Combined Effects of Drought and Density on Body and Antler Size of Male Iberian Red Deer Cervus Elaphus Hispanicus: Climate Change Implications

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Source: Wildlife Biology, 15(2) : 213-221

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/08-059

Wildl. Biol. 15: 213-221 (2009)
DOI: 10.2981/08-059

www.wildlifebiology.com

Short communication

Combined effects of drought and density on body and antler size of male Iberian red deer *Cervus elaphus hispanicus*: climate change implications

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Hunting management of red deer *Cervus elaphus* populations may tend to increase population densities to maximise annual yield. Some studies have shown that density and low winter temperatures affect red deer populations in central and northern Europe, but these results cannot be extrapolated to red deer populations in the Mediterranean region where the limiting season is summer instead of winter. The two regions are predicted to experience different climate change effects: while rainfall may increase in northern latitudes, heavier droughts are expected in the Mediterranean region. We studied red deer populations of different densities on 19 hunting estates in southern Spain during two years with contrasting precipitation levels. Our aim was to quantify the combined effects of drought and population density on the development of stags, which is the main economic objective of hunting management in these areas. We found that drought affected body and antler size negatively, and that the effects were more severe in populations of high density. On the basis of our results, we recommend reducing the current densities of red deer in southern Spain to maintain the economic and environmental sustainability of hunting exploitation in the context of global climate change.

Key words: Cervus elaphus, density, drought, game management, global climate change, Iberian red deer

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Received 3 September 2008, accepted 30 January 2009

Associate editor: Atle Mysterud

The warming of the climate is likely to be associated with changes in the distribution of precipitation throughout the world (IPCC 2007a). Studies on climate change indicate that the effects are likely to differ with latitude, resulting for instance in precipitation increments in northern Europe but reductions in more southerly Mediterranean areas, leading to increased risk of drought periods and fires in the south (IPCC 2007b). On the Iberian Peninsula, declines in rainfall are likely to be particularly marked in spring (MMA 2005), which may considerably worsen conditions during the dry and hot summer. Several studies have shown that local climatic variations affect ungulates in the northern hemisphere (e.g. Clutton-Brock & Albon 1989, Loison & Langvatn 1998, Coulson et al. 2000), but reports on the effects of climatic conditions on deer populations in southwestern Europe are very rare (Azorit et al. 2002).

The climate of southern Spain is very different from that of central and northern Europe. In northern latitudes, winter is the limiting season for growth and reproduction of ungulates as cold temperatures and snow reduce the food available to deer (Klein 1985), causing lower birth weights and increased mortality (Mitchell et al. 1976, Clutton-Brock & Albon 1982, Loison et al. 1999). In the Mediterranean, however, the limiting season is summer, when food availability is at its annual minimum and most herbaceous plants dry up, and deer have to increase browsing on less preferred shrub species (Rodríguez-Berrocal 1993, Bugalho & Milne 2003). Consequently, the effects of climate change on deer populations in northern Europe may not apply to deer populations in southern Europe.

Knowing the potential effects of drought on the development and reproduction of deer in these areas is of considerable importance, both from the point of view of the phenotypic plasticity of the characters involved (Emlen 1994, Gross 1996, Tomkins et al. 2005) and from its application to hunting management and conservation (Vargas et al. 1995, Carranza 1999, San Miguel et al. 1999). The objectives in our study were 1) to quantify the effects of current drought periods on the development of red deer *Cervus elaphus* stags, which constitute the objective of game management in these areas, and, as a result of this knowledge, 2) to provide practical recommendations in the face of expected changes in local climatic conditions, in order to maintain the sustainability of red deer populations in this region from the point of view of hunting exploitation and ecosystem conservation.

