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Reduced horn size in two wild trophy-hunted species of Caprinae

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Factors affecting horn size in wild Caprinae are of biological and socio-economic interest because several species are selectively harvested on the basis of this heritable character. We analysed temporal trends in horn size in two mountain ungulates from south-eastern Spain, the Iberian wild goat *Capra pyrenaica* and the aoudad *Ammotragus lervia*. Trophy harvest is the main way in which these two species are exploited, although 'poor-quality' aoudads are also selectively removed. In recent years, both populations have suffered drastic decreases in number due to outbreaks of sarcoptic mange that led to the suspension of hunting for several years. Horn length in harvested male wild goats and aoudads declined during our study period. Over an 18-year period, the mean age of male goats shot as trophies rose by four years, while the age of trophy-harvested aoudads decreased by around six months over a 9-year period. Age and environmental conditions during the first few years of life explained 20% of variance in horn size in Iberian wild goat and 53% in aoudad. Population density early in life explained much of the reduction in goat horn size over time. Nevertheless, the major fall in population densities after the sarcoptic mange outbreaks did not lead to a recovery in horn size in either species. We suggest that the selective removal of large-horned animals may contribute to a decline in horn size. Other factors that may also explain the observed pattern include changes in interspecific competition, long-lasting maternal effects and reduced carrying capacity due to overgrazing during high density periods. Unfortunately, our data sets did not allow us to account for the possible effects of these factors.

Key words: *Ammotragus lervia*, aoudad, *Capra pyrenaica*, horn size, Iberian wild goat, game management, population density, sarcoptidosis, trophy harvest

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Horn size in mountain ungulates has important and diverse implications for conservation biology and evolution (Coltman et al. 2002, Singer & Zeigenfuss 2002). Horn size signals individual quality (von Hardenberg et al. 2007) and reflects the environmental conditions experienced both during early development (Côté et al. 1998, Toïgo et al. 1999) and throughout an animal's entire life, especially in species where substantial horn growth continues throughout life. Horn growth is sensitive to changes in population density (Jorgenson et al. 1998), weather (Pérez-Barbería et al. 1996, Giacometti et al. 2002) and resource availability (Festa-Bianchet et al. 2004, Festa-Bianchet & Côté 2008). Males with greater horn growth obtain high-quality resources, are more resistant to parasites (Luzón et al. 2008) and have better sperm quality (Santiago-Moreno et al. 2007).

Artificial selective pressures such as trophy hunting may lead to a reduction in horn size in wild ungulates (Coltman et al. 2003, Garel et al. 2007, Bonenfant et al. 2009b) by removing individuals with large horns. Size-selective harvests usually center on males (Fenberg & Roy 2008). Given that horn and antler size are heritable and genetically correlated with fitness-related traits in both sexes (Kruuk et al. 2002, Coltman et al. 2005), selective hunting may lead to undesirable evolutionary consequences such as reduced body and horn size (Coltman et al. 2003). Clear evidence exists of the demographic consequences and phenotypic evolution caused by the selective harvesting practiced by fisheries (Law 2000, Hutchings & Fraser 2008). Yet, few studies have examined the potential selective effects of recreational hunting on wild mammals (Garel et al. 2007, Festa-Bianchet & Lee 2009). The potential selective effects of trophy hunting may undermine the economic and ecological value of hunted populations, although it is difficult to determine whether changes are an evolutionary response or a consequence of phenotypic plasticity (Fenberg & Roy 2008).

The trophy harvesting of Caprinae is economically important (Doris 2002, Harris & Pletscher 2002). In Europe, trophy hunting is a well-established tradition. In Spanish game reserves, hunting fees increase with the 'score' of the harvested animal, which depends mainly on horn size, horn symmetry and the animal's age. Since revenues from trophy hunting increase with the size of the horns of adult males, the management of

'trophy' species is focused on the production of large-horned males.

The endemic Iberian wild goat *Capra pyrenaica* and the exotic aoudad *Ammotragus lervia* are two of the most popular big game species in Spain. Given the lack of opportunities for hunting aoudad within its natural range, and because it develops larger horns in southeast Spain than in northern Africa, the demand to hunt this species in Spain is increasing. For example, in year 2000 a draw for 19 aoudad permits attracted > 3000 applications, mainly from international hunters (Serrano et al. 2002).

