



Short communication

Density-dependent decline of early horn growth in European mouflon

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ABSTRACT

The development of horns in Caprinae can be largely influenced by food-limiting factors such as population density and climate, as well as by negative evolutionary responses to size-selective harvesting. In this study, we investigated the effects of population density, environmental covariates and trophy hunting on horn development in a population of European mouflon *Ovis aries musimon* introduced to the Mediterranean region of Croatia in the early 1980s. The study population was subject to commercial trophy hunting on males since the mid-1980s. This allowed to analyse the temporal trend in early horn growth in 341 rams legally culled. Cohort-based linear model and analysis of deviance (ANODEV) revealed a significant negative trend in early horn growth, with a decline of ca. 10% over only 15 cohorts (1993–2007). The increase in population density (by ca. 600%) and summer temperature, selected via LASSO regression, explained about 61% and 13% of the decline in early horn growth, as revealed by the ANODEV R^2 . Our results suggest a prominent role of food-limiting factors in the decline of weapon size. We also found a negative relationship between age at death and early horn growth in our study population, which suggests the occurrence of hunters' selectivity towards large horns. The effect of trophy hunting on the decline in horn size, however, is difficult to quantify. Our analysis was largely influenced by the rapid increase of mouflon density after introduction, thereby limiting the possibility to detect potential effects of hunting selection, although the large number of rams shot before 5 years of age may possibly lead to undesirable consequences of trophy hunting on mating success. To clarify the consequences of commercial trophy hunting on the mouflon population, the long-term pattern of horn growth and the age-dependent male siring success should be further investigated.

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Male weapon size in large and polygynous ungulates plays a major role in evolutionary biology and wildlife management. Horns are considered honest indicators of phenotypic quality (Bonenfant et al., 2009) and trophy hunting can be a major source of revenue (Palazy et al., 2012). Consequently, temporal changes in horn size have attracted the attention of evolutionary biologists and wildlife managers over the past decades. Long-term variations in male weapon size may entail evolutionary responses to sexual or natural selection (Geist, 1996; Bro-Jørgensen, 2007) as well as to artificial selection through hunting (McDougall et al., 2006; Festa-Bianchet and Mysterud, 2018).

Males in wild sheep species allocate substantial energy resources to early horn growth to secure reproductive success (Coltman et al., 2002). In turn, the expression of this sexually-selected trait can be largely influenced by availability of food resources. The synergistic effect of food-limiting factors such as population density (Jorgenson et al., 1998), climate (von Hardenberg et al., 2004), geological substrate and topography (Chirichella et al., 2013), vegetation communities (Festa-Bianchet et al., 2004) and other habitat characteristics (Carvalho et al., 2017) indeed plays a major role in horn development (Jorgenson et al., 1998; Douhard et al., 2017). In addition, human-related factors such as trophy hunting (i.e., the selective culling of males with large horns or antlers) can be an important evolutionary force shaping weapons' growth in polygynous ungulates (Festa-Bianchet, 2017).

While the role of ecological factors on horn development is widely accepted, the methodological approaches used to support

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evolution through selective harvesting have been heavily criticised in the past (Hadfield et al., 2010), mainly due to the difficulty of distinguishing evolution from phenotypic plasticity (Fenberg and Roy, 2008; Festa-Bianchet and Mysterud, 2018). Recent works, however, have provided strong evidence for undesirable evolutionary consequences of selective hunting of Caprinae (e.g., bighorn sheep *Ovis canadensis*: Douhard et al., 2016 and Pigeon et al., 2016 or stone sheep *Ovis dalli stonei*: Douhard et al., 2016). Hunting regulations that allow shooting large-horned males before they can attain reproduction may favour siring success of older males with smaller horns (Coltman et al., 2003; Festa-Bianchet et al., 2004; Douhard et al., 2016). In turn, trophy hunting may trigger a long-term decline in horn length, provided that “traits that determine trophy quality confer a fitness advantage at an advanced age” (Douhard et al., 2016). Several factors can thus concur to shape horn growth, and disentangling the ecological and evolutionary causes of temporal changes in weapon size may be exceptionally challenging (Festa-Bianchet and Mysterud, 2018).

