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Original investigation

Evidence for phenotypic plasticity but not for compensatory horn growth in male Iberian ibex

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ABSTRACT

The description of horn growth patterns is of utmost importance for the sustainable management of wild ungulate populations subjected to intense trophy hunting. This is a topic of renewed interest because horn growth patterns seem to be contingent on region and population.

We sampled 2145 male Iberian ibexes (*Capra pyrenaica*) evenly distributed across the *Els Ports de Tortosa i Beseit* National Game Reserve, NE Spain. A total of 24,615 annual horn growth segments were measured and used to describe horn growth patterns of male ibexes and to test whether compensatory horn growth occurs in an heterogeneous area.

We found that individual heterogeneity explained more than a quarter (27.75%) of the variability in annual segment length and that habitat characteristics foster significant phenotypic differences among male ibexes. Our results corroborate previous studies by demonstrating that compensatory horn growth in male ibexes, as in other members of the tribe *Caprini*, is inexistent. Our study goes one step further and suggests that compensatory horn growth in male ibexes is neither promoted by cohort effects nor by habitat differences.

The absence of compensatory horn growth has important management implications, namely: (i) male ibexes are not able to recover from a bad start, and (ii) the species is prone to evolutionary effects from trophy hunting. We emphasize that the study of just one proxy of horn growth may hamper the current knowledge about compensatory mechanisms in wild ungulates and imperil the development of effective management measures.

Introduction

Horns are permanent epidermal structures whose size and shape contribute to establish dominance hierarchies amongst males of polygynous species (Geist, 1966). In *Caprinae*, horn growth continues throughout the animal's life but the rate to which it occurs varies with season and decreases with advancing age (Bergeron et al., 2008). Horn growth is not only driven by intrinsic factors such as age, sex or genetic variability of individuals, but also by the interactions between the individual characteristics and extrinsic variables such as resource availability and harvesting strategies (Monteith et al., 2013). Horns are generally considered honest signals of individual health (Ezenwa and Jolles, 2008) and are sometimes expected to provide an indication of habitat quality (Garel et al., 2007).

Trophy hunting of ungulate males with large and symmetric horns is widespread and can produce important revenues for game managers and wildlife conservation (Loveridge et al., 2006).

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The selective harvesting of these horn-like structures, too often intensive and unrestrictive, has raised an increasing concern about the evolutionary consequences and ultimately, the socio-economic implications of this activity. Recent studies have shown that trophy hunting causes a significant reduction in horn size and body weight on the short-term (Pigeon et al., 2016). This is partly because individuals with desirable phenotypes (valuable trophies) are more prone to be removed before they can breed (Coltman et al., 2003). Additionally, it may also trigger several demographic consequences such as males reproducing earlier and the consequent destabilization of social structures (Milner et al., 2007). Unequivocal evidence moreover shows that changes in observed phenotypic traits may result from a combination of size-selective harvesting and environmental factors (Douhard et al., 2017). The horns of bovids stop growing in winter, usually forming a distinct segment (annulus). Because large horns are energetically demanding, environmental variations able to impact forage availability and quality may affect the yearly-horn growth. For instance, it was demonstrated that a decrease in resource availability led to more resources being allocated to body growth than to horn growth in young bighorn rams (*Ovis canadensis*), possibly increasing short-term survival at the cost of decreased long-term reproductive success (Festa-Bianchet et al., 2004).

Compensatory growth is the mechanism whereby an organism compensates the growth depression, resulting from periods of food restriction and nutrients shortage, by increasing the relative resource allocation to a specific trait when environmental and nutritional conditions improved (Jobling, 2010; Metcalfe and Monaghan, 2001). Thereafter, the consequences of trophy hunting and unfavorable environmental conditions are particularly evident in species where compensatory horn growth is weak or absent (Festa-Bianchet, 2016). Empirical evidence suggests that compensatory horn growth may be significant in species where the majority of horn growth occurs at a young age (*e.g.* Mountain goats *Oreamnos americanus*, Côté et al., 1998; Alpine chamois *Rupicapra r. rupicapra*, Corlatti et al., 2015), but may be weak in species where horn growth occurs at high rates even in adulthood (*e.g.* Alpine ibex *Capra ibex ibex*, Toïgo et al., 1999). Although the species' ability to increase growth rates may mitigate the effects of a bad start, compensatory growth may carry long-term costs, and is often contingent on life stages and specific traits (Metcalfe and Monaghan, 2001). For instance, in species where the development of structural sexual ornaments is an inextricable aspect of reproductive success (e.g. horns in Caprinae are used in contests for mates), investment in sexual ornaments may lead to reduced individual body size and/or reduced chances of survival (Lindström et al., 2005).