Material and methods

Our study area is located in the southern part of the Iberian Peninsula in Sierra Morena, a chain of low mountains covered by Mediterranean shrub and forest. The main tree species in this area are holm oak *Quercus ilex* and cork oak *Quercus suber*, which usually coexist with a wide variety of shrub species of which *Cistus* is the most abundant genus. There are also plantation areas with pine trees *Pinus* sp. The climate is characterised by mild, rainy winters and dry, hot summers. Our fieldwork was carried out in 2004 and 2005, the latter being an extremely dry year with a total annual rainfall of only 341.6 mm, while in 2004 total annual rainfall was 608.8 mm. Average annual rainfall in the region during the seven years prior to our study period was 595.97 ± 124.28 SD (Consejería de Agricultura y Pesca), and thus 2004 can be considered normal for the area on the basis of rainfall, whereas 2005 was an extremely dry year.

Our study area included 19 hunting estates with a mean size of ca 1,300 ha. Some of these estates (6) were surrounded by 2 m high perimeter wire fences which prevented deer from leaving the area. The presence or absence of fences leads to marked differences in management which in turn affects the structure of populations (Carranza 1999). In particular, when the estate is fenced, the owner is able to manage the population inside the fence without interference by neighbouring managers. Stags in fenced areas are normally allowed to reach maturity whereas in open estates they are hunted at a much younger age, and the sex ratio of the population tends to maintain a strong female bias. We will consider these two types of estates when analysing the effects of drought and density.

To check the variations in food availability between the two years of study, we measured grass height in spring (April-May) at the same fixed points ($N = 46$) distributed throughout the study estates. Deer density on each estate was estimated by counting animals seen at open mating areas during late afternoon in September, when the animals gather at mating areas and are therefore more visible (Carranza et al. 1996). Since an indeterminate number of animals may remain outside the mating areas, we considered our estimation to be a minimum value of density. Density was used in the analyses as a two-level categorical factor, for which we arbitrarily used 0.3 deer per ha as the cut off point for the two levels of density.

We measured 415 stags in 21 hunts (monterías; 12 in 2004 and nine in 2005). In the type of hunt called montería, packs of dogs are released within a shrub area to move the deer outwards to the sites where hunters are waiting, and hunting pressure on males is essentially regulated by only allowing one montería per year in the same area. Because hunters are normally allowed to shoot any male over two years old there is little opportunity for hunting to bias particular males, and montería is the least biased procedure to obtain data from hunted red deer (Martínez et al. 2005). From animals culled in monterías, we measured body length and heart girth (to the nearest 0.5 cm) in the following way: body length was measured from the tip of the snout to the tip of the tail, excluding the hair and following the dorsal contour of the body of the animal lying on the ground; heart girth was measured as the chest perimeter behind the forelegs. The following antler measurements (to the nearest 0.1 cm) were also taken in the field:

- Antler length was measured from the burr (included) to the longest tip of the antler.
- Burr circumference was measured as the perimeter of the basal bone protrusion of the antler.
- Antler thickness was measured as the perimeter around the main trunk of the antler measured between the brow-tine and the trez-tine.

- Number of antler points was taken as the total number of tines ≥ 2 cm on both antlers.

We were unable to weigh the animals used in this work, but heart girth has been proven to be a good proxy of body weight for red deer in Spain (Alarcos 2007). It was not possible to take all measurements for all individuals, so our sample sizes differ among measurements. For analyses we used average values for both antlers.

Mandibles were removed for determination of deer age in the laboratory. Age was estimated by counting cementum growth marks at the interradicular pad under the first molar (Mitchell 1967), and checked by eruption patterns in younger animals. We expressed age in completed years from birth, so an animal aged N is living its N + 1 year of life.

We used covariance analyses (ANCOVA) to explore the differences in grass height between the two years of study regarding the date. To investigate whether independent factors influenced morphological variables, we used a Linear Mixed Model fitted by restricted maximum likelihood (REML: SPSS software version 11, SPSS Inc., Chicago, Illinois, U.S.A.). Age of individuals and its quadratic term were introduced in the analyses to control for the non-linear relationship between age and morphological variables. Other fixed factors were year (2004 and 2005), fence (whether the estate was or was not fenced) and density (above or below 0.3 deer per ha). Estates were introduced in the model as random factors. This model showed the best-fitting values of the information criteria (-2 Restricted Log Likelihood and Akaike's Information Criterion, AIC). We followed a backward stepwise procedure, by first including all fixed terms and their double and triple interactions, thereafter removing non-significant interactions up to the final model which included the fixed factors and significant interactions.