As for other wild sheep species, in European mouflon *Ovis aries musimon* the allocation of resources to sexually selected traits is highly susceptible to variations in forage availability and quality (Geiger et al., 1977). Furthermore, in wild sheep horn size is heritable and genetically correlated with fitness-related traits (Coltman et al., 2005; Pigeon et al., 2016). Density dependence, climate forcing and trophy hunting are thus expected to play important roles in shaping life history traits in these species. In turn, temporal changes in horn size in wild sheep offer the opportunity to measure the effect of different drivers on this sexually selected trait (Jonas and Perry, 2010; Cameron et al., 2016). Indeed, trophy hunting and changes in quality and availability of food resources have been suggested to negatively affect horn growth in European mouflon (Garel et al., 2007).

In this study we explore how early horn growth in males in a Croatian mouflon population was affected by population density, environmental factors and hunting pressure. After investigating the occurrence of hunting selection, we examine the temporal change in early horn growth over 15 cohorts between 1993 and 2007, and the variables that best explain this variation. We hypothesize that i) rams with fast-growing horns would be shot at a younger age since hunting had no age-restrictions, and ii) harsh environmental conditions and increasing population density would negatively affect horn growth by reducing availability of food resources (Jorgenson et al., 1998; Douhard et al., 2016). Finally, we discuss the potential role of selective hunting on mouflon.

The study population was introduced to the mainland of Croatia in the early 1980s using the source population of Brijuni island (Kusak and Krapinec, 2010). The study area is a typical Mediterranean ecosystem interrupted by ditches, bays and rocks where open areas prevail (80%) and scrublands of Euro-Mediterranean vegetation are sporadic (Seletković et al., 2011). After the introduction, mouflon increased rapidly and reached apparent asymptotic population size in the mid-2000s, with ca. 500 individuals (Fig. 1a). During the study period, population density ranged from 4.12 ind. / 100 ha in 1994 to 24.31 ind. / 100 ha in 2008. Currently, the mouflon population appears numerically stable (Anonymous, 2019) and the sex ratio is biased 1:3 towards females (J. Tomljanović, pers. comm.). This bias is largely explained by the intense commercial trophy hunting on males that has occurred in the study population since 1985. Commercial trophy hunting (i.e. hunting for a fee) was mostly performed by foreign tourist hunters. Besides the number of males allowed for harvesting (ca. 40 permits per year), no limitations were imposed on horn size. Hunters were often accompanied by a game warden and preferentially chose to shoot males with largest horns. The only factors limiting hunting selectivity during the study period were thus hunting effort (restricted to the weekends) and the increasing fees for larger trophies.

Legal hunting started in 1985 and allowed us to collect horn growth data for 431 rams over 28 years until 2012. Due to the limited number of measurements before the beginning of trophy hunting and after the cohort of 2007, however, for our data analysis we considered only horn growth measures for cohorts between 1993 and 2007 ($n = 341$). We determined the age of males by counting horn annuli (Geist, 1966) and considered the left horn only, as directional asymmetry is absent in Caprinae (von Hardenberg et al., 2004). Most horns showed some wear on the tip, thus we excluded the first segment from the analysis. Early horn growth was defined as the summed length of segments 2 and 3 (Hengeveld and Festa-Bianchet, 2011) and measured using a flexible ruler. Only complete segments were considered for analysis, and measurements were taken by the same experienced game warden using a standardized methodology where horn annuli were measured separately (Merchant et al., 1982). Population density and climate were considered as potential predictors of horn length variation. Population size was assessed through ground counts performed in spring by 3–5 experienced game wardens from vantage points. Count series often include errors due to imperfect detection probability, so that an observed time series is normally the outcome of an underlying process (i.e., the variation in true population size due to biotic or abiotic processes) plus observation error (i.e., noise due to imperfect detection probabilities) (Dennis et al., 2006). By assuming an underlying population process using different stochastic models, state-space models allow to decompose population time series into process variation (which we are normally interested in) and observation errors (which we normally want to filter out). We thus applied a linear state-space model and a Kalman filter approach to mouflon count data to eliminate observation noise, assuming a Gompertz density-dependent process using the package MARSS (Holmes et al., 2012). Further details about the structure and performance of state-space models applied to wildlife counts are available in Dennis et al. (2006) and in Ahrestani et al. (2013). Filtered yearly counts from 1994 to 2008 were used as a proxy of population abundance during the second year of horn growth for each individual. Climatic data were collected on a seasonal basis and obtained from a state hydrometeorological station located in close proximity of the study area. They included average of minimum and maximum temperatures in spring (March–May) and in summer (June–August), and average rainfall in the same seasons, as these parameters are expected to reflect environmental conditions during the period of horn growth (Chirichella et al., 2013; Büntgen et al., 2014; Douhard et al., 2017).