We used measurements of harvested males from both species to explore how factors such as population density, environmental conditions and long-term intensive trophy management (11 years for aoudads and 18 years for Iberian wild goats) have affected horn size and the mean age of harvested males. We examined data from two isolated populations in southeast Spain: Iberian wild goats from the Sierras de Cazorla, Segura y Las Villas Natural Park and aoudads from the Sierra Espuña Regional Park. We tested three hypotheses. First, for both species we expected a decrease in horn size with increasing population density (Jorgenson et al. 1998) and with the selective harvesting of large-horned males (Coltman et al. 2003). For aoudads, we also expected a positive effect of the removal of individuals of poor phenotypic quality on horn size of trophy-harvested animals. Second, if horn growth rates decrease over time, the age of males harvested during our study period should increase, as slow-growing males will require more time to develop into desirable trophies (Garel et al. 2007). Third, since food availability depends on temperature and rainfall, we expected a decrease in horn length of both species for individuals that grew during drought years.

Material and methods

Study area

The Sierras de Cazorla, Segura y Las Villas Natural Park (hereafter Cazorla) (37°43'-38°31'N, 2°29'-2°55'W; Fig. 1) covers over 2,143 km² of which > 50% is above 1,000 m a.s.l. with peaks of > 1,700 m a.s.l. The substrate is calcareous and the main vegetation consists of holm oak *Quercus rotundifolia* with reforested areas of European black pine *Pinus nigra*, maritime pine *P. pinaster* and Aleppo

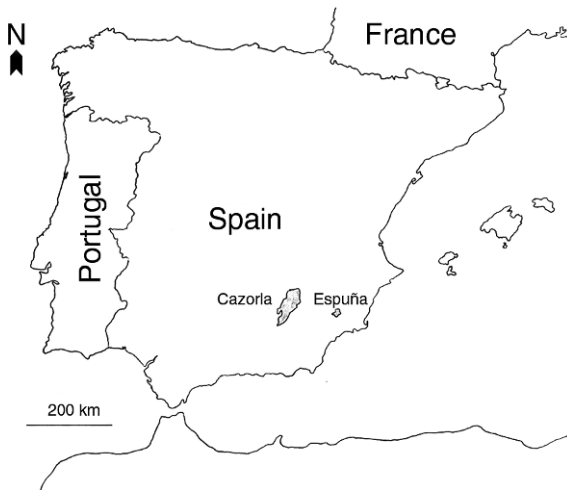


Figure 1. Our study areas in the southeast Iberian Peninsula. Cazorla: Sierras de Cazorla, Segura y Las Villas Natural Park and Espuña: Sierra Espuña Regional Park.

pine *P. halepensis*. Cazorla's population of wild goats peaked at nearly 10,000 in 1986 but was then seriously affected in 1987 by an outbreak of sarcoptidosis. Four years later, only a few hundred animals remained (Fandos 1991). Other ungulates in our study area include fallow deer *Dama dama*, red deer *Cervus elaphus*, European mouflon *Ovis aries* and wild boar *Sus scrofa*. The roe deer *Capreolus capreolus* became extinct in Cazorla in 1957. There are no large predators, given that the brown bear *Ursus arctos* disappeared during the 18th century, and the wolf *Canis lupus* and the Iberian lynx *Lynx pardinus* became extinct in the first half of the 20th century. The extirpation of predators presumably allowed ungulate populations to grow during subsequent decades. Wild ungulates compete with domestic sheep and goats (over 9,200 animals in 1983) and, to a lesser extent, cattle (Alados & Escós 1996). Wild goats and other ungulates are harvested within the 900 km² 'Coto Nacional de Caza' (currently an Andalusian Game Reserve) which was created in 1960 (Law 17/1960).