We present predicted values from the final models in figures for all individuals included in the analyses except in the case of body length. For this variable, the interaction between the factors age and year was significant, indicating that the poor year only affected some ages (younger ones). Hence, we present the predicted values for younger males (1-4 years old and still growing; Alarcos 2007).

Results

Food availability differed markedly between 2004 and 2005. The height of the grass in spring 2004 and 2005 was 21.52 cm $\pm$ 1.84 (SE) and 7.00 cm $\pm$ 1.84 (SE), respectively (ANCOVA: $F = 25.33$, $df = 1, 89$, $P < 0.001$), which fitted with the difference in rainfall between the two years.

For body size variables, density had a significant effect on body length and only marginally on heart girth (Table 1). The significant interaction between density and fence for body length (see Table 1) occurred because density only showed an effect on body length in fenced estates, while in non-fenced estates body length was equally low either at high or low density. The effect of drought (year factor) was not significant for heart girth. Body length, however, was strongly affected by drought conditions in year 2005, but the significant interaction with age indicated that the effect was only to reduce body growth of young males (see Table 1 and Fig. 1).

Antler size was affected mainly by fence, i.e. one or more of the variables antler length, burr, thickness or number of tines increased notably under fenced conditions (see Table 1 and Fig. 2). Antler length was more sensitive to density, and when density is high may completely outweigh the effect of fence, whereas all the remaining antler variables were more sensitive to drought conditions (see Table 1). The variables related to antler thickness and points showed reduced values for 2005 under all conditions of density and presence/absence of fence (see Fig. 2), although there was very little reduction in these values in fenced populations under conditions of low density (see Fig. 2) and these interactions were not significant (not shown).

For all morphological variables studied, we found significant differences between open and fenced estates, indicating that the conditions imposed by different management and hunting pressure in these types of estates have a clear impact on the size of stags, even after controlling by age.

The effect of year and other independent factors on antler size was not caused by differences in body size in general, since when we controlled by body length (which was significantly affected by year and other independent factors), antler size was still affected by year, fence and density (Table 2).

Discussion

Our results show that drought conditions negatively affected body and antler size. Body size was more affected in young males, which have not completed body growth (Clutton-Brock et al. 1982, Alarcos

Table 1. Mixed model (REML) results for the influence of independent variables on the different measures of body and antler size in the two years of study. Hunting estates were introduced in models as random factors. Fixed factors were year, fence and density, as well as age and age^2, which were introduced to control for the quadratic relationship with morphology. Only significant interactions were included. Parameter estimates and standard errors are shown for year 2005, fenced estates and high density with respect to their alternatives, when significant.