To test if trophy hunting led to earlier mortality in rams with rapid early horn growth, we applied a one-tailed non-parametric Kendall rank correlation test between early horn growth and age at death under the assumption that greater age at death would associate with smaller horn growth (cf. Douhard et al., 2016). To test for the occurrence of temporal trend in early horn size we first fitted a simple linear model, regressing early horn growth against cohort fitted as a continuous predictor (Garel et al., 2007; Douhard et al., 2016). Linear model assumptions were checked by visual inspection of residuals. To avoid reporting spurious results, we conducted a further analysis of temporal trend in early horn growth using analysis of deviance (ANODEV: Skalski et al., 1993). This procedure compares the fit of a covariate model (i.e., cohort as a continuous variable) relative to that of both the baseline (i.e., constant) and the full time-dependent (i.e., cohort as a discrete factor) models (cf. Grosbois et al., 2008). ANODEV returns an F -statistics that tests the null hypothesis that the continuous covariate “cohort” has no impact on the variation of early horn growth. Finally, to investigate the importance of density and climate in explaining the temporal trend in early growth, we calculated the R^2 values of the ANODEV tests on a subset of selected variables. Variable selection was performed using Least Absolute Shrinkage and Selection

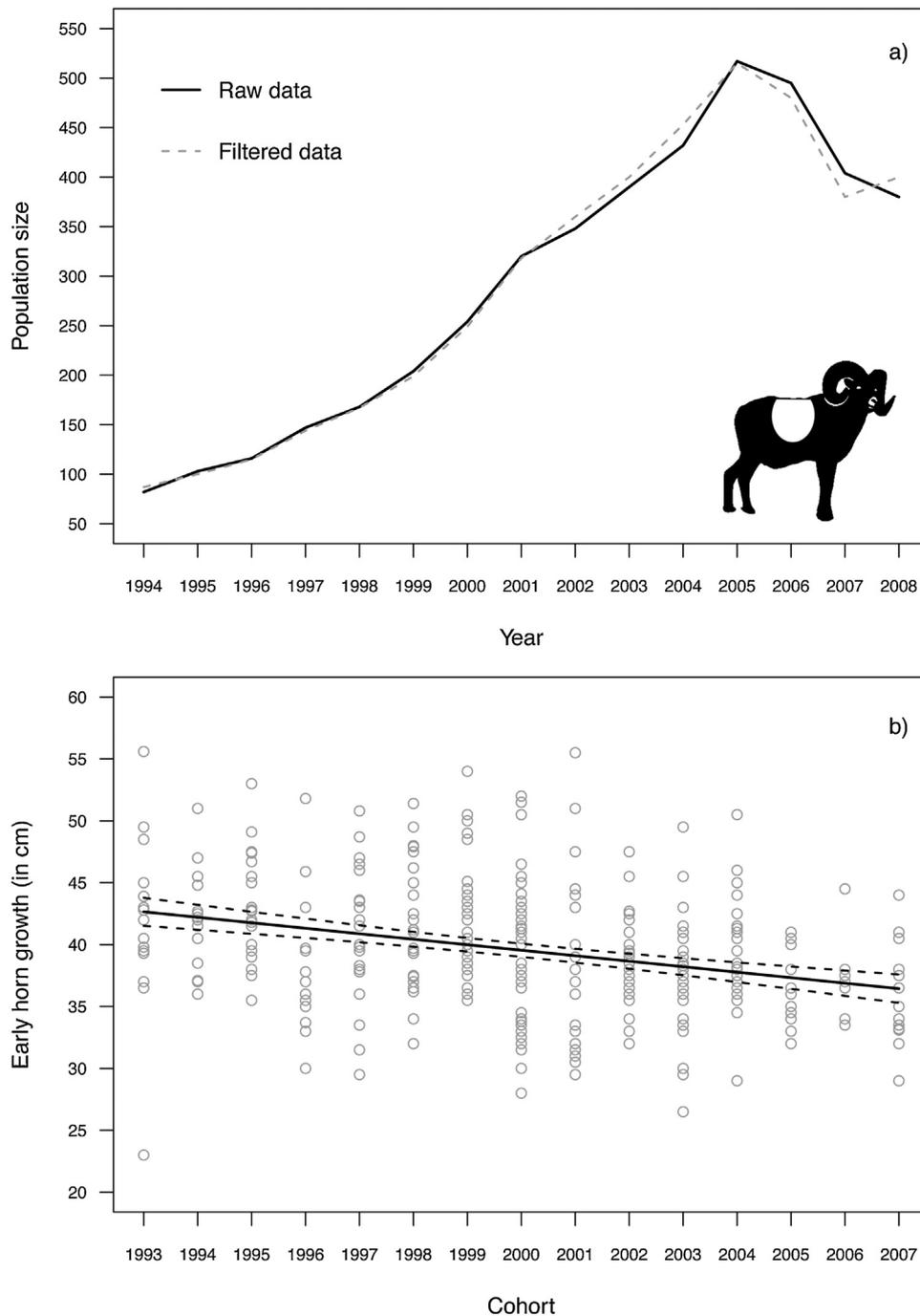


Fig. 1. Relationship between cohort (year of birth) and: a) population size (raw and filtered data) and b) early horn growth (in cm) for European mouflon rams hunted in the study site in Croatia between 1993 and 2007. The dashed lines in b) represents 95% confidence interval.

Operator (LASSO) regression (Tibshirani, 1996) based on the minimization of the predicted mean square error. Early horn growth was fitted as a response variable, while population size and all climatic variables were fitted as predictors. LASSO applies a regularization process where it penalizes the coefficients of the regression variables, and coefficients shrinking to zero are excluded from the final model (Tibshirani, 1996). LASSO is also tolerant to multicollinearity issues (Dormann et al., 2013). This is a desirable property especially when the functional relationships between the response variable and the predictors are not known in advance, thereby circumventing the problem of deciding which collinear variable to exclude a priori from the model. The selected predictors were standardized and included in a linear model to obtain final estimates. Significant

