

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

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1 **Abstract**

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

6 We sampled 2,145 male Iberian ibexes (*Capra pyrenaica*) evenly distributed across the  
7 *Els Ports de Tortosa i Beseit* National Game Reserve, NE Spain. A total of 24,615 annual horn  
8 growth segments were measured and used to describe horn growth patterns of male ibexes and to  
9 test whether compensatory horn growth occurs in an heterogeneous area.

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

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

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

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## 1        **1. Introduction**

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

12            Trophy hunting of ungulate males with large and symmetric horns is widespread and can  
13 produce important revenues for game managers and wildlife conservation (Loveridge et al.,  
14 2006). The selective harvesting of these horn-like structures, too often intensive and unrestrictive,  
15 has raised an increasing concern about the evolutionary consequences and ultimately, the socio-  
16 economic implications of this activity. Recent studies have shown that trophy hunting causes a  
17 significant reduction in horn size and body weight on the short-term (Pigeon et al., 2016). This is  
18 partly because individuals with desirable phenotypes (valuable trophies) are more prone to be  
19 removed before they can breed (Coltman et al., 2003). Additionally, it may also trigger several  
20 demographic consequences such as males reproducing earlier and the consequent destabilization  
21 of social structures (Milner et al. 2007). Unequivocal evidence moreover shows that changes in  
22 observed phenotypic traits may result from a combination of size-selective harvesting and  
23 environmental factors (Douhard et al., 2017). The horns of bovids stop growing in winter, usually  
24 forming a distinct segment (annulus). Because large horns are energetically demanding,  
25 environmental variations able to impact forage availability and quality may affect the yearly-horn  
26 growth. For instance, it was demonstrated that a decrease in resource availability led to more  
27 resources being allocated to body growth than to horn growth in young bighorn rams (*Ovis*  
28 *canadensis*), possibly increasing short-term survival at the cost of decreased long-term  
29 reproductive success (Festa-Bianchet et al., 2004).

30            Compensatory growth is the mechanism whereby an organism compensates the growth  
31 depression, resulting from periods of food restriction and nutrients shortage, by increasing the  
32 relative resource allocation to a specific trait when environmental and nutritional conditions  
33 improved (Jobling, 2010; Metcalfe and Monaghan, 2001). Thereafter, the consequences of trophy  
34 hunting and unfavorable environmental conditions are particularly evident in species where  
35 compensatory horn growth is weak or absent (Festa-Bianchet, 2016). Empirical evidence suggests  
36 that compensatory horn growth may be significant in species where the majority of horn growth  
37 occurs at a young age (*e.g.* Mountain goats *Oreamnos americanus*, Côté et al., 1998; Alpine

1 chamois *Rupicapra r. rupicapra*, Corlatti et al., 2015), but may be weak in species where horn  
2 growth occurs at high rates even in adulthood (e.g. Alpine ibex *Capra ibex ibex*, Toïgo et al.,  
3 1999). Although the species' ability to increase growth rates may mitigate the effects of a bad  
4 start, compensatory growth may carry long-term costs, and is often contingent on life stages and  
5 specific traits (Metcalf and Monaghan, 2001). For instance, in species where the development  
6 of structural sexual ornaments is an inextricable aspect of reproductive success (e.g. horns in  
7 Caprinae are used in contests for mates), investment in sexual ornaments may lead to reduced  
8 individual body size and/or reduced chances of survival (Lindström et al. 2005).

9 As variation in horn size and shape of male *Caprinae* subjected to intensive harvesting  
10 regimes, and variable environmental conditions, can have demographic, evolutionary and socio-  
11 economic implications, assessing the possibility of compensatory horn growth on those  
12 populations is becoming of growing importance for many wildlife managers. This is obviously a  
13 subject of concern since the lack of compensatory horn growth typically means that slower-  
14 growing young males become small-horned mature males (Toïgo et al., 2013). Furthermore,  
15 although recent studies did explore the possibility of compensatory growth in *Bovidae* (Alpine  
16 ibex: Toïgo et al., 1999, Bergeron et al., 2008, Toïgo et al., 2013; Bighorn rams: Festa-Bianchet  
17 et al., 2004), the relative importance of habitat characteristics in shaping horn growth remains  
18 largely unknown. The Iberian ibex (*Capra pyrenaica*) is the most economically valuable species  
19 in Spain and its management is focused on the production of large-horned males. Trophy hunting  
20 of male ibexes is widespread throughout the country and it is based on the overall rank of horn  
21 size, horn symmetry and age (Pérez et al., 2011). In the *Els Ports de Tortosa i Beseit* National  
22 Game Reserve, NE Spain, Iberian ibex males have been trophy-harvested over the last four  
23 decades. Individuals of low phenotypic value are also selectively removed in an attempt to reduce  
24 the intraspecific competition and to limit the reproduction of undesired phenotypes (Pérez et al.,  
25 2011). This harvesting regime has been seen as a management strategy to ensure the long-term  
26 sustainability of the hunting activity because it counteracts the undesirable effects of trophy  
27 hunting on the distribution of the affected phenotypic trait, the horn size and shape. Although this  
28 strategy might be enough to offset the evolutionary consequences of trophy hunting (Mysterud  
29 and Bischof, 2010), the lack of knowledge on how environmental conditions may affect horn  
30 growth patterns hampers the implementation of spatially explicit countermeasures to alleviate  
31 trophy hunting impacts. A better understanding of horn growth patterns would therefore be a most  
32 welcome first step towards the effective management of this species. Taking advantage of a long-  
33 term monitoring of an Iberian ibex population, we here aim to: i) explore whether individual  
34 heterogeneity, cohort and sampling locations foster well-differentiated horn growth patterns in  
35 male ibexes and ii) assess if compensatory horn growth occurs. Horn growth patterns and  
36 phenotypic quality differ sharply between individuals and this difference may be exacerbated by  
37 environmental conditions (Alpine ibex, Bergeron et al., 2008; thinhorn sheep *Ovis dalli*, Loehr et