The Sierra Espuña Regional Park (hereafter Espuña) (37°48'-37°57'N, 1°22'-1°37'W) covers about 178 km² and has peaks > 1,300 m a.s.l. The predominant vegetation consists of reforested Aleppo pine woods and shrubs. The aoudad was introduced in 1970 by the former Spanish Fish, Game and National Park's Service for recreational hunting (Cassinello 1998). The founder population consisted of 11 males and 24 females brought from several European and African zoos. The area where

the aoudads were released measures 142 km² and was declared a National Game Reserve in 1973 (Law 2/1973). This population was affected by a sarcoptic mange outbreak in 1991 and within four years had fallen by > 80% (González-Candela et al. 2004). Wild boars are also present and hunted in this game reserve.

Data collection

For each harvested animal, a gamekeeper confirmed the sex (aoudad females have large horns) and estimated the age by counting the horn segments as Fandos (1991) did for Iberian wild goats and Gray & Simpson (1985) did for aoudads. The gamekeeper then used a tape to measure total horn length as instructed by the Junta Nacional de Homologación de Trofeos de Caza (an institution created in 1962 by the Ministry of Agriculture). At the beginning of each hunting season, each gamekeeper received a new tape measure and participated in a seminar in which the measurement protocol was reviewed. Gamekeepers only measured each animal once and, therefore, we cannot estimate the error in horn measurements. We estimated a repeatability of horn length of > 0.9 and a measurement error of < 3% by measuring a sample of 20 male wild goats twice from a neighbouring population. According to Harper (1994), this repeatability is excellent. Inter-observer repeatability and its associated error were not estimated, but we assume that it was negligible in light of work in related species (von Harderberg et al. 2007).

Wild goats

Over 21 years (from 1968 to 1986 and from 2001 to 2003, i.e. before and after the mange outbreak) 1,005 male wild goats, aged 8-13 years, were shot during trophy hunts (the only type of harvesting permitted) in Cazorla. We also know the number of male goats harvested each year and have an estimate of population density for the period 1968-1986. During our entire study period, monthly precipitation (mm) and temperatures (°C) were recorded at a meteorological station inside the study area.

Aoudad

In Espuña, 853 aoudads (568 females and 285 males) were harvested during 1980-1999. Only 230 males, aged 4-11 years, were taken as trophies. The other animals were females shot in order to reduce density and males killed because of undesirable horn size or shape. Monthly precipitation (mm) and

temperatures (°C) were recorded at a meteorological station 5 km from the study area.

Data analysis

Temporal trend in horn size

To investigate potential changes in horn size while accounting for the effects of age, environmental conditions, population density and year of birth (cohort effect), we fitted several models in which horn length was explained by the following variables:

1) age; horns of wild goats grow throughout their lifetime, although > 80% of asymptotic horn size is achieved during the first five years, following a sigmoid model (Álvarez 1990). Our data set included only animals > 8 years old and, according to Granados et al. (2001), after this age there is a linear relationship between horn length and age. A linear model explained more variability ($R^2=0.044$, $F_{1, 1003}=46.56$, $P < 0.01$) than exponential, polynomial or sigmoid models (results not shown). According to Gray & Simpson (1985), horn size in male aoudads reaches 81% of its asymptote by four years of age. Most aoudads in our data set were > 4 years old and a linear fit between age and horn length was appropriate ($R^2=0.52$, $F_{1, 228}=243.83$, $P < 0.01$) for correcting for age. Thus, in all statistical models for both species we included age as a covariate;

2) environmental conditions; we accounted for environmental variation with the integrated Gaussean aridity index: $GI = \sum \text{Mean precipitation} - (2 \times \text{mean temperature})$ (Gaussean & Bagnouls 1953). This index is positively correlated with primary productivity in Mediterranean environments, since negative values correspond with dry periods (Peñuelas et al. 2007). GI was estimated in spring, the peak growth period for vegetation (Palacio & Montserrat-Martí 2007) and horns in both study species (Gray & Simpson 1985, Fandos 1991). Because the relationship between horn growth and environmental conditions in these species are poorly known, we tested models that included the integrated Gaussean index during the main period of horn growth, i.e. the first five years of life for wild goats and the first four years for aoudads (Early GI), as well as during an animal's entire

life (Lifetime GI). In both species, most horn growth occurs during the first few years of life and no compensatory growth has been reported. Therefore, environmental conditions early in life or during the entire lifespan should affect horn size at harvest;

