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Horn growth variation and hunting selection of the Alpine ibex

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Summary

1. Selective hunting can affect demographic characteristics and phenotypic traits of the targeted species. Hunting systems often involve harvesting quotas based on sex, age and/or size categories to avoid selective pressure. However, it is difficult to assess if such regulations deter hunters from targeting larger 'trophy' animals with longer horns that may have evolutionary consequences.

2. Here, we compile 44'088 annually resolved and absolutely dated measurements of Alpine ibex (*Capra ibex*) horn growth increments from 8'355 males, harvested between 1978 and 2013, in the eastern Swiss Canton of Grisons. We aim to determine if male ibex with longer horns were preferentially targeted, causing animals with early rapid horn growth to have shorter lives, and whether such hunting selection translated into long-term trends in horn size over the past four decades.

3. Results show that medium- to longer-horned adult males had a higher probability of being harvested than shorter-horned individuals of the same age, and that regulations do affect the hunters' behaviour. Nevertheless, phenotypic traits like horn length, as well as body size and weight, remained stable over the study period.

4. Though selective trophy hunting still occurs, it did not cause a measurable evolutionary response in Grisons' Alpine ibex populations; managed and surveyed since 1978. Nevertheless, further research is needed to understand if phenotypic trait development is co-influenced by other, potentially compensatory factors that may possibly mask the effects of selective, long-term hunting pressure.

Key-words: Alpine ungulate, *Capra ibex*, evolutionary change, horn growth, phenotypic plasticity, Swiss Alps, trophy hunting, wildlife management.

Introduction

Anthropogenic selection pressure has been documented to change life history and morphology in a broad range of taxa, including fishes (Kuparainen & Merilä 2007), birds (Bosse *et al.* 2017) and ungulates (Pigeon *et al.* 2016). Selective hunting, the directed removal of animals with specific traits, can result in undesired demographic, genetic and phenotypic changes in the target population (Jachmann *et al.* 1995; Whitman *et al.* 2004; Garel *et al.* 2007; Allendorf & Hard 2009; Croes *et al.* 2011; Coltman *et al.* 2003; Packer *et al.* 2011; Bro-Jorgensen 2014; Douhard *et al.* 2016; Pigeon *et al.* 2016). Evolutionary responses are expected to be most severe when hunters preferentially and continuously harvest males possessing large antlers and horns, i.e. when harvesting is strongly selective and acts on heritable traits. Trophy hunting has been found to trigger phenotypic changes in ungulate populations, such as reductions in body weight and size, as well as the dimension and symmetry of horns (Coltman *et al.* 2003; Garel *et al.* 2007; Pérez *et al.* 2011; Douhard *et al.* 2016; Pigeon *et al.* 2016). To avoid evolutionary consequences in managed populations (Allendorf *et al.* 2008), harvests should not impose a strong selection (Festa-Bianchet 2016; Begg *et al.* 2017). Yet it is still debatable (Ripple *et al.* 2016) whether a properly managed trophy harvest can be used as a conservation tool for maintaining biodiversity (Di Minin *et al.* 2016).

Understanding the role of trophy hunting as an evolutionary driver, depends on a number of factors related to both the hunt's impact, through its intensity and selection (Festa-Bianchet 2016), as well as the age-specific importance of antler or horn size on mating success. Those studies reporting observed effects of selective hunting pressure either come from management systems where a threshold horn sizes defines the legal limit, or there are no specific harvest restrictions for large males. Since both systems are highly selective, it remains to be seen to what extent alternative management regimes can affect the likelihood of

negative trait changes. For example, a decline in the horn size of one Stone sheep population was found under intensive hunting pressure, whereas no such effects occurred when harvesting rates were reduced (Douhart *et al.* 2016). Species' age distribution and life history should be further considered in order to develop sustainable hunting systems that minimize negative impacts on the target population. An alternative management option to relieve some of the overall hunting pressure is to implement age-specific harvest quota that hinder the selection of males simply based on their antler or horn size. Whether or not long-term management systems can reduce selective harvest pressure is, however, not well understood.

Assessing the effects of trophy hunting is particularly challenging because highly resolved, sufficiently replicated, long-term surveys (Imperio *et al.* 2010; Chase 2014), combined with state-of-the-art model approaches are rare (Pigeon *et al.* 2016; Festa-Bianchet 2016; Schindler *et al.* 2017). In addition, the potentially rapid evolutionary adaptation by short-lived species to climate and environmental changes, as well as the behavioural ecology of larger animals, may offset the negative effects of selective hunting or, at the very least, cloud the distinctions.

The managed Alpine ibex populations in the eastern Swiss Alps describe an unprecedented setting for researching potential long-term effects of hunting (www.jagd-fischerei.gr.ch), because the Canton of Grisons has documented each ibex harvest since hunting of this reintroduced species started (Büntgen *et al.* 2014, 2017). Between 1978 and 2013, professional game wardens measured the lengths of 44'088 annual horn growth increments from 8'355 male Alpine ibexes, harvested in eight hunting units, across the eastern Swiss Alps. In addition to the individual increment and accumulated horn length measurements, Grisons' game inventory includes data on hind leg lengths and eviscerated body weight of all the harvested animals. The Alpine ibex (*Capra ibex*) is a sexually dimorphic species of the subfamily *Caprinae* characterized by old males carrying sizable

horns. Increasing with age, body mass and horn length are key traits for male reproductive success (Bergeron *et al.* 2010; Willisch *et al.* 2015). It has been shown that horn growth, an important secondary sexual trait of male ibexes (Büntgen *et al.* 2014), is a reliable indicator of their quality (von Hardenberg *et al.* 2007). Moreover, the Alpine ibex has a slow life history and does not exhibit strong compensatory horn growth (Toïgo *et al.* 1999; Carvalho *et al.* 2017) unlike in chamois (*Rupicapra rupicapra*; Rughetti & Festa-Bianchet 2010). Ibexes therefore cannot compensate for poor early-life growth performance later on (Toïgo *et al.* 2007), which makes this species more susceptible for selective harvest pressure.

