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 2,145 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.

Keywords *Capra pyrenaica*, habitat, game management, horn growth patterns, phenotypic plasticity, population management, size-selective harvesting, trophy hunting.

1. 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). 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).

2. Material and methods

2.1. Study area

We used accurate measurements of 24,615 annual horn growth segments from 2,145 male ibexes sampled at “Els Ports de Tortosa i Beseit” National Game Reserve, north-eastern Spain (PTB, hereafter; 40º48’N, 0º19’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.

2.2. 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.

2.3. Statistical analyses

By performing a k-means cluster analysis, we identified two distinct clusters that explain 73.11% of the spot variability in terms of habitat characteristics. The first cluster (cluster 1, n = 28 spots) is represented by areas with a great proportion of dense Mediterranean forests (north and west of PTB), while the second cluster (cluster 2, n = 14 spots) is characterized by shrublands interspersed by pasture or agricultural areas (east of PTB). The habitat cluster was used as a fixed factor in the subsequent models. The habitat classification took into account the food availability and quality based on the diet of the studied population (Martínez, 1994).

We explored the horn growth patterns as a function of age (years), cohort and habitat cluster using generalized additive mixed models (GAMM). We considered annual segment length (cm) as the response variable, and male identity (ID) as a random factor with varying intercepts and fixed slopes. We fitted ID as a random factor to avoid pseudo-replication and to explore individual heterogeneities in male horn growth. We tested the significance of ID using the likelihood ratio test (LRT, Steele and Hogg, 2003). Out of a total of 50 spots, eight were excluded from the analyses given the low representativeness of male samples ($n < 20$).

We followed the methodological framework adopted in previous studies (Alpine ibex: Toïgo et al., 2013; Alpine chamois: Corlatti et al., 2015) to explore whether compensatory growth occurred. We performed a regression model between the length of the second segment (log-transformed L2) and the cumulative length of the third, fourth, fifth and sixth segments (log-transformed L3-L6, inflection point; Álvarez, 1990; Sarasa et al., 2012). We fitted the cohort and habitat cluster as fixed factors to account for temporal and spatial variability in environmental conditions, respectively. To explore the possibility of fine-scale compensatory growth we ran multiple regressions between subsequent horn growth segments (L3-L2, L4-L3, L5-L4 and L6-L5). Alternative models were compared by applying an information-theoretic approach. The Akaike information criterion (AIC; Akaike, 1974) and the deviance information criterion (DIC; Spiegelhalter et al., 2002) were used as the parsimony criteria. A model was selected over another whenever it reduces the AIC in 2 (two) units (Burnham & Anderson 2002). Statistical significance was set at $P \leq 0.05$ for all tests. The amount of variation explained by each mixed model (R^2) was calculated following the recommendations of Nakagawa and Schielzeth (2013). The software R 3.4.0 (R Development Core Team, 2017) was used to perform the analyses. The “mgcv” package (Wood, 2012) and the “gamm4” (Wood and Scheipl, 2016) were used for GAMM analyses and the “nlme” package (Pinheiro et al., 2012) for linear mixed-effects models.