3) population density; for wild goats, density estimates were based on line transects (Burnham et al. 1980). Seven transects, each 14 km in length, were sampled two or three times a month by two observers. Estimates of annual and seasonal densities were obtained by pooling observations from surveys carried out during the corresponding period. Data were analysed with Linetran and Transect programs and the coefficient of variation associated with the estimated density ranged from 27.6% in fall to 35.2% in spring (Fandos 1991). Following the same rationale, we included the mean population density experienced during the main period of horn growth (Early Density) and over the lifetime (Lifetime Density) in statistical models. During our study period, aoudad densities were estimated using different methods, and for several years no estimates were available, and, hence, we could not include density in models for this species. No correction for date of harvesting was required, as all animals were harvested in autumn-winter when horn growth in both species is negligible (Gray & Simpson 1985, Toledano-Díaz et al. 2007).

Finally, since the linear regression between year of harvest and horn length showed a clear residual pattern (results not shown) due to a non-linear relationship (Fig. 2), we used generalised additive models (GAMs with a Gaussian error structure and the identity link function) with year of harvest as the smoothed variable (Wood 2006, Zuur et al. 2007) to analyse changes in horn length over time before the mange outbreak (from 1975 to 1986 for wild goats and from 1980 to 1992 for aoudads). Because our main interest was the temporal trend after accounting for the effects of age, environmental conditions and population density, we included the factor year in all models as a covariate following Garcia-Berthou (2001) and Freckleton (2002).

Age of harvested animals

We used linear models to explore temporal trends in the mean age of wild goats and aoudads harvested as

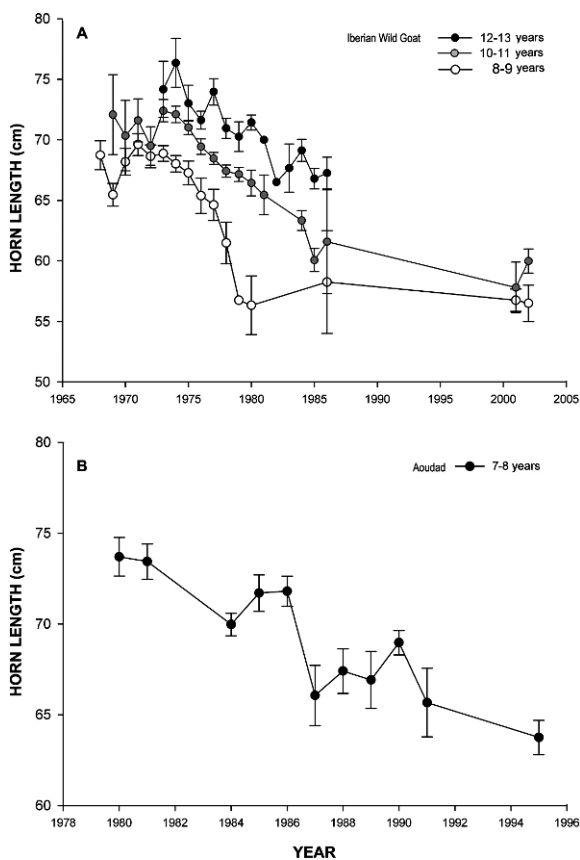


Figure 2. Horn length (mean \pm SE) of trophy-harvested male Iberian wild goats (A) and aoudads 7-8 years old (B) over time.

trophies, with year of harvest as a fixed factor. We only considered the period before the mange outbreaks, since hunting regulations changed after the population crashed and no permits were awarded in the years immediately after the die-offs.

Management strategies and horn size

The selective removal of animals of low phenotypic quality may improve trophy quality by (i) limiting reproduction of undesired phenotypes and (ii) decreasing intraspecific competition.

We explored whether the number of aoudads harvested in order to improve trophy quality affected the horn size of males harvested as trophies. We fitted a set of linear mixed models in which horn length was explained by the average number of females and 'undesirable' males shot each year, first during years when aoudads were aged 1-4 years ('females + selective males when young') then over their entire lifespan ('females + selective males'). For this analysis, the influence of both age and early

environmental conditions on aoudad horn length (the main factors selected from the 'temporal trend' analysis) was corrected by including both variables as covariates in all models. Year of harvest was included as a random factor to avoid pseudoreplication (Zuur et al. 2009).

