Data were collected from Cabaniers National Park, located 10 km from our study.
Age structure index. Based on the data of known-age males harvested during the period 2002 to 2016 (n = 2835), we reconstructed the age-structure of the male population prospectively (i.e. knowing the age of each male at death we calculated its age during the previous years). Hence, we obtained a yearly male age structure based on a mean of 790 ± 62 known-age males which corresponded to more than 80% of the estimated male population. Age was determined by histological examinations of incisors using cementum annuli counts (Low & Cowan, 1963). Finally, we obtained the age structure for the subset of males harvested during the period 2002 to 2016 (POP_t). Therefore, we built a linear model with left antler gross score (n = 2350) as the response variable and the following predictors: Population traits (POP_t), Acorn yield index (ACORN), RBI during autumn and winter (RBI_aut_win) and RBI during spring (RBI_spr). We centered all predictors (Schielzeth, 2010) and included two-way interactions of population traits and the other variables to account for food availability per individual.

Because we considered left and right antlers as independent samples, we kept the right-side subset (n = 2406) to validate the results from the left side model. Hence, we performed Pearson’s χ² tests to assess correlations between left-side model predictions and mean right antler gross scores by year. All analyses were performed using the R statistical software v3.2.1 (http://www.r-project.org/). To fit the model, we used the function ‘lm’ of the package ‘stats’. We used the function dredge to rank all possible models based on the lowest weighting provided by the Akaike information criterion (AIC) and selected the simplest model (least number of parameters) among all candidate models within ΔAIC<2 following the principle of parsimony (Burnham & Anderson, 2002). To estimate the amount of variance explained by each predictor we performed variance partitioning with the function ‘varpart’ included in the R package ‘vegan’. Finally, as density and age structure were correlated, the effect size of the variable Population traits accounted for both variables. To assess their relative importance, we calculated to what extent the observed changes in age structure during our study period could have modified mean population antler size. First, we calculated mean antler gross score based on data of males harvested during a management regime called ‘Monterías’ before and after the study period (1997; density of 36 ind/km², 2012 and 2013; density of 26 ind/km², n = 247; Fig. S2). Martínez-Jauregui et al. (2005) concluded that size or age selection by hunters was less pronounced in Monterías than for other hunting methods such as trophy-stalking and management hunting. Using the annual percentage of males of each age and the mean antler size by age, we calculated the yearly mean population gross score and the potential increase in antler size caused by changes in age structure.

Results

Over the 10 years of the study, mean left antler gross score was 126 ± 19 (score ± sd; n = 2350). Inter-annual variation in mean gross score varied from 111 ± 15 in 2005 to 138 ± 18 in 2011 (Fig. 1). Mean deer population density decreased throughout the years (40.3 deer/km² in 2003 and 29.6 deer/km² in 2011) while all male age structure variables followed an increasing trend (Fig. 2b, c). Acorn production showed high inter-annual variability, with lower acorn crops during 2005 and 2006 and highest in 2009 (Fig. 2d). RBI during spring and RBI during autumn and winter showed high inter-annual variability (mean 0.99 ± 0.40 and 0.22 ± 0.21, respectively; Fig. 2e, f). Finally, it is worth noting the low values of 2005 for all variables reflecting plant productivity (Acorn yield, RBI during spring and RBI during autumn and winter).

Following the principle of parsimony we selected the best fitting model that contained the following predictors: Acorn yield, RBI during spring and their interactions with Population traits (Table 1). Pearson correlation showed a high correlation...
between model predictions and mean right antlers gross score by year. Acorn yield and RBI during spring showed a positive relationship with gross antler score while Population traits showed a negative relationship (Table 2). Population traits was the variable explaining the highest amount of variance, followed by Acorn yield and, to a lesser extent, RBI during spring. Based on the age structure of males each year and the calculated mean antler size by age, we observed a maximum increase in 6.4% in antler gross score (from a score of 106 in 2003 to 113 in 2008; Table S3) due to age structure, while the total predicted increase in gross score due to the variable Population traits was 13.2%. This indicates that age structure alone cannot explain the total effect produced by the variable Population traits, most likely changes in population density explained the rest of the variance (6.8%). During years with highest acorn crop (controlling for the rest of the variables), mean antler gross score was ca. 13% greater than in years with poor acorn crops. This is a very strong effect because the total variation on mean antler score during the study period was 24%. The effect size of RBI during spring, when controlling for the rest of the variables, showed approximately a 7.0% antler score difference between the year with maximum and minimum plant productivity. Finally, the interaction between Population traits and Acorn yield suggested a greater negative effect of a poor acorn crop when density was high or age structure was younger (Fig. 3a). On the other hand, the interaction between RBI during spring and Population traits revealed only a positive effect of RBI on antler size when density was medium or low and/or age structure was balanced or older (Fig. 3b).