	df	F	P	Estimate ± SE
Effects on body length				
Intercept	1, 320	2529.060	<0.001	161.11 ± 3.80
Year	1, 328	14.891	<0.001	-20.46 ± 5.30
Fence	1, 20	20.048	<0.001	13.58 ± 2.60
Density	1, 15	5.228	0.037	ns
Fence*Density	1, 15	5.730	0.030	-8.93 ± 3.73
Year*Age	1, 362	9.644	0.002	8.48 ± 2.73
Year*Age^2	1, 367	5.580	0.019	-0.71 ± 0.30
Age	1, 363	55.417	<0.001	6.59 ± 1.86
Age^2	1, 362	28.337	<0.001	-0.46 ± 0.19
Random factor (estates): Variance ± SE = 8.87 ± 4.57, Wald Z = 1.941, P = 0.052				
Effects on heart girth				
Intercept	1, 300	2255.981	<0.001	96.26 ± 2.13
Year	1, 89	1.067	0.304	ns
Fence	1, 20	19.682	<0.001	7.00 ± 1.57
Density	1, 16	3.476	0.080	ns
Age	1, 364	37.963	<0.001	5.87 ± 0.95
Age^2	1, 363	21.800	<0.001	-0.46 ± 0.10
Random factor (estates): Variance ± SE = 6.51 ± 2.91, Wald Z = 2.238, P = 0.025				
Effects on antler length				
Intercept	1, 288	76.308	<0.001	24.57 ± 2.89
Year	1, 14	13.670	0.002	-8.15 ± 2.72
Fence	1, 14	18.661	0.001	6.41 ± 2.37
Density	1, 10	10.184	0.009	ns
Fence*Density	1, 10	7.206	0.023	ns
Fence*Density*Year	3, 16	4.696	0.015	10.44 ± 3.43
Age	1, 370	106.981	<0.001	13.39 ± 1.29
Age^2	1, 369	45.132	<0.001	-0.93 ± 0.13
Random factor (estates): Variance ± SE = 6.20 ± 4.09, Wald Z = 1.514, P = 0.130				
Effects on burr circumference				
Intercept	1, 311	222.291	<0.001	9.26 ± 0.62
Year	1, 35	12.609	0.001	-1.08 ± 0.30
Fence	1, 18	18.442	<0.001	1.78 ± 0.41
Density	1, 15	2.299	0.150	ns
Age	1, 378	75.046	<0.001	2.54 ± 0.29
Age^2	1, 376	23.131	<0.001	-0.15 ± 0.03
Random factor (estates): Variance ± SE = 0.43 ± 0.22, Wald Z = 1.969, P = 0.049				
Effects on antler thickness				
Intercept	1, 290	164.776	<0.001	5.45 ± 0.42
Year	1, 29	10.165	0.003	-0.69 ± 0.22
Fence	1, 16	12.279	0.003	1.02 ± 0.29
Density	1, 13	3.292	0.091	ns
Age	1, 366	66.333	<0.001	1.59 ± 0.19
Age^2	1, 364	21.823	<0.001	-0.09 ± 0.02
Random factor (estates): Variance ± SE = 0.22 ± 0.11, Wald Z = 1.942, P = 0.052				
Effects on number of antler tines				
Intercept	1, 321	20.678	<0.001	2.86 ± 0.67
Year	1, 42	16.469	<0.001	-1.21 ± 0.29
Fence	1, 18	23.783	<0.001	2.06 ± 0.42
Density	1, 15	1.100	0.311	ns
Age	1, 388	84.048	<0.001	2.96 ± 0.32
Age^2	1, 387	45.167	<0.001	-0.23 ± 0.03
Random factor (estates): Variance ± SE = 0.40 ± 0.23, Wald Z = 1.770, P = 0.077				