For all analyses, model selection was based on Akaike's Information Criterion corrected for small sample sizes (AIC_c ; Anderson et al. 2001, Burnham & Anderson 2002, Johnson & Omland 2004). When the ΔAIC_c was < 2 units, we chose the model with fewest parameters. We also estimated the Akaike weight (w_i), which is the probability that a model is the best among those compared (Burnham & Anderson 2002). Once the best model was selected, we checked for normality and the absence of residual pattern in data variation. All statistical analyses were performed using R version 2.9.2 (R Development Core Team 2010).

Results

Temporal trends in horn size

For wild goats, uncorrected horn length decreased during the study period (see Fig. 2). For example, the average horn length of animals aged 10-11 years in 1985 was 15.4% less than in 1975. This decline apparently persisted during the mange outbreak (1987-1988) when hunting was suspended.

For aoudads, horn length declined gradually over time. For example, in animals aged 7-8 years old (see Fig. 2), the most common age in our data set, horns decreased in length by 10.9% over 11 years (from 73.7 ± 1.06 cm in 1980 to 65.7 ± 1.89 cm in 1991). As in wild goats, the decline continued for eight years after the mange outbreak in 1991.

Model selection showed that horn-size variability in male Iberian wild goats was best explained by age, the year of harvest and population density during early life, accounting for 33.5% of variability (Table 1). The next best model also included environmental conditions during early life (see Table 1) and had substantial support ($\Delta AIC = 0.94$), indicating that factors experienced in the first five years of life influence adult horn size. Considering only the two best models, population density during early life (corrected for age and harvest year) explained 21.5% of variability in horn length, whereas year of harvest (corrected for age and population density) and environmental conditions during the first five years of age (Early GI) explained 8% and

Table 1. Model selection for horn-size variability in 362 Iberian wild goats. This analysis includes only animals harvested in years for which information on population and local weather conditions was available. K = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c = difference of AIC with respect to the best model, w_i = Akaike weight, M_0 = null model only with the constant term. Only models with substantial support ($\Delta AIC_c < 10$) are shown, including the first model above this cut-off and the null model. The best models are indicated in italics.

Model	K	AIC_c	ΔAIC_c	w_i
<i>Age + Year shot + Early Density</i>	12	2053.90	0.00	0.42
<i>Age + Year shot + Early Density + Early GI</i>	13	2054.85	0.94	0.26
Age + Year shot + Early Density + Lifetime GI	13	2056.01	2.10	0.15
Age + Year shot + Lifetime GI	12	2057.32	3.42	0.08
Age + Year shot + Lifetime Density	12	2058.75	4.85	0.04
Age + Year shot + Lifetime Density + Early GI	13	2059.22	5.31	0.03
Age + Year shot + Early GI	12	2060.34	6.44	< 0.01
Age + Year shot + Lifetime Density + Lifetime GI	13	2060.87	6.96	< 0.01
M_0	2	2196.27	142.37	< 0.01

0.9%, respectively, of observed variability in horn length (Fig. 3). Thus, in addition to a progressive decrease in horn size over time (see Fig. 3), wild goats had shorter horns if they grew under high