Discussion

Our study highlights the strong role that seed masting, RBI during spring and population traits (deer density and age

Figure 1  Inter-annual variation in cast antler gross score for Iberian red deer from south-central Spain during 2002-2011 (observed mean gross score (●) 95% CI) and predicted (■) values from the top model.

Figure 2  (a) Observed (●) mean left antler gross score of Iberian red deer from south-central Spain (2002-2011), (b) annual deer population estimates by year (density (■) ± CV), (c) age structure variation through time (% of males ≥ 6 years old (d) mean acorn yield (acorn (■) ± so); (e) mean RBI during spring (RBI (■) ± CV); (f) mean RBI during autumn and winter (RBI (■) ± CV).
The influence of both population density (Clutton-Brock & Albon, 1989; Schmidt et al., 2001; Kruuk et al., 2002) and spring nutrition (Gaspar-López et al., 2010) on antler development has been previously reported. However, to the best of our knowledge, no study has shown an effect of acorn crop on red deer antler development (but see for white-tailed deer: Wentworth et al., 1992), even though acorns have been previously described as a crucial source of high-quality food for deer during autumn and winter in oak-dominated systems (Picard et al., 1991; San Miguel et al., 2000; Azorit et al., 2012). In addition, we demonstrated that changes in male age structure can significantly affect the mean size of cast antlers at the population level. Consequently, although cast antlers may represent a useful tool to monitor the effect of key environmental conditions (e.g. food availability per capita) on

<table>
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<tr>
<th>Table 1</th>
<th>Model selection describing the factors affecting Iberian red deer antler size (gross score) in south-central Spain, 2002-2011</th>
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<td>7</td>
</tr>
<tr>
<td>2 ACORN + POP_t + RBI_spr + RIBI_aut_win + POP_t + ACORN + POP_t + RBI_spr</td>
<td>8</td>
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<td>3 ACORN + POP_t + RBI_spr + RIBI_aut_win + POP_t + ACORN + POP_t + RBI_spr + POP_t + RIBI_spr</td>
<td>9</td>
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<tr>
<td>4 ACORN + POP_t + RBI_spr + RIBI_aut_win + POP_t + RIBI_spr</td>
<td>7</td>
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<tr>
<td>5 ACORN + POP_t + RBI_spr + RIBI_aut_win + POP_t + RBI_spr + RIBI_aut_win</td>
<td>8</td>
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<tr>
<td>6 ACORN + POP_t + RBI_spr + POP_t + ACORN</td>
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d.f. indicates degrees of freedom, LogLik denotes maximum log likelihood, ΔAIC is the difference in Akaike criterion scores between the top and the actual model and w represents AIC weights.

ACORN, Acorn yield index; POP_t, population traits; RBI_spr, RBI during spring and RBI_aut_win, RBI during autumn and winter.

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<th>Table 2</th>
<th>Summary of the best-fitting linear model describing the factors affecting antler size (gross score) in Iberian red deer from south-central Spain, 2002-2011.</th>
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<td>Population traits</td>
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<td>RBI_spr</td>
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<tr>
<td>ACORN * POP_t</td>
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<tr>
<td>RBI_spr * POP_t</td>
<td>−1.6</td>
</tr>
</tbody>
</table>

AdjR² left = 0.12. Adjusted R squared is the proportion of variance explained by the model selected. POP_t, population traits; ACORN, Acorn yield index; RBI_spr, RBI during spring.

Model estimates and standard errors are presented for each variable and interaction.

All variables were centered on their mean.

P-values indicate statistical significance.