Results

Total horn length are driven by the male's age (β = 5.19, SE = 0.02, t = 330.30, P < 0.0001, R^2 = 0.51, Fig. 2). Regarding the growth patterns of annual segments, the most parsimonious model included the effects of age, cohort, habitat cluster and the interaction between age and habitat cluster (AIC = 97961.71, DIC = 97867). The second most competitive model only includes the effects of age and habitat cluster, however was at approximately 80 AIC units from the most parsimonious model (AIC = 98041.68, ΔAIC = 79.97, DIC = 98041.68). LRT demonstrated that male identity was highly significant (LRT between the full model and the model without random effect = 702.99, d.f. = 7, P < 0.001). Among-individual variations accounted for 27.75% of observed differences in annuli length, confirming our first hypothesis (Hypothesis 1). As expected, we reported a significant decrease of the annual segment length during adulthood (β = -0.24, SE = 0.003, t = -66.38, P < 0.001), particularly evident after the age of eight (Fig. 3). On the other hand, cohort had no significant effect on the growth patterns of annual segments (β = 0.002, SE = 0.003, t = 0.60, P = 0.55). The annual segments of males harvested in shrubland habitats are significantly longer than the segments of males harvested in forest-dominated areas (β = 0.43, SE = 0.05, t = 9.23, P < 0.001). This result indicates that male ibexes exhibit substantial phenotypic differences among habitats, confirming our expectations (Hypothesis 2). Male's age and habitat interacted significantly suggesting that the pace of horn growth decreased faster in the shrubland habitats (β = -0.05, SE = 0.01, t = -10.13, P < 0.001). With regards to compensatory horn growth, our results (the length of L2 was positively correlated with the length of L3-L6: β = 0.42, SE = 0.03, t = 13.55, P < 0.001) corroborate the third hypothesis (Hypothesis 3, Fig. 4), and reinforce the conclusions of previous studies that this mechanism in species belonging to the tribe *Caprini* is weak or absent. Our results further suggested that neither cohort effects (β = -0.0004, SE = 0.0003, t = -1.31, P = 0.18) nor habitat differences (β = -0.05, SE = 0.06, t = -0.82, P = 0.41) promote the occurrence of this mechanism. The pairwise analyses showed that the length of subsequent annual segments are positively correlated and therefore no evidences for fine-scale compensatory growth were detected (L3-L2: β = 0.42, P < 0.001; L4-L3: β = 0.74, P < 0.001; L5-L4: β = 0.71, P < 0.001; L6-L5: β = 0.64, P < 0.001).

Discussion

The characteristics of our dataset (*e.g.* large number of yearly-horn segments taken from many individuals evenly distributed over the study area) provides an excellent opportunity to explore horn growth patterns and test for compensatory horn growth in male Iberian ibexes. Our results show that individual characteristics lead to well-differentiated horn growth trajectories and provide statistical support for an evident phenotypic plasticity in horn growth, probably due to differences in habitat characteristics and quality of food resources. We reported a positive relationship between L2 and the horn length between the annuli L3-L6, which confirms that compensatory growth of horns length does not occurs in male ibexes, a pattern already described in other studies on ungulates (Alpine ibex: Toïgo et al., 1999, Bergeron et al., 2008, Toïgo et al., 2013; Bighorn rams: Festa-Bianchet et al., 2004). Our study goes one step further suggesting that the absence of compensatory horn growth in Iberian ibex does not depend on the cohort or habitat characteristics. The positive correlation between L2 and L3-L6 indicates that L2 could be used as a reliable proxy of horn size at older ages and suggests that males with fast-growing horns early in life will probably become large-horned mature males. The absence of compensatory horn growth may exacerbate individual differences in total horn length among mature males because small-horned young males will not be able to catch-up large-horned young males later in life (Bergeron et al., 2008).

Taken as a whole, our findings suggests that variable environmental conditions, here represented by habitat characteristics, experienced throughout life foster well differentiated phenotypes among individuals (Dmitriew, 2011). In fact, individuals born in areas or periods of poor food provisioning tend to exhibit slower growth rates throughout life than those born under favorable conditions (Hamel et al., 2016). The effects of habitat changes and diet shifts on the phenotypic traits of a wild ungulate species were demonstrated by a long-term study carried out in southern France (Garel et al. 2007). By analysing the consequences of habitat loss on body mass, horn size and horn shape of mouflon (*Ovis gmelini musimon*), the authors reported that changes in quality and availability of food resources were crucial to the decline in phenotypic quality of mouflon. Our results support this finding, as ibex males inhabiting shrub- and grass-rich open areas (cluster 2) are characterized by longer annual segments than those inhabiting forest and closure habitats (cluster 1). Surprisingly, the horn growth rates decreased faster with advancing age in males sampled in shrub- and grass-rich open areas than in males sampled in forest and closure habitats. This result suggested that males may face a trade-off limiting horn growth or that once a horn size threshold is achieved, further growth has no effect on male performance. However, the exact causes for this trend are difficult to pinpoint as more detailed information is lacking.