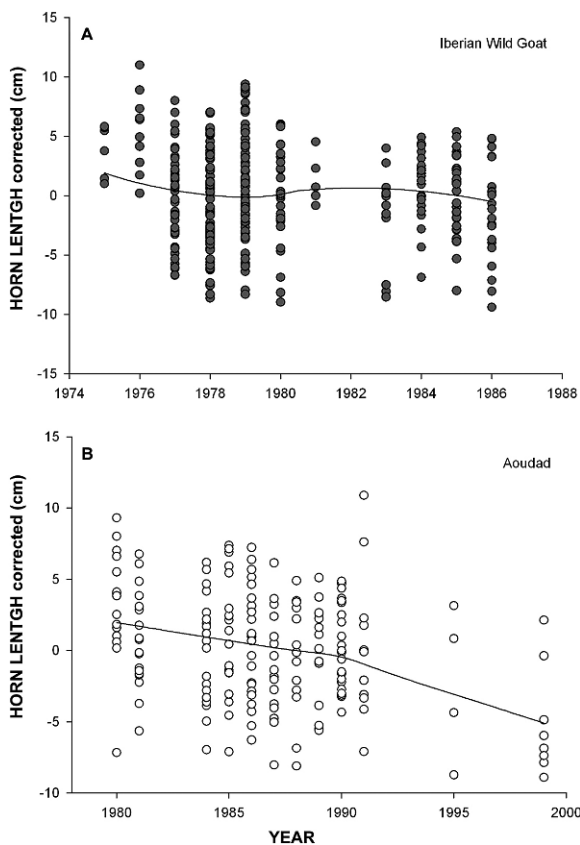


Figure 3. Residual horn length of trophy-harvested male Iberian wild goats (A) and aoudads (B) over time fitted by a general additive model. Horn length measurements were corrected for age, population density (only for wild goats), and the Gaussien index for the spring experienced during the main period of horn growth (five years for wild goats and four for aoudads).

densities (slope = -6.88, SE = 0.62) or during droughts (slope = 0.05, SE = 0.03).

Horn length in aoudads was affected by age, year of harvesting and environment during the first four years of life (Table 2), which accounted for 56.2% of variability. Year of harvest explained 7.2% of variability (see Fig. 3), while 4.5% was explained by environmental conditions. Horns of aoudads that grew during rainy and cool conditions (positive GI values) were longer (slope = 0.16, SE = 0.04) than those that grew during drought years. The cohort effect was negligible in both species, since all models incorporating this factor were > 20 AIC units from the best models.

Age at harvest

In bovids, a trophy's 'score' is based on measurements of horn length, basal perimeter and maximum separation. If the animal is > 10 years old, an extra point per year is added.

The mean age of goats harvested as trophies increased by four years (slope = 0.24, SE = 0.008; Fig. 4) over 18 years of trophy management (AIC of

Table 2. Model selection for horn-size variability in 230 male aoudads. This analysis includes only animals harvested in years for which information on population and local weather conditions was available. K = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c = difference of AIC with respect to the best model, w_i = Akaike weight, M_0 = null model only with the constant term. Only models with substantial support ($\Delta AIC_c < 10$) are shown, including the first model above this cut-off and the null model. The best model is indicated in italics.

Model	K	AIC_c	ΔAIC_c	w_i
<i>Age + Year shot + Early GI</i>	5	1305.72	0	0.73
Age + Year shot + Lifetime GI	5	1307.79	2.07	0.26
M_0	2	1490.54	184.61	< 0.01

model including year = 2876.52, explaining 46.7% of observed variability in age; AIC of constant model = 3488.86, $\Delta AIC = 612.34$). On the other hand, the age of trophy-harvested aoudads decreased by about six months (slope = -0.131, SE = 0.027; see Fig. 4) over nine years (AIC including year = 703.85, explaining 9.9% of observed variability in age; AIC of constant model = 723.95, $\Delta AIC = 20.1$).

Effects of harvest strategies

For aoudad males, model selection suggested that harvest of non-trophy animals had no effect on the horn size of males harvested as trophies (Table 3).

Discussion

As expected, population density reduced horn growth in Iberian wild goats, suggesting that