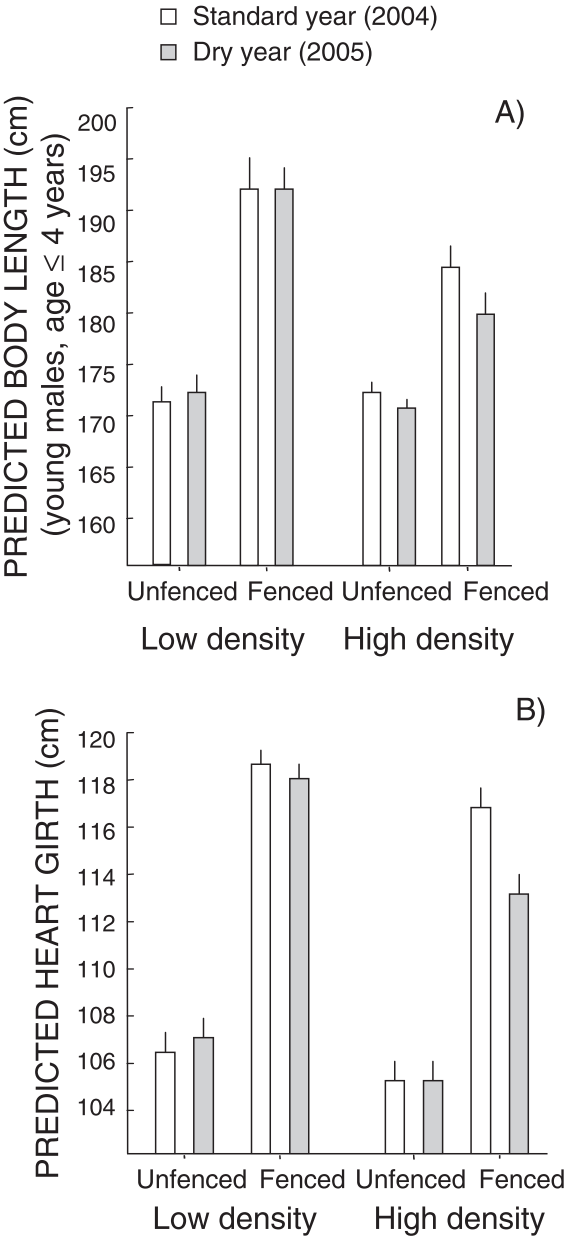

Figure 1. Body size of red deer males (predicted values from REML Mixed Models) as a function of independent factors in the two years of study: A) body length of young males (1 - 4 years old) as a function of density, presence or absence of perimeter fence in the estate, and year; B) predicted heart girth of all males as a function of density, presence or absence of perimeter fence, and year.

2007), but antlers were affected in individuals of all ages. Also, the effects on antlers remained after controlling by body size, indicating lower allocation of resources to antlers relative to body during adverse environmental conditions (Mysterud et al. 2005) like a dry year in Mediterranean habitats.

Male body size in red deer (Loison & Langvatn 1998) and other cervid species (Leberg & Smith 1993, Ferguson et al. 2000) mostly depends on resource availability, which is also greatly influenced by population density (Bonenfant et al. 2002, Weladji & Holand 2003). The phenology and key factors that limit deer performance in northern and southern regions of Europe are markedly different. While low winter temperatures determine the limiting season in many northern areas of red deer distribution (Klein 1985), high temperatures and absence of rainfall during the summer in Mediterranean habitats reduce vegetation productivity and resource availability for deer, thus making summer the limiting season for herbivores in Mediterranean areas (Carranza et al. 1990, Carranza 1995, Rodríguez-Berrocal 1993, Bugalho & Milne 2003).

Our data show that larger body and antler size are produced in fenced rather than open areas. The main difference between the two types of estates is that in fenced areas managers can maintain sex ratio equilibrium and age structure of the population, including mature stags, whereas in open areas hunting pressure from neighbouring estates affects the whole population, leading to strongly female biased sex ratios and age structures which are heavily skewed towards younger males (Carranza 1999; see also Langvatn & Loison 1999). Contrasting sex ratios and population structure between fenced and open estates are likely to affect male growth and antler development (Singer & Zeingenfuss 2002, Yoccoz et al. 2002, Mysterud et al. 2003), although this issue deserves further research.

Our data show that in open estates the effects of density are not apparent, probably because deer can move freely according to the availability of resources in each area at different times of the year, so the observed differences in density may not reflect differences in competitive conditions. In fenced estates, on the contrary, high density related to marked decreases in body and antler sizes when environmental conditions deteriorated, suggesting that these estates were maintaining deer densities according to an optimum level for average years but probably too high for drier years.

Elevated densities under drier conditions have implications not only for the economy of hunting exploitation but also for the conservation of natural vegetation. Red deer management in fenced estates is normally oriented towards the improvement of trophies (antler size), therefore density should be reduced to maintain performance under conditions