As variation in horn size and shape of male *Caprinae* subjected to intensive harvesting regimes, and variable environmental conditions, can have demographic, evolutionary and socio-economic implications, assessing the possibility of compensatory horn growth on those populations is becoming of growing importance for many wildlife managers. This is obviously a subject of concern since the lack of compensatory horn growth typically means that slower-growing young males become small-horned mature males (Toïgo et al., 2013). Furthermore, although recent studies did explore the possibility of compensatory growth in *Bovidae* (Alpine ibex: Toïgo et al., 1999; Bergeron et al., 2008, Toïgo et al., 2013; Bighorn rams: Festa-Bianchet et al., 2004), the relative importance of habitat characteristics in shaping horn growth remains largely unknown. The Iberian ibex (*Capra pyrenaica*) is the most economically valuable species in Spain and its management is focused on the production of large-horned males. Trophy hunting of male ibexes is widespread throughout the country and it is based on the overall rank of horn size, horn symmetry and age (Pérez et al., 2011). In the *Els Ports de Tortosa i Beseit* National Game Reserve, NE Spain, Iberian ibex males have been trophy-harvested over the last four decades. Individuals of low phenotypic value are also selectively removed in an attempt to reduce the intraspecific competition and to limit the reproduction of undesired phenotypes (Pérez et al., 2011). This harvesting regime has been seen as a management strategy to ensure the long-term sustainability of the hunting activity because it counteracts the undesirable effects of trophy hunting on the distribution of the affected phenotypic trait, the horn size and shape. Although this strategy might be enough to offset the evolutionary consequences of trophy hunting (Mysterud and Bischof, 2010), the lack of knowledge on how environmental conditions may affect horn growth patterns hampers the implementation of spatially explicit countermeasures to alleviate trophy hunting impacts. A better understanding of horn growth patterns would therefore be a most welcome first step towards the effective management of this species. Taking advantage of a long-term monitoring of an Iberian ibex population, we here aim to: (i) explore whether individual heterogeneity, cohort and sampling locations foster well-differentiated horn growth patterns in male ibexes and (ii) assess if compensatory horn growth occurs. Horn growth patterns and phenotypic quality differ sharply between individuals and this difference may be exacerbated by environmental conditions (Alpine ibex, Bergeron et al., 2008; thinhorn sheep *Ovis dalli*, Loehr et al., 2010). Because horns are energetically costly to produce and carry, we expect marked individual heterogeneities in their expression (Hypothesis 1) and evident plasticity in horn growth patterns between habitats, i.e. the correlation between successive horn growth segments is expected to be influenced by the habitat characteristics (Hypothesis 2). Growing evidence from field studies suggests that compensatory horn growth is negligible in tribe *Caprini* (e.g. Toïgo et al., 2013; Festa-Bianchet et al., 2004), however, the relationship between compensatory horn growth and habitat characteristics remains little explored in species belonging to this prominent tribe (but see Corlatti et al., 2015 who explored this relationship in Alpine chamois, tribe *Rupicaprini*). We here hypothesise that the large variability in habitat characteristics found in our study area may allow for compensatory horn growth to occur in male ibex inhabiting specific locations (Hypothesis 3).

Material and methods

Study area

We used accurate measurements of 24,615 annual horn growth segments from 2145 male ibexes sampled at "Els Ports de Tortosa i Beseit" National Game Reserve, north-eastern Spain (PTB, hereafter; 40°48′N, 0°19′E, Fig. 1). PTB covers an area of 28,587 ha. The landscape is heterogeneous and encompasses a range of Mediterranean-type habitats interspersed by pastures and crops. The substrate is calcareous and the vegetation is mainly composed by Mediterranean forests of *Quercus ilex* and *Pinus halepensis*. The evergreen sclerophyll shrubland characterizes the east part of the study area and harbors the greatest diversity of plant species.

Iberian ibex sampling

All sampled animals were legally and selectively hunted over 21 years (from 1995 to 2016). Sex was determined by visual inspection and age (years) was visually assessed from horn-segment counts (see for details Fandos, 1991). The measurements of annual segments were taken to the nearest mm with a nylon tape measure. The oldest and outermost annual segment was excluded from our analyses due to abrasion (Álvarez, 1990) and maternal effects (Giacometti et al., 2002). Most ibexes had 10–14 growth segments per horn which indicates that they were 11–15 years old when hunted. More than 14 or less than 10 segments per horn were only found in 25% of males.