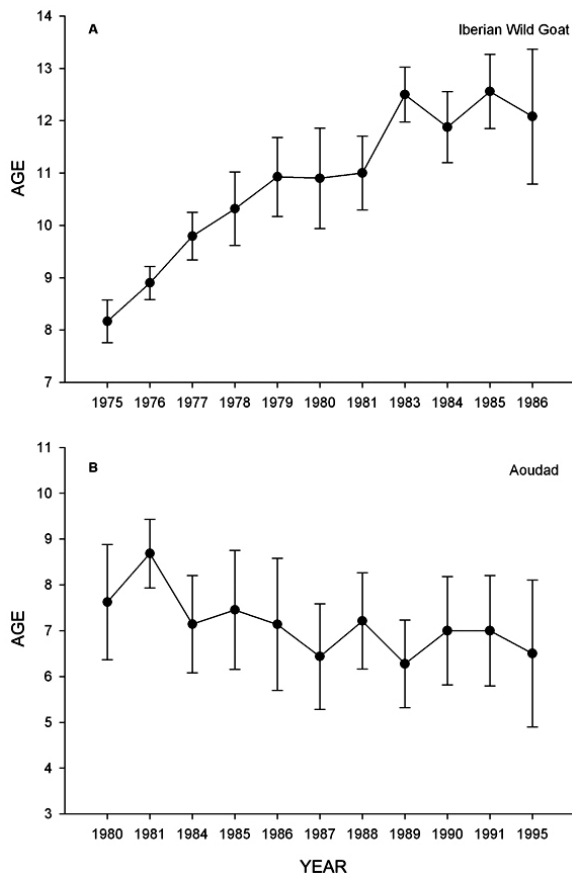


Figure 4. Age (mean \pm SE) of male Iberian wild goats (A) and aoudads (B) harvested as trophies in Cazorla and Espuña, respectively, before the outbreaks of sarcoptic mange.

Table 3. Model selection of the effects of the number and kind of aoudads harvested for trophy improvement in Espuña, Spain, on the horn length of males harvested as trophies. This analysis includes only animals harvested in years for which information on local weather conditions was available. 'Selective females when young' and 'Selective males when young' are the average number of females or 'undesirable' males harvested during the first four years of the life of males harvested as trophies. 'Total females' and 'Total selective males' are the average number of females and 'undesirable' males harvested per year over the lifetime of each trophy-harvested male. All models include the age of animals and the environmental conditions experienced during the first four years of life (Early GI), in addition to year of harvest as a random factor. Only models with substantial support ($\Delta AIC_c < 10$) are shown, including the first model above this cut-off and the null model. The best model is indicated in italics.

Model	K	AIC _c	ΔAIC_c	w_i
<i>M_o</i>	4	697.08	0.00	0.97
Total males	6	705.48	8.40	0.01
Selective males when young	6	706.27	9.19	< 0.01
Selective females when young	6	709.64	12.56	< 0.01
Total females	6	709.72	12.64	< 0.01
Total females + Total selective males	7	711.84	14.75	< 0.01
Total females + Selective males when young	7	713.18	16.09	< 0.01

management strategies that permit high goat densities are likely to lead to a decrease in trophy production. Outbreaks of disease led to serious decreases in density in both populations. Nevertheless, horns of animals harvested after the re-opening of trophy hunting showed no sign of increase (see Fig. 2), despite over a decade of low density and no persisting symptoms of disease.

Changes in the density of other wild and domestic ungulates in Cazorla could explain the observed trend in goat horn size. Crespo-Guerrero (2003) reported increases in numbers of red deer (from 400 to 4,800), fallow deer (from 120 to 1,700) and mouflon (from 140 to 400) in Cazorla between 1963 and 1984. These increases could increase interspecific competition and reduce horn growth, but we could not compare Iberian goat horn size with the density of possible competitors, due to a lack of census data for these other species in most years.

In addition to affecting the demography of large herbivores (Bonenfant et al. 2009a), population density can affect the growth of females and the amount of maternal care they devote to offspring (Festa-Bianchet & Jorgenson 1998). A time-lagged maternal effect may have reduced the growth of males born during years of high density, thereby

delaying the increase in body and horn size expected after population densities declined.

An additional possibility that we cannot exclude is that overgrazing during the high density phase may have permanently lowered habitat carrying capacity, possibly through erosion or invasion by grazing-tolerant plants. If overgrazed, forage plants take over a decade to recover and the resulting lag in resource limitation could have hampered horn growth in males.

The results of our analyses of two long-term data sets of trophy-harvested mountain ungulates are, however, also compatible with the hypothesis that the removal of large-horned males by hunters led to a lower rate of horn growth, even after accounting for the effects of environment and population density on horn phenotype. The suspension of hunting for 13 years during a mange epizootic failed to reestablish greater horn growth rates, supporting claims that artificially-selected changes in phenotype may not be quickly reversed by natural selection once the artificial pressures cease (Walsh et al. 2006).