There are some possible explanations, ranging from ontogenetic to environmental, to explain the effects of temporal and spatial variability of forage quality in alpine ungulates. First, seasonal and environmental-driven variations in forage availability/quality may lead to poor maternal cares during prenatal and postnatal stages, which affects offspring mass and survival (Landete-Castillejos et al., 2009). Second, because the synchrony of parturition time plays an important role in among-individual variation, too early or too late neonates may mismatch the peak of vegetation productivity and/or climate mildness (Feder et al., 2008). This seems to be set a vicious circle as early nutritional deficits can have negative effects on the adult survival and its offspring (Burton and Metcalfe, 2014).

The absence of compensatory horn growth have important implications for the Iberian ibex management because i) young males presenting a smaller horn growth are not able to recover from a bad start and will become small-horned mature males and, (ii) the species is more prone to suffer strong evolutionary effects of trophy hunting (Festa-Bianchet, 2016). Although this result corroborate previous findings, there are some considerations worth highlighting. The traits measured to evaluate compensatory horn growth in most studies (*e.g.* horn length), including our own, are often the most accessible and seldom the most functional. Few studies explored other horn growth parameters (*e.g.* apical/base circumference, segment volume) to test the occurrence of this mechanism (see Festa-Bianchet et al. 2004), which prevents generating conclusive remarks (Sarasa et al., 2012). The fighting behavior of male Iberian ibexes poses a strong pressure on the basal sections of horns, so horn volume is considered an important feature to maintain the integrity of these structures (Álvarez, 1990). High-quality males with massive horns fight for longer times and are best suitable to withstand heavy blows from other males. This gives an important competitive advantage on female choice and mating partners’ defense. Horn volume is therefore an important trait that might be safeguarded. An alternative hypothesis can be proposed to explain the absence of compensatory horn growth. For instance, harsh environmental conditions during early growth affect all individuals of the same cohort simultaneously (Hamel et al., 2016). Therefore, allocating a substantial amount of resources to compensate horn growth in adverse environments might not be a good strategy once all the male competitors shared the same environmental constraints and it can entail survival costs. This conservative strategy of resource allocation that tracks environmental variation and resource availability is usually displayed by large herbivores inhabiting seasonal environments (Descamps et al., 2016). In this case, the genetic and parental effects can make the difference between small-horned and large-horned mature males. Additionally, recent studies reported a significant reduction of male-male interactions during the mating season (Willisch and Neuhaus, 2010) and showed that young adults of male Alpine ibex participate in the rut through coursing, a low-cost reproductive tactic (Willisch and Neuhaus, 2009). This energetically conservative reproductive behavior, that still needs to be confirmed in the Iberian ibex, makes the recovery of horn size throughout life an optional strategy with unnecessary survival costs.

Our study is correlative which represents an important caveat to our analyses. We do not control for genetic effects, that may represent an evolutionary constraint to compensatory horn growth, or for the nutritional value of vegetation units, which hampers the description of the relationships between differences in habitat characteristics and the possibility of compensatory horn growth. Experimental long-term studies need to be run in order to shed light about cause-effect relationships of compensatory horn growth in ungulates. Because trade-offs in relative allocation depends on environmental conditions and total resource acquisition (Descamps et al., 2016), we argue that compensatory horn growth may be adaptive and contingent on region. We also advocate that future approaches beholding a geographically extensive sampling and the incorporation of ecologically, epidemiologically and genetically related variables, as well as the study of others morphological parameters, are increasingly necessary to understand the long-term consequences of size-selective harvesting and nutritional deficits on horn growth patterns of *Caprinae* populations. Nevertheless, we demonstrated that habitat characteristics are one of the key variables that foster significant differences in the males horn length. This information is of great interest for hunting associations and wildlife managers as it provides scientific support for design habitat management actions aimed at improving the phenotypic quality of ibex males and mitigating the impacts of trophy hunting.

Author contributions

JC, JMP, CF, NP and ES conceived the study. OE, JMP and XOB collected the data. JC and ES analysed the data. JC, JMP, NP and ES wrote the paper. All authors contributed to the development of ideas and approved the final version of the manuscript.