Here, we test the hypothesis that evolutionary effects of long-term harvesting can be neutral despite hunters' preference for large trophies. Taking advantage from Grisons' hunting inventory that includes all harvested ibex males from 1978-2013 in the eastern Swiss Alps, we assess specifically the predictions of whether 1) hunters are still able to preferentially harvest larger horn sized animals within their prescribed age-class, and 2) if the strict regulations and penalties of such a management system are sufficient to counter harvest-induced long-term effects on horn size development of the Alpine ibex over the past four decades of survey.

Materials and methods

SPECIES HISTORY, STUDY SITE AND HUNTING SYSTEM

The Alpine ibex almost went extinct in the 18th century when its distribution was reduced to a single population of a few individuals in the western Italian Alps (Maudet *et al.* 2002). Animals from this remnant population were taken to Swiss zoos for captive breeding before being re-introduced to Grisons in 1920 (Ratti 1994; Biebach & Keller 2012). In this part of the eastern Swiss Alps, the native ibex population went extinct in the 17th century (Giacometti 1991). After a period of full protection, ibex hunting resumed in 1978 under the

control of Grisons' Department of Wildlife and Fishery Service (www.jagd-fischerei.gr.ch). The Grisons' hunting system has been designed to reduce potentially undesirable evolutionary effects by minimizing both the sex and age bias in the annual hunting bags.

Since then, professional game wardens have documented the location of each harvested animal as well as several morphological traits (Table S1), including the length of every annual horn growth increment (Büntgen *et al.* 2014, 2017). The resulting dataset is exceptionally unique due to its resolution, duration and replication. The Grisons' complete ibex inventory contains 44'088 annually resolved and absolutely dated measurements of horn growth increments from 8'355 males that were harvested between 1978 and 2013. Moreover, the population size of eight Alpine ibex hunting units (HU) in Grisons is counted every year between March and May when most animals gather in known areas and are relatively easy to observe (Ratti 1994). These annual censuses provide fairly accurate population estimates (Sæther *et al.* 2002; Largo *et al.* 2008). The autumnal hunting quota is re-calculated annually based on the standardized spring surveys and regional population trends. As a result, each year's ibex harvest is tuned to inter-annual population fluctuations. Since Grisons' hunting system is designed to maintain stable population sizes, authorized hunters must target both sexes in all age-classes. Individual hunters can apply for the ibex hunt every 10–15 years only. From the hunters' registry, a preliminary number of hunters are granted licences by a lottery system. After participating in an age-identification course provided by the game wardens, the selected hunters are allowed to hunt for 20 days in October (Büntgen *et al.* 2017). A hunter's first kill must be a non-lactating female (≥1-year old); only then the hunter can – in the remaining time of the hunting period – target a male in one of five age-classes assigned to that specific hunter. If a hunter fails to take a male within his/her designated age-class, a penalty is paid and the kill is confiscated. The age-classes are: 1–2-year old, 2–3, 4–5, 6–10 and ≥11-years old male ibexes. It is important to note that, in the case of male ibexes,

age-specific hunting is possible because their annual horn grow increments accumulate into substantially longer horns with increasing age (Fig. 1). The total horn lengths of 2–3-year-old male ibexes are ~20 cm, whereas total horn lengths of individuals ≥10 years are, on average, between 60 and 80 cm.

The 8'355 animals included in this study represent an update of the dataset introduced by Büntgen *et al.* (2014). It contains 44'088 annual horn growth increment measurements from Grisons' eight geographically distinct hunting units (Fig. S1a). The Alpine ibex lives at elevations between ~1600 and 3100 meters a.s.l. (Giacometti *et al.* 2002). At these elevations, Alpine meadows above the upper tree line are composed of grasses, herbs and dwarf shrubs, and represent 7'106 km^2 of suitable ibex habitat in the eastern Swiss Alps. Under the direction of a government game warden, every animal taken in the annual hunt is shot by a locally registered hunter. The official hunting management protocol, together with the total number of registered hunters, has remained fairly stable since 1977 (Büntgen *et al.* 2017).

STATISTICAL ASSESSMENT

The total horn length, at a specific age, is considered the sum of all annual horn growth increments present at that age. The outermost, first increment is removed from all analyses, because it is highly susceptible to abrasion which if included, negatively biases the total horn length (Giacometti *et al.* 2002). This abrasion effect obviously increases with age (Büntgen *et al.* 2014). Hunting age one thus refers to animals in their second year of life.

Over the period 1978–2013, changes in horn length, hind leg length and eviscerated body weight over time, were analysed by linear regressions to assess temporal changes in the age-dependent morphology of these physical traits. Wilcoxon Signed Rank (Wilcoxon 1945) tests were performed to compare the mean value of those physical traits at each hunting age,

during two equally long, early/late split-periods (1978–1995 and 1996–2013). To compare the annual horn growth increments, and total horn lengths between animals of different ages, we normalized the measurements by converting them to Z-scores (i.e. standardized values with a mean of zero and a standard deviation of one) as follows: $Z = (X - \mu) / \sigma$. In this equation Z is the standardized variable of interest (i.e. annual horn growth increment or total horn length), X is the non-standardized variable, μ is the mean of the variable at each age, and σ is the standard deviation of the variable at each age.