R squared was calculated based on the proportion of the total variance explained by each variable (without interactions) and the independent fraction as the individual variance explained by each variable that is not explained by any other variable.

| Figure 3 | Predicted antler gross score of Iberian red deer from south-central Spain (2002-2011) as a result of the interactive effect between: (a) Acorn yield and population traits and (b) RBI during spring and population traits. Both interactions are represented at three different levels of population density and/or age structure. |

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antler attributes, we recommend not to use cast antlers unless reliable data on age structure are available given the strong influence of age structure on population antler size.

Our study revealed that two main food resources influenced inter-annual variation in antler size: (1) acorn production, and (2) spring plant productivity. In addition, the absence of an effect of autumn-winter RBI on antler size was only partial because we could not test its potential influence during non-mast years (the 2 years with lowest acorn crop coincided with the driest autumn and winter recorded; Fig. 2d, f). Nevertheless, we were able to conclude that during years of medium and high acorn crop there was no significant influence of autumn/winter plant productivity, suggesting a greater effect of seed mast over the autumn-winter green forage on antler size. However, the chemical composition of acorns is low in essential elements required for antler development (proteins and minerals; Landete-Castillejos et al., 2012) compared to that of autumn/winter grasses (Rodríguez-Estévez et al., 2007). Hence, we suggest that acorn production does not have a direct effect on antler development by providing the necessary nutrients for their formation but, instead, may have an indirect effect by helping males build up body fat reserves rapidly after the mating effort (Azorit et al., 2012), enabling them to later concentrate in alternative, more specific nutrients for antler formation.

In addition, our predictor ‘population traits’ accounted for two highly correlated variables (density and age structure) and, thus, we could not discriminate the effect of each variable in the models. However, an alternative approach based on antler data of harvested males helped elucidate that the total observed variation in antler size could not be due to the sole effect of age structure. Age structure explained ca. half of the variation in antler scores, which leads to the conclusion that the rest of the variation was likely due to changes in population density. Nevertheless, the strong influence of high population density on antler size has been widely described (Schmidt et al., 2001; Kruuk et al., 2002; Azorit et al., 2002) because: (1) it limits per capita food intake of high quality and, hence, resources available for antler growth (Mysterud et al., 2005) and (2) it produces a negative delayed effect on adult body size due to poor early life nutrition (Landete-Castillejos et al., 2005; Gómez et al., 2006; Ceacero et al., 2010; Dryden, 2016).

Finally, the significant interacting effects among the variable population trait (density and age structure) and the two variables used as proxy of food resources (acorn crop and RBI during spring) could help to elucidate two points: (1) during mast years there was little or no effect of the variable population trait on antler size while a greater effect was observed during non-mast years, and (2) during years of higher spring plant productivity the variable population traits had a positive effect on antler size but no significant effect occurred during unfavorable years. Nevertheless, further studies should control for both population trait variables to clarify the relative importance of population density and age structure in the observed interactions with acorn crop and RBI during spring.

Finally, our results have important management implications particularly in the current context of increasingly higher deer populations (Cóte et al., 2004; San Miguel, Perea & Fernández, 2010; Perea, Girardello & San Miguel, 2014). First, high deer densities decrease per capita resource availability leading to high intraspecific competition for food, which, in environments with high variation in resources, favors larger inter-annual fluctuations of antler size. Second, high deer densities also limit oak recruitment (Perea & Gil, 2014; López-Sánchez et al., 2016), which reduces the abundance of mature oak trees and thus overall acorn crop. Hence, we recommend reducing deer densities in Mediterranean environments to the estimated optimal for these environments (below 20 to 25 deer km⁻²). Soriguer et al., 1994 to ensure oak recruitment and improve antler size of unsupplemented red deer populations.

Acknowledgments

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**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Retrospective estimation of the population structure for males ≥ 2 years old.

**Figure S2.** Averaged antler gross score of males harvested during “Monterías” before and after the study period (1997; density 36 ind/km² and 2012-2013 density 26 ind/km²).

**Table S1.** Modified gross score of red deer antlers

**Table S2.** Changes in age structure for the Iberian red deer male population subset (≥ 2 years old) during the study period.

**Table S3.** Assessment of the impact of male age structure on antler gross score between the year with the lowest proportion of older males (2003 - 2004) and the year with the highest (2007 - 2008). Age structure was calculated as the percentage of males of each age.