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Fig. 1. Location of the study area. the “*Els Ports de Tortosa i Beseit*” National Game Reserve. Main habitat characterization is also presented.

Fig. 2. Relationship between total horn length (cm) and age at harvest (years). The red solid line represent the relationship in forest and closure habitats; the red dashed line represent the relationship in shrub- and grass-rich open areas.

Fig. 3. Variation in annual segment length (cm) in relation to age (years) considering forest and closure habitats (dark grey box plots) and shrub- and grass-rich open areas (light grey box plots). Solid black squares represent the overall mean annuli length.

Fig. 4. Relationship between log-transformed L2 and log-transformed L3-L6. The black dashed line represent the L2/L3-L6 relationship considering all the sampled males; the red solid line represent the L2/L3-L6 relationship in forest and closure habitats; the red dashed line represent the L2/L3-L6 relationship in shrub- and grass-rich open areas and the grey lines represent the L2/L3-L6 relationship *per* spot.

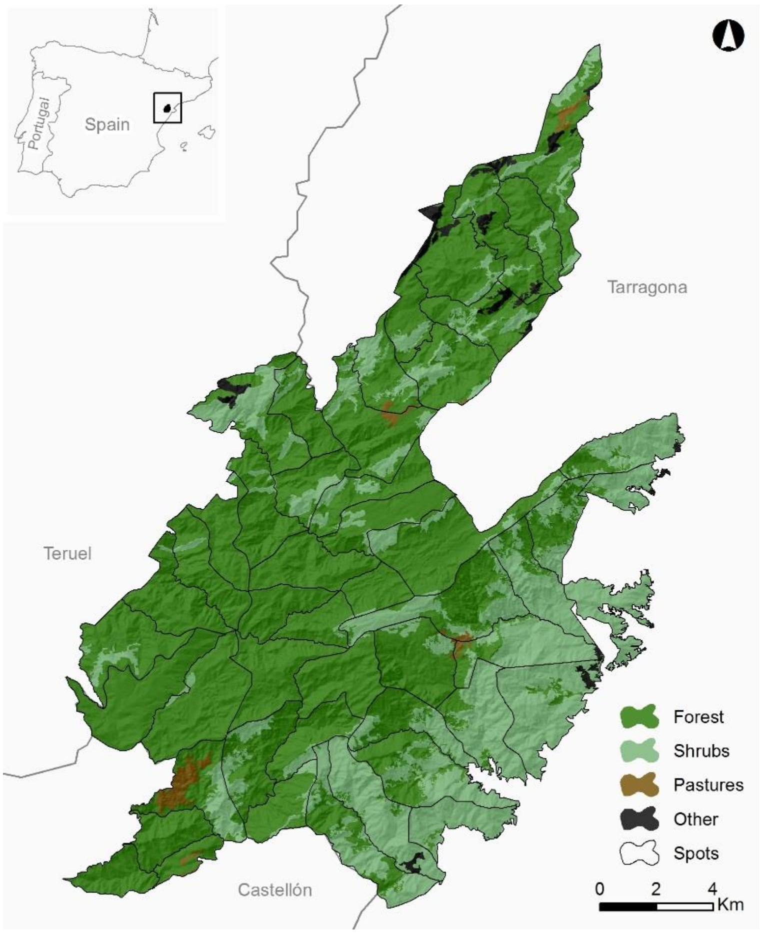
Portugal
Spain
Tarragona
Teruel
Castellón
Forest
Shrubs
Pastures
Other
Spots
0
2
4
Km

Figure 1.