To explore the influence of horn length on the likelihood of being harvested, we compared accumulated horn lengths of the same age between harvested animals, and those harvested at older ages, then calculated horn length differences between the two groups.

A generalized additive model with mixed effects was used to test the significance of the identified patterns. This appraoch allows for non-linear relationships and can account for any dependency structure in the data (Wood 2006). The model's response variable is the conditional harvesting probability (*CHP*). The term *conditional* stresses the point that we are estimating the probability of an animal being harvested at a given age, given that the individual is eventually shot (as only hunt tally data are available). With this, we refer to the fact that time-series of horn lengths and hunting ages are not equivalent to cross-sectional data. Primarily, this has implications for the age-specific hunting probability, because the sampling scheme includes horn lengths for many young individuals but only few old ibexes. The proportion of harvested ibex therefore increases with age in the dataset used. However, this does not imply that hunters favour older ibex, but rather that age must be included in the hunting model to control for the confounding effect of the sampling. At the same time, it is important to note that ibex survival is extremely high for 1–10-year old individuals, and therefore is unlikely to have a strong bias on our results. We fitted the following mixed additive logistic regression model:

$$\log\left(\frac{CHP_{ijk}}{1 - CHP_{ijk}}\right) = \beta_0 + s_p(stHL_{ijk}) + s(age_{ijk}) + u_j + v_k + \varepsilon_{ijk}$$

with *CHP* being the conditional hunting probability of individual *i* in hunting unit *j* and calendar year *k*, β_0 is the overall intercept and u_j and v_k are the random effects on the intercept associated with hunting unit *j* and calendar year *k*, respectively. Standardized (Z-scores) of horn length (*stHL*) and ibex age were incorporated via thin plate regression splines (s). Since hunters may favour different horn lengths, depending on penalties for shooting an individual of the adjacent age-class, we created a categorical penalty variable (*p*) assigning each age to the lower or upper age range of each age-class (Table 1). Close to the *lower limit*, we assume selection of longer horns; close to the *upper limit*, we assume selection of shorter horns or indifferences. For both penalty conditions an individual effect function of *stHL* is fitted. Finally, *εijk* is the error term. The discriminative power of the model was assessed using the area under the receiver operation curve (AUC). Generalized additive models were fitted using the *gam* function in the R-language (version 2.11.1; R Development Core Team 2017) package *MGCV* (Wood 2011).

Results

The distribution of the harvesting locations of all 8'355 Alpine ibex males reveals a clear geographical concentration to the eight hunting units across the Canton Grisons (Fig. S1). The total horn lengths and the annual horn growth increments show a strong age trend, with younger individuals possessing smaller horn lengths but higher annual horn growth rates (Figs. 1, S2). The majority of animals were two to five years old when harvested (Fig. S3), and the number of animals killed depended on the aforementioned spring population size (Fig. S4).

   A careful assessment of the age-specific accumulated total horn length, as well as the eviscerated body weight and hind leg length, independently calculated over the two equally

long early/late split-periods 1978–1995 and 1996–2013 reveals statistically no difference (Figs. S5-9). None of the physical traits measured showed evidence of long-term changes in ibex morphology over the study period. Neither positive nor negative trends were found in the mean horn-length time-series over the full 1978–2013 period (Fig. S10). These calculations were based on the slopes of linear models (P <0.05) with horn length and time as the dependent and independent variables, respectively.

The comparison of total ibex horn lengths from animals harvested at earlier or later ages shows a clear tendency for selective hunting (Fig. 2). Without selective hunting pressure, we would expect no slope in the data points of Figure 2A that excludes measurements of the animals' outermost, first horn, increment (see Fig. S5 for comparable data using the entire horn length). In fact, the total horn lengths of the harvested ibexes are on average 15.6 mm longer than the accumulated horn length of the same number of increments on animals that were harvested at older ages (Fig. 2B). For example, the total horn length of all ibex males that were harvested at the age of 12 years is on average 19 mm longer than the sum of the corresponding growth increments of all those males that were harvested at older ages (Fig. 2B). The largest age-specific difference of nearly 50 mm is seen between the 13-year and older individuals. Differences >10 mm were evident in nine out of 15 age-classes, whereas almost no difference was found for 10-year old animals (Fig. 2B). Without ignoring some bias due to the way hunters are able to recognise the size and age of animals in the field, this study finds the hunters' preference for targeting longer-horned male ibexes within a given age-class, to avoid a penalty for overshooting (Fig. 2B). The consequence of this behaviour is obvious when comparing the annual horn-length differences within the two largest age-classes; 6–10-year-old and ≥11-year-old male ibexes (Fig. 2B). Within the 6–10-year-old age-class, the largest differences are found for the seven and eight-year-old males, whereas

basically no difference exists for the 10-year-old individuals. Within the ≥11-year-old age-class, there is a tendency for increasing horn-length differences with increasing age.