variables were then selected to perform separate ANODEV tests to quantify the amount of variation in early horn size accounted for by each covariate. Specifically, covariate models were run separately for each of the predictor included in the final linear model, and the R^2 values significant ANODEV tests were calculated. All statistical analyses were performed in R 3.3.2 (R Core Team, 2016) in RStudio 1.1.423 (RStudio Team, 2016). We considered an alpha-level of $p = 0.05$ as statistically significant for all analyses.

The one-tailed nonparametric Kendall rank correlation test revealed a significant negative relationship between early horn growth and age at death ($\tau = -1.763$, $p = 0.039$), suggesting a potential for hunters' selectivity towards large trophies. The male early horn growth declined significantly by ca. 10% for cohorts between

Table 1

Estimates of the standardized effects of the linear model build with the variables selected by LASSO regression for early horn growth in mouflon rams in Croatia, between 1993 and 2007: cohort population size, average minimum spring temperature (Min. spring T), average maximum summer temperatures (Max. summer T) and average amount of rainfall in spring (Rain spring) and in summer (Rain summer). The table reports Beta coefficients (β), standard errors (SE), t-statistics (t) and p-values (p). Significant variables in bold.

Coefficient	β	SE	t	p
Intercept	39.574	0.270	146.488	<0.001
Population size	-1.408	0.288	-4.885	<0.001
Min. spring T	0.353	0.355	0.994	0.321
Max. summer T	-0.861	0.431	-1.999	0.046
Rain spring	-0.629	0.352	-1.788	0.075
Rain summer	0.119	0.405	0.293	0.770

1993 and 2007 ($\beta = -0.44$, $SE = 0.073$, $t = -6.062$, $p < 0.001$) (Fig. 1b). The results of the ANODEV test on cohort as a continuous variable confirmed the significant negative temporal trend in early horn growth ($F_{1,13} = 27.89$, $p < 0.001$). The values of filtered counts returned by the state-space model were similar to raw counts, suggesting that in our study population the observation error was low (Fig. 1a). LASSO excluded average minimum temperature in summer and average maximum temperatures in spring as potential predictors of early horn growth. Of all the remaining predictors included in the final linear model, only density and average maximum summer temperature were significantly and negatively related to early horn growth (Table 1). The significant variables were used to perform separate ANODEV tests. Population density accounted for about 61% of the temporal variation in early horn growth, while the average maximum summer temperature accounted for only 14%.