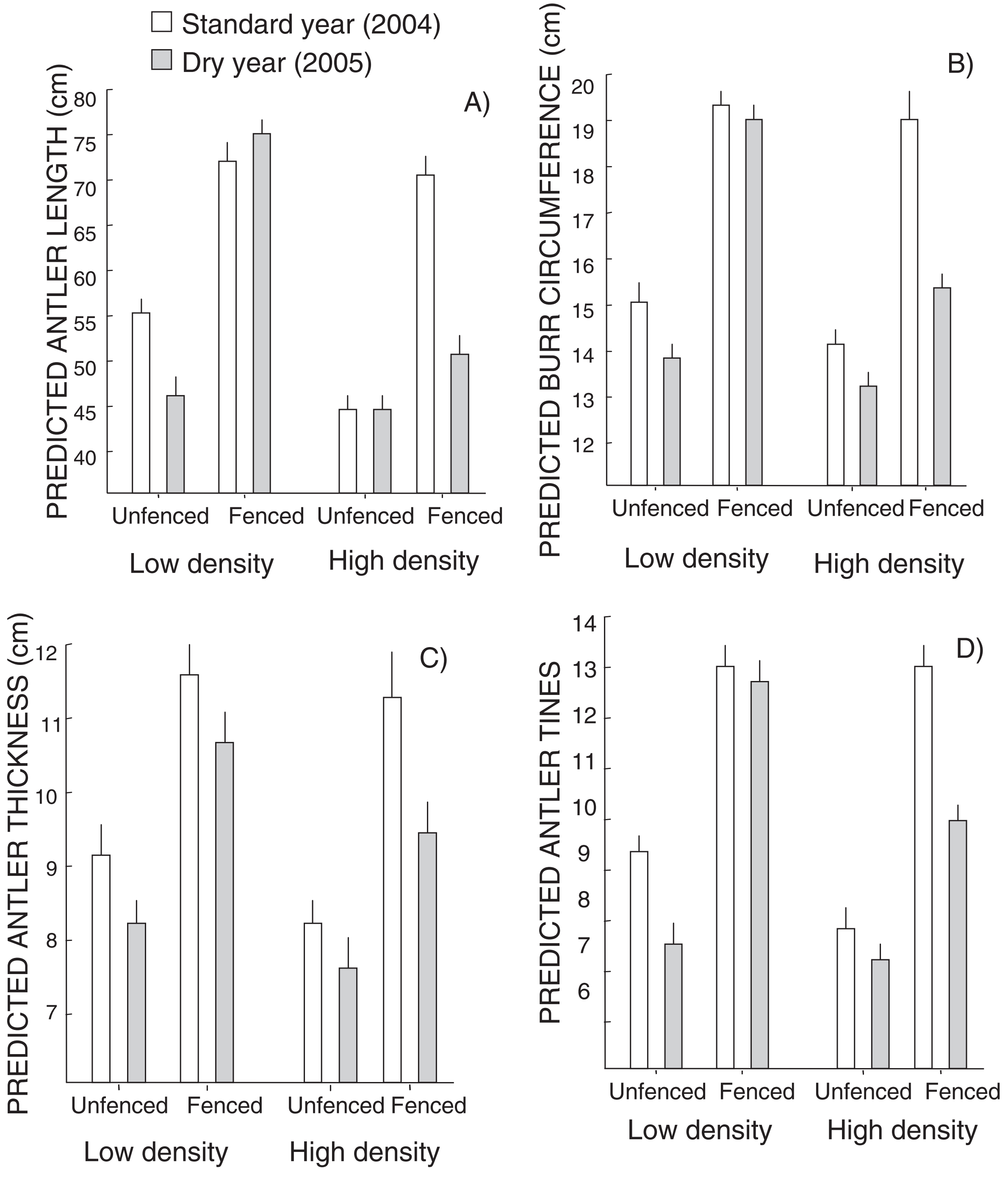

Figure 2. Antler size of red deer males (predicted values from REML Mixed Models) as a function of density and the presence of perimeter fence in the estate for the two years of study; A) antler length, B) burr circumference, C) antler thickness, and D) number of antler tines (see Table 1 for model results).

of low rainfall. However, our data also show that drought conditions affected body growth in young males. Growth during the first year of life has been demonstrated to have a strong influence on the future development of antlers in red deer (Clutton-Brock et al. 1982, Schmidt et al. 2001). Thus, a single year with poor conditions might have lifetime consequences for a complete cohort of stags (Albon

Table 2. Mixed model (REML) results for the influence of independent variables on the four measures of antler size in the two years of study, controlled by body size. Hunting estates were introduced in models as random factors. Fixed factors were year, fence and density, the covariates were body length as well as age and age^2, which were introduced to control for the quadratic relationship with morphology. Only significant interactions were included. Parameter estimates and standard errors are shown for year 2005, fenced estates and high density with respect to their alternatives, when significant.