The mixed additive logistic regression models (Table 2, Figs. 3-4), designed to test if horn length and the risk of penalty have an influence on the conditional harvesting probability (*CHP*), while taking into account the dependency structure in the data, confirmed the observation of selective hunting. Horn length significantly influenced the conditional harvesting probability, and the effect differed between the (*upper* and *lower*) penalty conditions. Close to the *lower limit*, hunters clearly favoured longer horns; close to the *upper limit*, hunters tended to shoot animals with average horn lengths. The confounding age variable reflects a sampling scheme with an increasing proportion of older ibexes. The model achieves an acceptable discrimination performance (AUC) of 0.72 (Hosmer & Lemeshow 2000). Though the effect of horn length and penalty varies between the age-classes, the patterns in each age class are similar (results not shown).

Discussion and conclusions

This study provides another independent line of evidence for hunting selection in a managed hunting system. Even though strict age-specific harvesting criteria have been implemented by the Canton of Grisons in eastern Switzerland since 1977, medium- to longer-horned Alpine ibex males had a higher probability of being harvested than shorter-horned individuals of the same age. Nevertheless, no signs for phenotypic trait changes were found over the past four decades (Figs. S6-10). Hence, evolutionary effects of harvesting depend on the details of a management system, as these ultimately determine harvest selectivity and pressure.

HUNTING REGULATION

Since its establishment in 1977, Grisons' official Alpine ibex hunting system aims to regulate the species' population development. There are many factors that can lead hunters to be less precise with their selection (Mysterud 2011), principal among them is the economic incentives to not lose an opportunity before the close of the hunting season (Diekert *et al.* 2016). In Grisons, this time constraint is magnified by the fact that each hunter must first harvest a female before being allowed to hunt a male of a pre-defined age-class. Independent of weather conditions, the autumnal ibex hunting period is restricted to only 20 days in October, which markedly reduces the time available for being selective. Furthermore, shooting a male outside the assigned age-class incurs a financial penalty and confiscation of the bag and trophy. Such regulations are an attempt to limit the potential for hunters to perform a preferential trait selection towards longer horned males. Strict harvesting regimes aim to protect against external forcing of phenotypic traits vis-a-vis affecting gene frequencies in the populations. The Grisons' hunting regulations are likely one reason why this study finds no evidence of long-term changes in physical traits like the total horn length, as well as eviscerated body weight and size (Figs. S6-10).

SELECTIVE HUNTING

Despite the aforementioned hunting regulations, we find evidence of the hunter's selection for medium- to longer-horned animals, especially at older ages (Figs. 2-4). Considering a hunter can only shoot a single male from one of the five age-classes (1–2, 2–3, 4–5, 6–10 and ≥11-year-old), and that killing an older animal would incur a penalty, hunters favour the relatively longer-horned animals within the younger portion of their assigned age-range (Figs. 2B, 3-4). Such a strategy reduces the probability of harvesting an animal from the next lower age-class with similar horn lengths and/or body attributes, and at the same time satisfies the desire for large trophies Conversely, to protect against accidentally taking an animal in the

next higher age-class, hunters aim at medium-horned animals within the older portion of the assigned age-range, which is reflected by the slightly negative selection effect on 10-year old animals (Fig. 2B). The strong effect on the very oldest ibex >11 years could be partially explained by the greater mortality of older males with large horns as reported by Toigo et al. (2013). Overall, these preferences may result in a larger hunting probability for individuals with faster horn growth.

It should be further noted that the effects seen in the data and model are conditional upon the sampling scheme that includes data of only those male ibexes that are eventually hunted. The part of the male ibex population that died because of natural death is not included, thus we lack information on selective disappearance due to natural death (Rebke *et al.* 2010). Yet, Toïgo *et al.* (2013) found no effect of early horn growth on survival until 12 years of age for male ibexes in the French Alps, supporting the robustness of our results. Moreover, the survival rate of male ibexes until age 9–10 years is with ~85% much higher than for most other ungulates for which the natural male survival rate during the first 10 years ranges from 10-40% (Toïgo et al. 2007).

LONG-TERM EFFECTS

As a species the Alpine ibex fulfils all the requirements for exhibiting an evolutionary response due to selective harvesting. The ibex has a slow life history and it is unlikely that they can compensate for poor early-life growth performance (Toïgo *et al.* 1999; Willisch *et al.* 2015). In some species like the chamois, as much as ~90% of the total horn growth occurs in the first three to four years of life. Therefore, slow growing individuals at an early age, due to unfavourable environmental conditions, can still compensate for a poor start of horn growth later in life (Rughetti & Festa-Bianchet 2010). Harvesting is therefore unlikely to yield an evolutionary response in chamois. By contrast, ibex horns grow much longer, and it

is unlikely these animals can compensate for a slow juvenile growth rate. In addition, horn size is more important for male mating success in ibex and bighorn sheep than in chamois and mountain goats (Festa-Bianchet *et al.* 2000; Côté & Festa-Bianchet 2001; Coltman *et al.* 2002; Mainguy *et al.* 2009), since the latter two species show strong compensatory growth that reduces the relevance of horn size for male mating success.

Possible explanations for our results, separately or combined, are the following (i-iii): (i) In spite of the hunter's selection for medium to longer horns when targeting male ibexes, the long-standing hunting policies in Grisons successfully balance a sustainable harvest without no detectable long-term effect on phenotypic traits. (ii) Any potential effect of the observed hunting selection on ibex horn length was too weak to elicit a response on decadal time-scales. In fact, horn growth responses to environmental changes seem to be more common (Douhard *et al.* 2017), and appear sooner and stronger, than evolutionary responses (Giacometti *et al.* 2002; von Hardenberg *et al.* 2004; Merilä & Hendry 2014; Festa-Bianchet 2016). (iii) Any potential decline in horn growth due to the selective hunting could be masked by positive influences of more favourable climate conditions, as manifest in the recent increase in spring temperatures over the entire Alpine arc (Büntgen *et al.* 2014) (Fig. S10).