Our results revealed that a significant declining trend of early horn growth occurred in mouflon rams over only 15 years of hunting. While there is some evidence of an effect of trophy hunting, our data analysis suggests a prominent role of food-limiting factors (mainly density dependence) in the decline of weapon size.

Population density and weather conditions are considered among the main factors influencing food quantity and quality, thus the development of horns in polygynous ungulates (Jorgenson et al., 1998; Bonenfant et al., 2009; Douhard et al., 2017). In our study, cohort population size was the most important driver of variation in early horn growth, explaining about 61% of the trend. This result is not surprising, given that our study population sharply increased its size after introduction, and that the effect of density should be weaker in populations that have continuously retained stable numbers (cf. Festa-Bianchet et al., 2014 on Bighorn sheep). Density dependence likely reduced the availability of forage through increased intraspecific competition, thus causing a decline in the investment of resources in weapon size (Douhard et al., 2017). Besides population abundance, maximum summer temperatures accounted for some 13% of the decline in early horn growth. Summer droughts and heat waves can severely reduce vegetation growth in the study area (Tadić et al., 2014). High temperatures may cause heat stress, thus reducing mouflon foraging activity and their ability to invest energy in growth (cf. Northern chamois *Rupicapra rupicapra*: Mason et al., 2014; Alpine ibex *Capra ibex*: Aublet et al., 2009). Conversely, increasing spring rainfalls are expected to favour horn growth through the increase of primary production (Chirichella et al., 2013; Büntgen et al., 2014).

A similar trend in horn growth was found in a hunted mouflon population in France (Garel et al., 2007). However, in their numerically stable study population, Garel et al. (2007) suggested that selective harvesting and habitat loss were the major determinants of the (ca. 20%) decline in horn length over some 28 years. Although their study population was hunted under regulations comparable

to those adopted in our study population, and despite we found an effect of trophy hunting on rams in Croatia, it is difficult to quantify the effect of hunters' selectivity on the observed decline in horn size. The evolutionary consequences of trophy hunting can manifest as long as harvest mortality is positively related to weapon size, large-horned males are harvested before attaining reproduction, and persistent harvest of young large-horned males increase the siring success of short-horned males (Festa-Bianchet, 2017).

Hunting bag data suggest that hunters' selection might have played a role in early horn growth decline, and may possibly lead to undesirable consequences on life history traits. The commercial hunters (i.e. tourists) are mostly limited by the short time frame available for hunting, which is restricted to the weekends (H. Bezjak, pers. comm.). Thus, even though hunters tended to select males with largest horns, they probably chose a less risky strategy to compensate for potential hunting failure by accepting to cull younger males with fast-growing horns. In fact, about 78% of rams in our study population were shot before reaching 6 years of age, and 56% before 5 years of age. The mean age at death of rams with rapid early horn growth (> 50 cm) was 3.86 years, while it was 4.64 years for rams with slower early horn growth (< 50 cm). Although no data are available on the age-specific relationship between age and siring success in European mouflon, the majority of mating events in captive rams were attained by individuals older than 4 years of age (Lincoln, 1998). Therefore, intense trophy hunting during the study period might have provided small-horned rams with greater opportunities of siring success, due to the lack of large-horned competitors (Hengeveld and Festa-Bianchet, 2011). On the other hand, intense removal of mouflon rams, irrespective of horn size, might affect the strength of sexual selection by reducing male-male competition (cf. Myrsterud et al., 2008; Clutton-Brock, 2017). In fact, mating events between 2-year old rams and ewes have been often observed (J. Tomljanović, pers. comm.). If so, trophy hunting might not have as strong an evolutionary effect, although it could lead to the disruption of the mating system.

To clarify the consequences of environmental change and commercial trophy hunting in the study population it is necessary to investigate the horn growth pattern and the age-dependent male siring success over a longer period than currently available, especially under condition of numerical stability. Although it is unclear whether trophy hunting might have caused undesirable consequences on mouflon rams, it is worth noticing that the study population is still subject to commercial harvesting. Management actions and research activities should thus focus on harvest sustainability – including the study of potential evolutionary effects of trophy hunting – to ensure future maintenance of commercial and economic benefits.

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Declaration of Competing Interest

None.

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