	df	F	P	Estimate ± SE
Effects on antler length				
Intercept	1, 329	17.646	<0.001	-30.57 ± 7.15
Year	1, 12	10.751	0.006	ns
Fence	1, 18	9.518	0.006	4.75 ± 2.09
Density	1, 9	7.390	0.024	ns
Fence*Density	1, 9	3.937	0.079	ns
Fence*Density*Year	3, 14	3.819	0.035	ns
Body length	1, 324	70.187	<0.001	0.36 ± 0.04
Age	1, 333	41.431	<0.001	8.59 ± 1.33
Age^2	1, 331	16.225	<0.001	-0.55 ± 0.13
Random factor (estates): Variance ± SE = 2.53 ± 2.55, Wald Z = 0.989, P = 0.322				
Effects on burr circumference				
Intercept	1, 307	6.270	0.013	-4.28 ± 1.70
Year	1, 22	17.084	<0.001	-0.95 ± 0.22
Fence	1, 26	11.256	0.002	1.06 ± 0.31
Density	1, 14	0.839	0.375	ns
Body length	1, 299	75.174	<0.001	0.08 ± 0.01
Age	1, 342	22.636	<0.001	1.46 ± 0.30
Age^2	1, 339	4.370	0.037	-0.06 ± 0.03
Random factor (estates): Variance ± SE = 0.09 ± 0.09, Wald Z = 1.028, P = 0.304				
Effects on antler thickness				
Intercept	1, 329	4.476	0.035	-2.43 ± 1.20
Year	1, 28	10.384	0.003	-0.63 ± 0.19
Fence	1, 21	5.069	0.035	0.60 ± 0.26
Density	1, 14	1.361	0.262	ns
Body length	1, 328	49.598	<0.001	0.05 ± 0.01
Age	1, 331	23.214	<0.001	1.02 ± 0.21
Age^2	1, 327	5.989	0.015	-0.05 ± 0.02
Random factor (estates): Variance ± SE = 0.13 ± 0.07, Wald Z = 1.697, P = 0.090				
Effects on number of antler tines				
Intercept	1, 335	20.184	<0.001	-8.92 ± 1.88
Year	1, 26	16.737	<0.001	-0.94 ± 0.25
Fence	1, 33	13.416	0.001	1.53 ± 0.37
Density	1, 15	0.024	0.879	ns
Body length	1, 325	42.792	<0.001	0.07 ± 0.01
Age	1, 351	40.677	<0.001	2.20 ± 0.34
Age^2	1, 349	24.192	<0.001	-0.17 ± 0.03
Random factor (estates): Variance ± SE = 0.15 ± 0.13, Wald Z = 1.168, P = 0.243				

et al. 1987, Langvatn et al. 1996, Post et al. 1997, Rose et al. 1998, Kruuk et al. 1999, Lindström 1999, Forchhammer et al. 2001).

Our results indicate a likely effect of climate change on red deer populations in the Iberian Peninsula through potential impacts on natural vegetation, and we recommend adapting population composition and management to the likely new scenario of reduced productivity of natural vegetation. Thus, the density should match a new optimum according to the expected productivity. On the other hand, our results also show that populations in fenced estates are more sensitive to environmental changes. Stags in fenced areas show larger body and antler size but they also suffer more dramatic reductions under worsening conditions. This suggests that fenced areas will experience higher impacts from climate change under current management practices and we therefore recommend that the sustainability of this type of management should be reviewed.

Acknowledgements - Our study was conducted through a collaborative agreement between the University of Extremadura and 'Consejería de Medio Ambiente' of 'Junta de Andalucía'. We thank R. Arenas and the staff at 'Consejería de Medio Ambiente' in Córdoba, as well as L. Arias de Reyna of the University of Córdoba, for their support at different stages of our study. We are also grateful to the owners and wardens of the estates studied and to the hunters. P. Montero, S. Alarcos, J.M. Seoane, M.J. Taboada, I. Parrillo, O. Linares, C. Sánchez-Prieto, L. Castillo, M. Núñez and M.J. Brito helped in fieldwork. A. Mysterud made helpful comments to previous versions of the manuscript. This work complies with current Spanish laws. Additional financial support came from Spanish Ministry of Education and Science, projects CGL2004-05993 and CGL2007-63594.

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