Ibex total horn length may partially reflect short-term climate fluctuations (Büntgen *et al.* 2014). Phenotypic features like horn, antler and body size of different species are well known to be sensitive to direct and indirect climatic influences, such as temperature variability and its control on the availability and quality of nutrition (Giacometti *et al.* 2002; Schmidt *et al.* 2001; Festa-Bianchet *et al.* 2004; Mysterud *et al.* 2005; Ozgul *et al.* 2009; Loehr *et al.* 2010; Sheridan & Bickford 2011; Douhard *et al.* 2017). Warmer springs can enhance both the quality and quantity of food for the Alpine ibex by initiating an earlier snowmelt and the advanced onset of vegetation growth (Büntgen *et al.* 2014). Indeed, similar relationships have been found for other species like reindeer (*Rangifer tarandus*; Pettorelli *et al.* 2005; Tveraa *et*

al. 2013) and the chamois (*Rupicapra rupicapra*; Garel *et al.* 2011). However, warmer and earlier spring conditions are also linked to faster vegetation growth and maturation (i.e. green-up) after winter. This can leave the herbivores with a lower quality food for an extended period, which has been shown to have a negative impact on the performance and fitness of the Alpine ibex, bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*; Pettorelli *et al.* 2007). Moreover, the nutrition of the dam probably matters more than that of growing males (Jorgenson *et al.* 1993; Festa-Bianchet & Jorgenson 1998; Festa-Bianchet *et al.* 2004; Monteith *et al.* 2018).

The extant populations of the Alpine ibex across the European Alps have experienced several severe genetic bottlenecks (Maudet *et al.* 2002; Giacometti 1991). Compared to its ancestral population the present ibexes are characterized by relatively low genetic variability (Biebach & Keller 2009). A limited gene pool tends to lower the potential for natural selection. In this regard, smaller genetic variability also reduces the opportunity to respond favourably, or in a compensatory manner, to selective hunting pressures, as well as to short-term habitat disturbances and/or long-term environmental changes, such as increasing temperatures that have been observed in the eastern Swiss Alps over the studied period (Fig. S10).

CONCLUSIONS

This study shows that even a strict management system cannot fully prevent a harvesting preference towards longer-horned animals. However, no long-term changes were found in the horn length of Grisons' male ibexes, which is most likely related to the fact that the hunting selection is too weak to impose a strong evolutionary effect. Furthermore, it's debatable if the combined effects of little variation in genetic traits (Giacometti *et al.* 2002; von Hardenberg *et al.* 2004; Merilä & Hendry 2014; Festa-Bianchet 2016), and improved climate/nutritional

conditions, are possibly compensating for any long-term hunting-induced decrease in horn length (Pettorelli *et al.* 2005; Tveraa *et al.* 2013; Büntgen *et al.* 2014).

Although, our observations emphasize the importance of continuous monitoring of hunting practices, especially in those systems where hunting management allows for the selection of animals with preferred traits, caution is advised when interpreting long-term harvest inventories due to possible uncertainties (Pelletier *et al.* 2012; Monteith *et al.* 2013; Festa-Bianchet *et al.* 2015). A more comprehensive evaluation of the sustainability of Grisons' governmental ibex management would require a comparative study, in which horn growth characteristics and individual biometric traits of a target population are compared with those of a fully protected population regulated only by natural mortality only (Büntgen *et al.* 2014). The Department of Wildlife and Fishery Service in Grisons is currently working on the development of such a dataset.

Finally, we suggest environmental conditions should be considered when linking phenotypic plasticity and/or genetic adaptation to the putative influences of long-term harvesting (Douhard *et al.* 2017). External, abiotic factors such as climate that may influence secondary sexual traits, including horns and antlers, are likely most pronounced in the extreme, marginal arctic and alpine ecosystems, where recent warming is considered the leading driver of the functioning, productivity and viability of most species.

Authors' contributions

H.J. developed, archived and provided the Alpine ibex horn growth dataset; U.B. conceived the study with input from K.B., J.D.G. and J.S.; U.B., K.B. and J.D.G. coordinated the project over two consecutive project phases; J.D.G. and L.H. performed statistical analyses with input from A.M.; U.B., P.J.K., J.D.G., K.B., A.M. and L.H. wrote the manuscript with input

from all others. Each author contributed to the discussion and gave final approval for this submission.

Data accessibility

The dataset supporting this article is available via the Dryad Digital Reposity http://doi.org/10.5061/dryad.k5p5cm1 (Büntgen et al. 2018).

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Tables and Figures

Table 1. Assignment of ibex age to the penalty variable, which was created to describe if hunters face a penalty for shooting an individual of the adjacent smaller or larger age-class. *Lower* and *upper limit* assign each age to the lower or upper age range of each age-class, assuming selection of longer horns close to the lower limit and selection of shorter horns or indifference close to the upper limit. Note that we collapsed the age-classes 1–2 and 2–3 due to an overlap for 2-year-old animals.

Age-classes	1-2 / 2-3			4-5		6-10					≥11
Hunting age	1	2	3	4	5	6	7	8	9	10	≥11
Penalty	lower limit	lower limit	upper limit	lower limit	upper limit	lower limit	lower limit	lower limit	upper limit	upper limit	lower limit

Table 2. Statistical parameter of the selected additive logistic regression model fitted to the conditional harvesting probability (*CHP*). The influence of *stHL* was significant for both penalty conditions (*upper* and *lower limit*). The confounding age variable accounts for the sampling scheme. Random effects on the intercept were assigned for individuals nested within hunting units (*u*) and for calendar years (*v*).