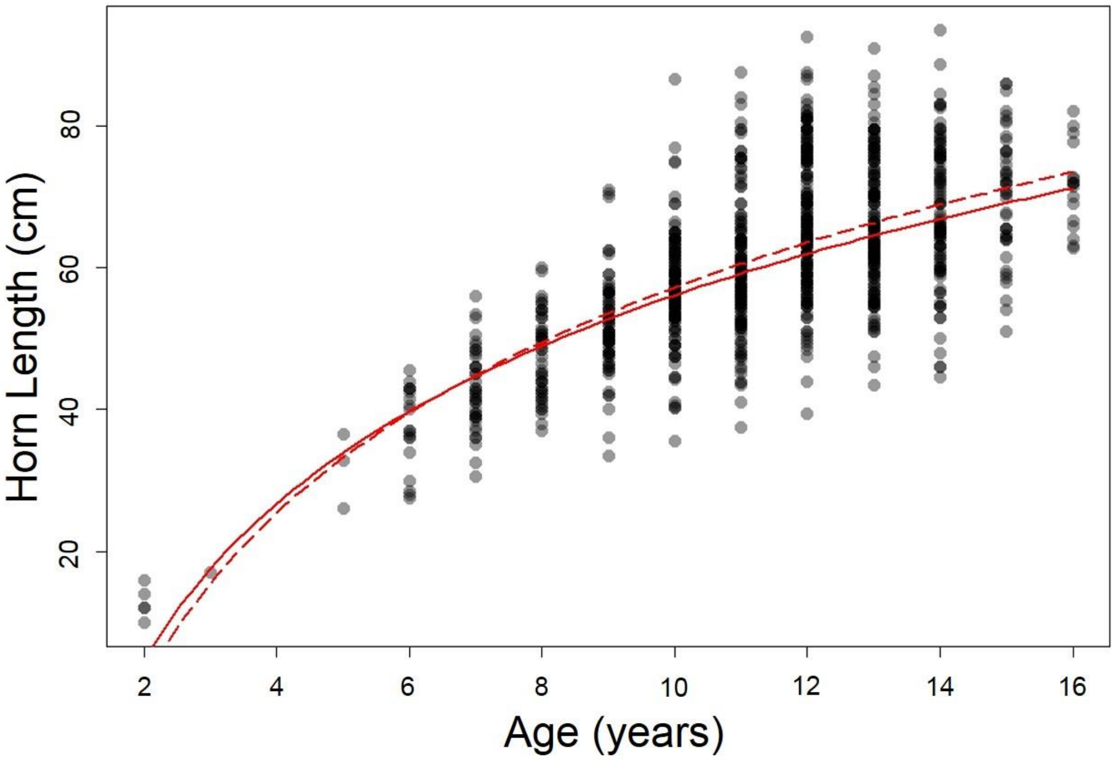

Figure 2.

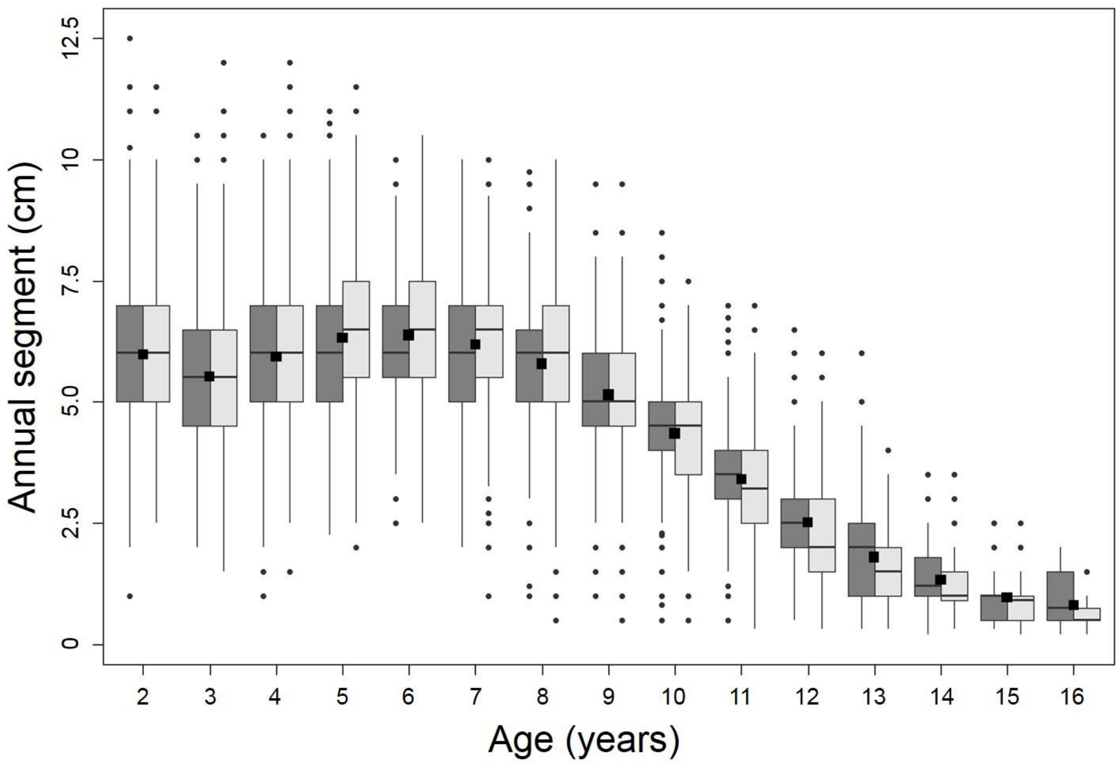
12.5
10
7.5
5.0
2.5
0
Annual segment (cm)
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Age (years)