For male goats shot as trophies, horn length decreased over time while average age at harvest increased substantially. If most hunters refuse to shoot males with horns below a given size threshold, this increase in age suggests that males took longer to reach 'desirable trophy' size. Garel et al. (2007) found similar results in mouflon. Male goats developed into acceptable trophies by 8-9 years of age in the late 1960s, but apparently required an extra 3-4 years to reach a horn size that would interest a hunter 15 years later. An increase in the average age of harvested males should reduce selection against large horns because males shot at an advanced age are likely to have had some reproductive success. In the Ram Mountain population of bighorn sheep, trophy hunting had an evolutionary effect, in part because rapidly-growing males were shot at 4-5 years, before they could obtain the high reproductive success associated with large horns in older rams (Coltman et al. 2002, 2003).

We suggest that the increase in age of harvested wild goats was due to the scarcity of large young males as a result of the combined effects of higher density and intense artificial selection, rather than any planned strategy aiming to increase the reproductive success of trophy animals. A key concern here is that, even though the average age of harvested males increased, the age at which individual males were harvested was probably

related to their individual rate of growth, since fast-growing males are likely shot at a younger age than slow-growing males (Festa-Bianchet et al. 2004).

The age-adjusted length of aoudad horns also decreased over time, possibly because of the selective effect of trophy hunting. However, contrary to results for wild goats, there was a slight decrease in the average age of males harvested as trophies. This change in age may indicate high hunting pressure; a decrease in the age of harvested males might be expected if, instead of only harvesting males above a threshold size, hunters shoot the largest-horned male they encounter. Over time, as old males are removed by hunting, the 'largest' males are inevitably younger. Clearly, more information is required about what affects a hunter's decision to harvest a male of the two study species.

The relationships between horn size and age-specific mating success must be elucidated to properly assess the potential selective impact of trophy hunting (Festa-Bianchet & Lee 2009). Its evolutionary impact is likely to be highest wherever the phenotypic characteristics selected by hunters confer high reproductive success on males. No data exist on individual reproductive success in either study species, although similarities in sexual dimorphism, age-specific horn growth patterns and mating systems suggest that horn size is likely to play a similar role in wild goats and aoudads as in bighorn sheep rams, where a negative impact of intense trophy hunting on the evolution of horn size has been reported (Coltman et al. 2003). Our study, however, was not able to establish whether the observed trend in horn length is due to an evolutionary response to trophy harvesting, or whether it is partly affected by environmental variables other than those we controlled for. Selection on a heritable trait does not necessarily lead to phenotypic change (Kruuk et al. 2002, Teplitsky et al. 2008, Ozygul et al. 2009).

We suggest that harvesting programs that attempt to mimic natural patterns of mortality, including an emphasis on culling juveniles and senescent individuals and the avoidance of phenotype-based harvesting, would have fewer undesirable demographic, phenotypic or genetic consequences than trophy hunting. This harvesting strategy may be particularly desirable if natural mortality is altered by the absence of natural predators (Bischof et al. 2008), as is the case for

most Iberian wild goat or aoudad populations in Spain. A combination of compensatory culling and trophy hunting may make trophy hunting sustainable (Mysterud & Bischof 2010). For our study species and other ungulates managed for trophy hunting, a better understanding of the likely impacts of selective hunting requires data on individual reproductive success of males in terms of age, horn size and the age structure of competing males.

Conclusion

When revenue from trophy hunting is used for conservation, trophy harvesting can become a useful conservation tool, as in some populations of markhor *Capra falconeri*, urial *Ovis vignei* and Asiatic ibex *Capra ibex sibirica* in Pakistan (Johnson 1997). However, the selective exploitation of wild Caprinae based purely on horn size leads to a reduction in size and number of mature males. Possible demographic side effects include female-biased adult sex ratios, increasing recruitment rates and low mean male age, as well as changes in parturition dates, birth synchrony and offspring sex ratio (Milner et al. 2007). Selective hunting may also have unpredictable consequences because of genetic correlations between horn size and other fitness-related traits. Trophy hunting should, therefore, be replaced by harvests that mimic natural mortality.

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