Parametric coefficient:

	Estimate	Std. Error	Z-value	p-value
Intercept	-1.095	6.202	-0.177	0.86

Approximate significance of smooth terms:

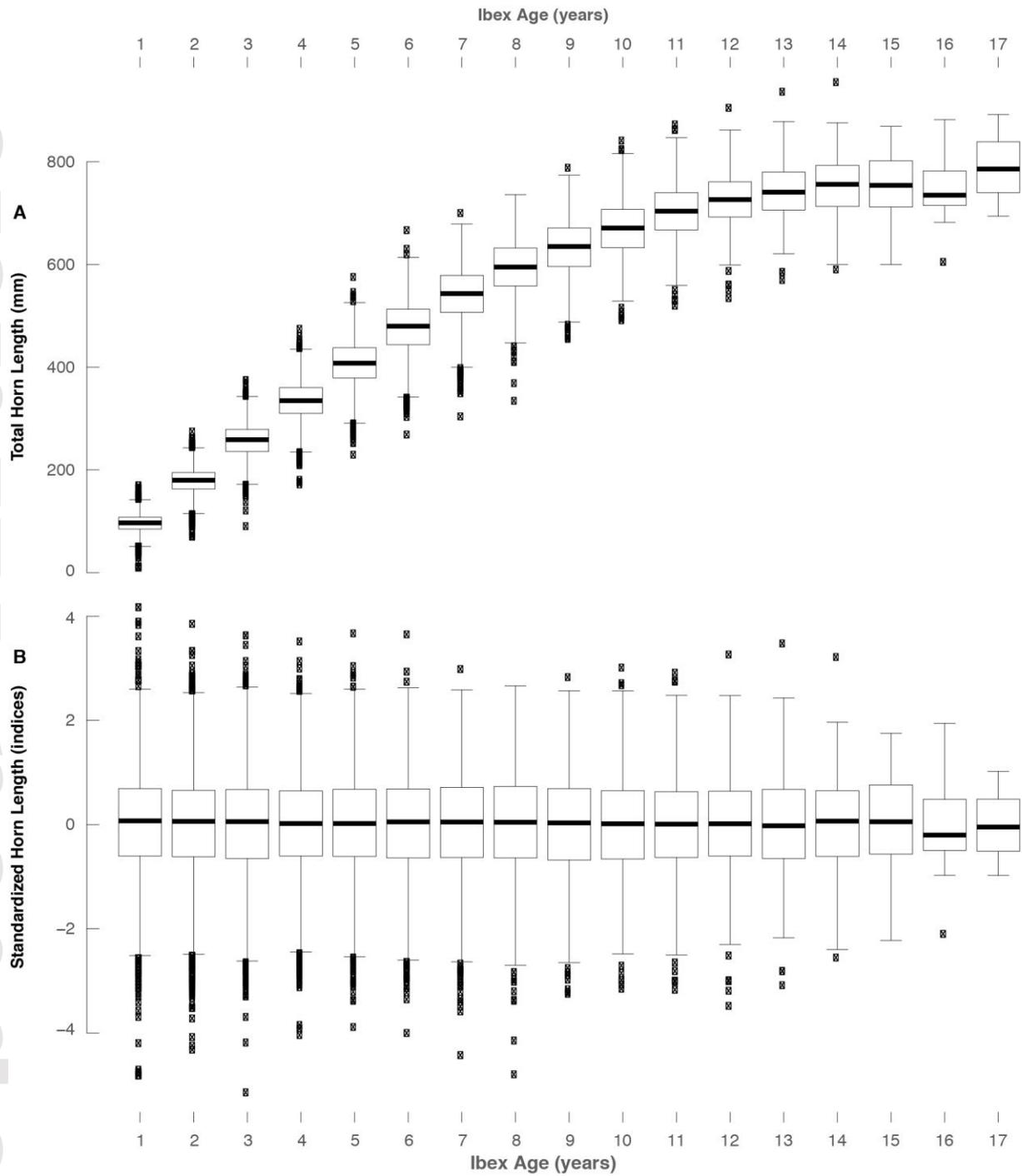|	edf	Ref.df	Chi-square	p-value	
$s_{lower\ limit}(stHL)$	3.400	4.330	34.190	1.22e-06	***
$s_{upper\ limit}(stHL)$	3.600	4.510	32.250	4.99e-06	***
s(*age*)	8.815	8.978	1050.030	< 2e-16	***
u	5.975	7	734.550	2.33e-05	***
v	23.917	24	364.850	< 2e-16	***