Figure 3.

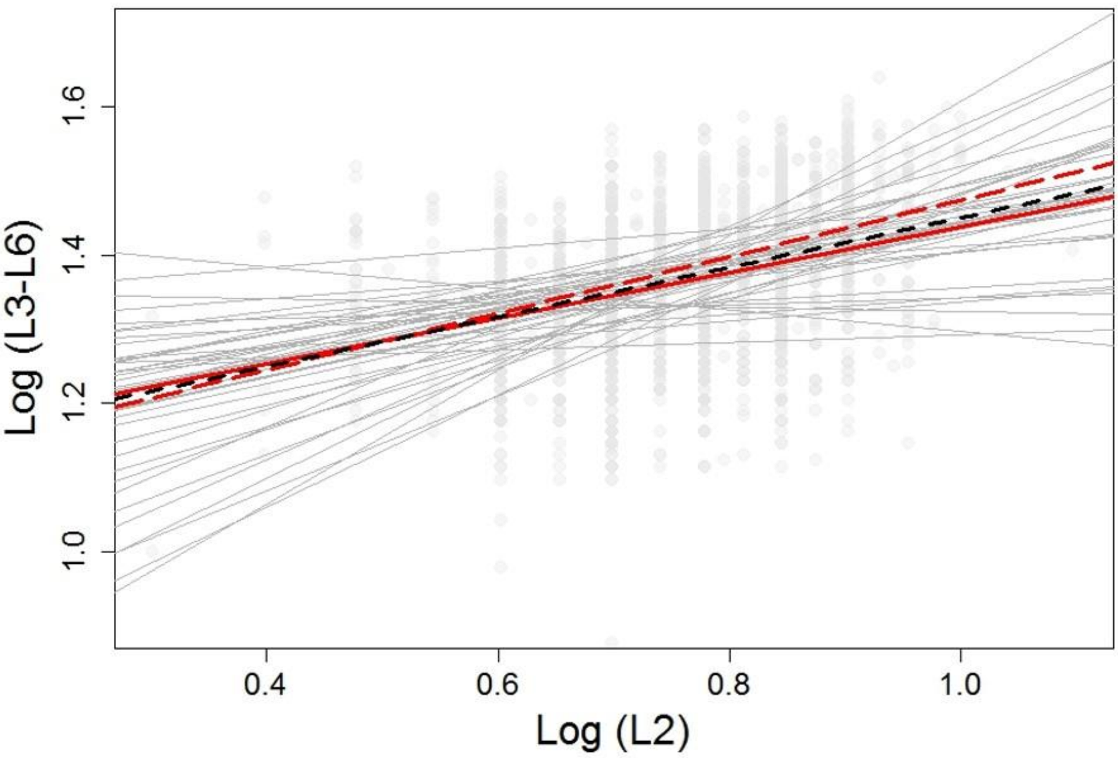

Figure 4.