Fig. 1. (**A**) Characteristic age trend in Alpine ibex horn growth, and (**B**) corresponding indices after standardization by age-specific mean and standard deviation values.
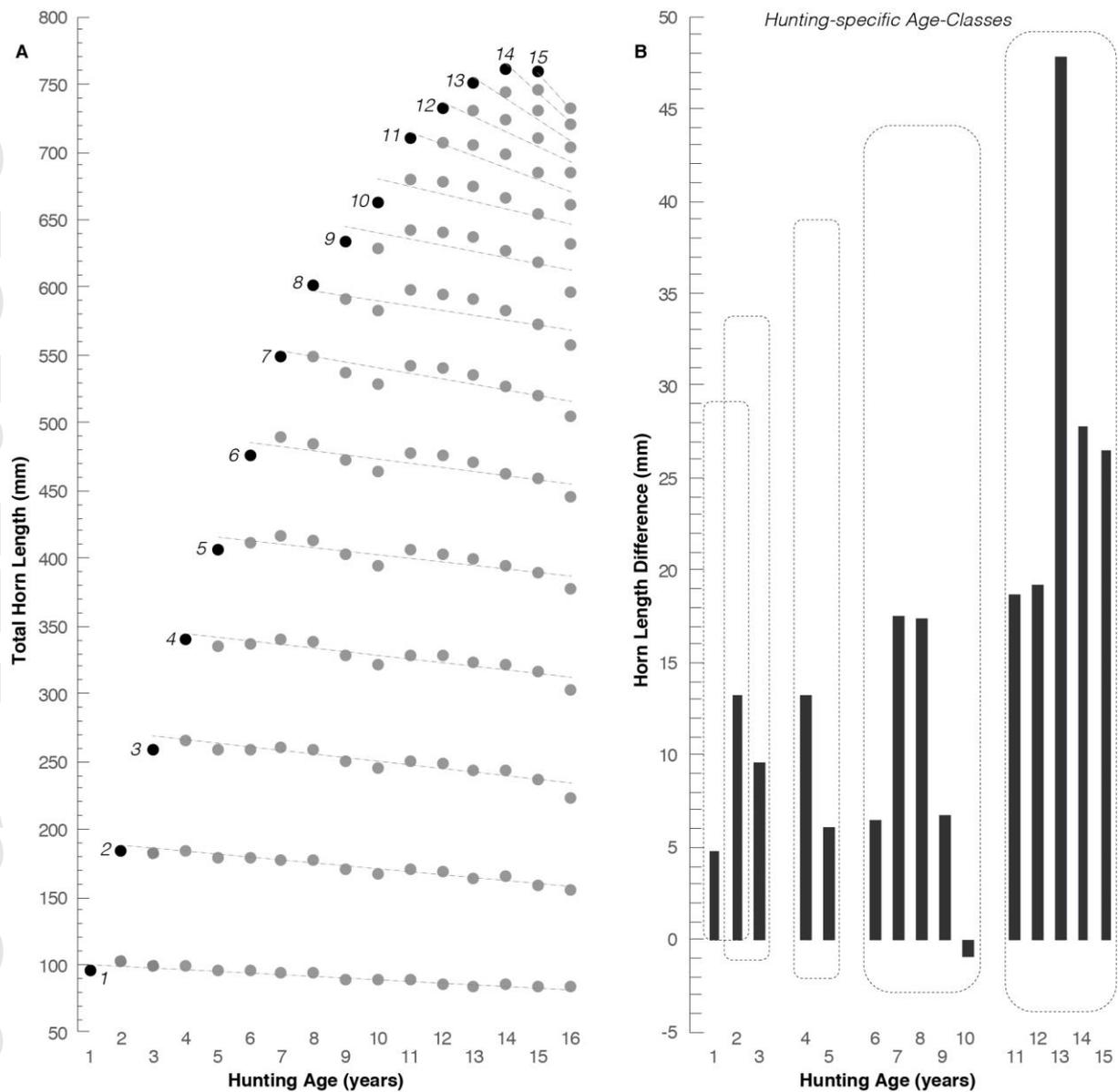
Fig. 2. (**A**) Accumulated total horn length (y-axis) at different harvesting ages (x-axis; from young to old ibex males from left to right). Black dots refer to total horn length at different harvesting ages, whereas grey dots show the length of the corresponding horn growth increments of animals that were harvested at later ages. Dashed grey lines are linear trends, with R^2 ranging from 0.49 at age-class 9 to 0.94 and 0.97 at age-class 2 and 14, respectively. (**B**) Differences in the total horn length of harvested animals and the accumulated length of the same number of horn increments of those male ibexes that were harvested at later ages. Grey-dashed frames show age-classes in which hunters are allowed to harvest. The outermost, first increment has been removed in this data (see Fig. S5 for more details).
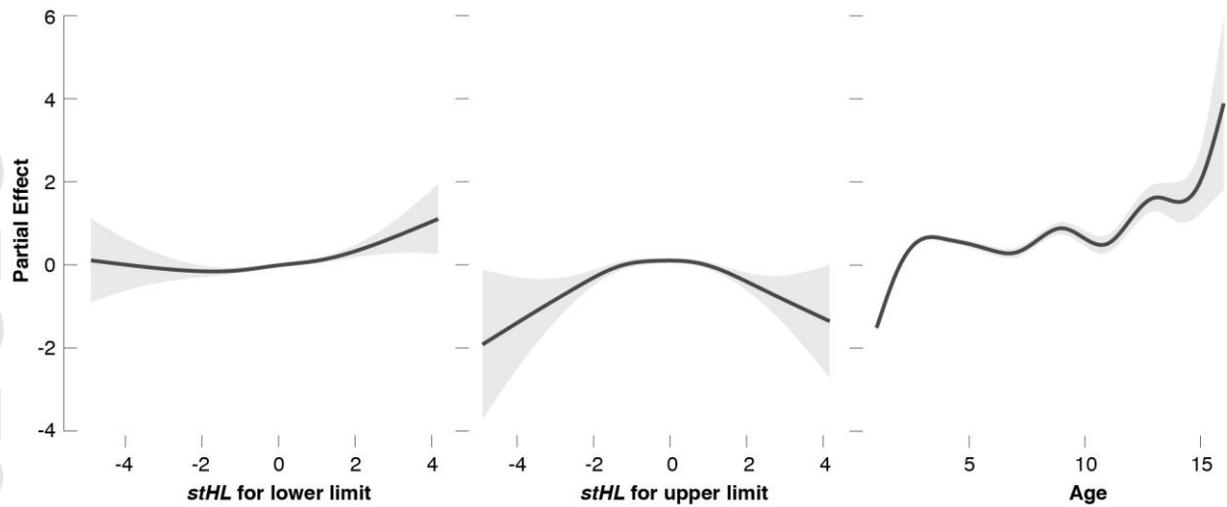
Fig. 3. Partial effects of standardized horn length (*stHL*) and *age* on the conditional harvesting probability (*CHP*) with 0.95 confidence intervals from the mixed additive logistic regression model. The effect of *stHL* on *CHP* is shown for two penalty conditions (Table 1): Close to the *lower limit* of each age class, hunters favoured longer horns; close to the *upper limit*, hunters tended to shoot animals with average horn length. Note that the increasing effect of age on *CHP* does not imply that hunters favour older ibex, but rather that age must be included in the hunting model to control for the confounding effect of the sampling scheme.
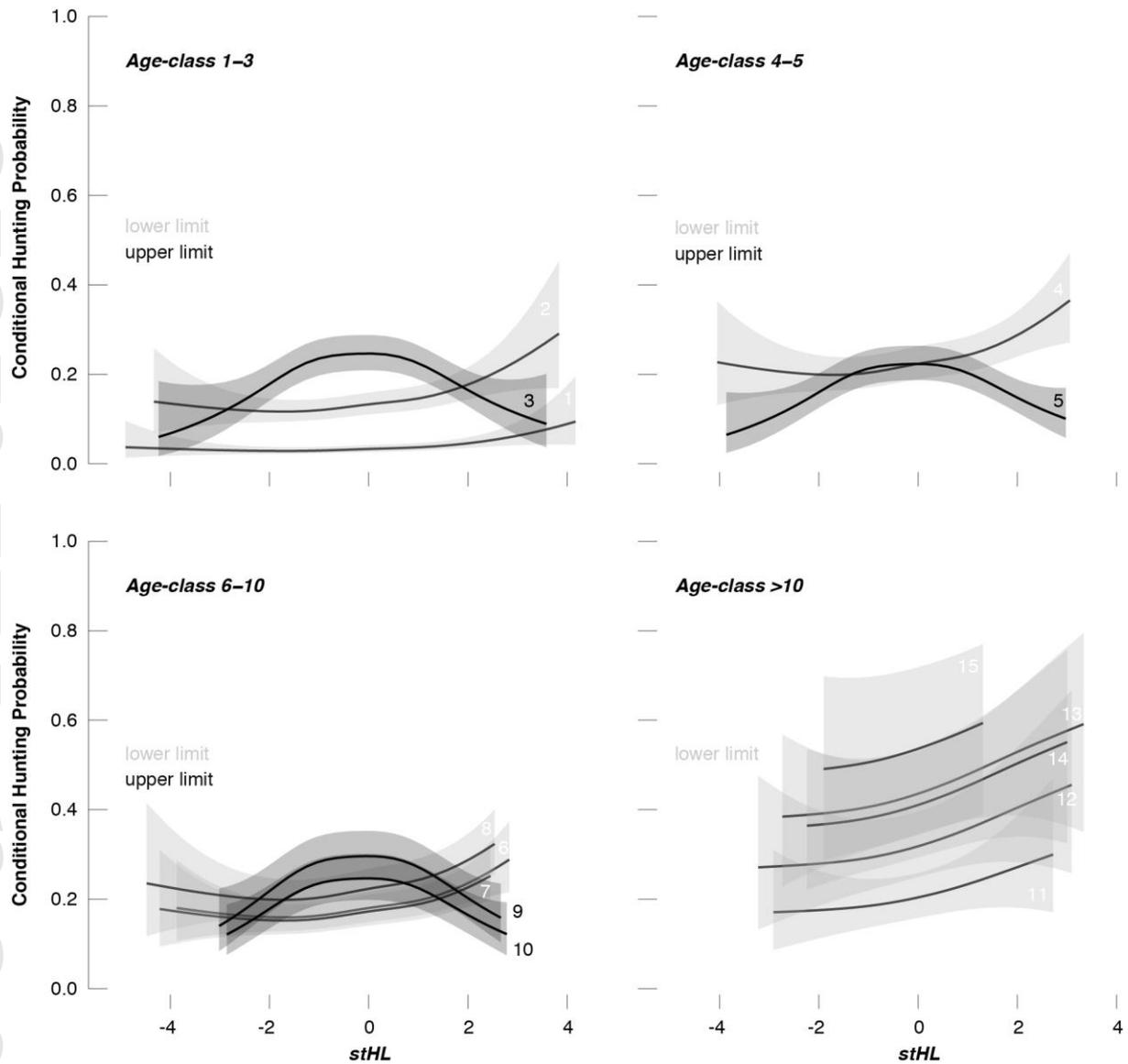
Fig. 4. Predicted conditional harvesting probabilities (*CHP*) with 0.95-confidence intervals from the mixed additive logistic regression model. Predictions are shown for different standardized horn lengths (*stHL*) and ages, exemplarily for adult ibex males in hunting unit 8 in calendar year 1990. Each panel corresponds to one of the age-classes assigned to the hunters. Light (*lower limit*) and dark grey (*dark limit*) shadings refer to the penalty-term in the model, with the corresponding right-side numbers indicating the ibex age.