1 al., 2010). Because horns are energetically costly to produce and carry, we expect marked  
2 individual heterogeneities in their expression (Hypothesis 1) and evident plasticity in horn growth  
3 patterns between habitats, *i.e.* the correlation between successive horn growth segments is  
4 expected to be influenced by the habitat characteristics (Hypothesis 2). Growing evidence from  
5 field studies suggests that compensatory horn growth is negligible in tribe *Caprini* (*e.g.* Toïgo et  
6 al., 2013; Festa-Bianchet et al., 2004), however, the relationship between compensatory horn  
7 growth and habitat characteristics remains little explored in species belonging to this prominent  
8 tribe (but see Corlatti et al. 2015 who explored this relationship in Alpine chamois, tribe  
9 *Rupicaprini*). We here hypothesise that the large variability in habitat characteristics found in our  
10 study area may allow for compensatory horn growth to occur in male ibex inhabiting specific  
11 locations (Hypothesis 3).

## 12 13 **2. Material and methods**

### 14 15 **2.1. Study area**

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17 We used accurate measurements of 24,615 annual horn growth segments from 2,145 male  
18 ibexes sampled at “Els Ports de Tortosa i Beseit” National Game Reserve, north-eastern Spain  
19 (PTB, hereafter; 40°48’N, 0°19’E, Fig. 1). PTB covers an area of 28,587 ha. The landscape is  
20 heterogeneous and encompasses a range of Mediterranean-type habitats interspersed by pastures  
21 and crops. The substrate is calcareous and the vegetation is mainly composed by Mediterranean  
22 forests of *Quercus ilex* and *Pinus halepensis*. The evergreen sclerophyll shrubland characterizes  
23 the east part of the study area and harbors the greatest diversity of plant species.

### 24 25 **2.2. Iberian ibex sampling**

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27 All sampled animals were legally and selectively hunted over 21 years (from 1995 to  
28 2016). Sex was determined by visual inspection and age (years) was visually assessed from horn-  
29 segment counts (see for details Fandos, 1991). The measurements of annual segments were taken  
30 to the nearest mm with a nylon tape measure. The oldest and outermost annual segment was  
31 excluded from our analyses due to abrasion (Álvarez, 1990) and maternal effects (Giacometti et  
32 al., 2002). Most ibexes had 10-14 growth segments per horn which indicates that they were 11-  
33 15 years old when hunted. More than 14 or less than 10 segments per horn were only found in  
34 25% of males.

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### 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.

## 1           **Results**

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3           Total horn length are driven by the male's age ( $\beta = 5.19$ ,  $SE = 0.02$ ,  $t = 330.30$ ,  $P <$   
4  $0.0001$ ,  $R^2 = 0.51$ , Fig. 2). Regarding the growth patterns of annual segments, the most  
5 parsimonious model included the effects of age, cohort, habitat cluster and the interaction between  
6 age and habitat cluster ( $AIC = 97961.71$ ,  $DIC = 97867$ ). The second most competitive model only  
7 includes the effects of age and habitat cluster, however was at approximately 80 AIC units from  
8 the most parsimonious model ( $AIC = 98041.68$ ,  $\Delta AIC = 79.97$ ,  $DIC = 98041.68$ ). LRT  
9 demonstrated that male identity was highly significant (LRT between the full model and the  
10 model without random effect = 702.99, d.f. = 7,  $P < 0.001$ ). Among-individual variations  
11 accounted for 27.75% of observed differences in annuli length, confirming our first hypothesis  
12 (Hypothesis 1). As expected, we reported a significant decrease of the annual segment length  
13 during adulthood ( $\beta = -0.24$ ,  $SE = 0.003$ ,  $t = -66.38$ ,  $P < 0.001$ ), particularly evident after the age  
14 of eight (Fig. 3). On the other hand, cohort had no significant effect on the growth patterns of  
15 annual segments ( $\beta = 0.002$ ,  $SE = 0.003$ ,  $t = 0.60$ ,  $P = 0.55$ ). The annual segments of males  
16 harvested in shrubland habitats are significantly longer than the segments of males harvested in  
17 forest-dominated areas ( $\beta = 0.43$ ,  $SE = 0.05$ ,  $t = 9.23$ ,  $P < 0.001$ ). This result indicates that male  
18 ibexes exhibit substantial phenotypic differences among habitats, confirming our expectations  
19 (Hypothesis 2). Male's age and habitat interacted significantly suggesting that the pace of horn  
20 growth decreased faster in the shrubland habitats ( $\beta = -0.05$ ,  $SE = 0.01$ ,  $t = -10.13$ ,  $P < 0.001$ ).  
21 With regards to compensatory horn growth, our results (the length of L2 was positively correlated  
22 with the length of L3-L6:  $\beta = 0.42$ ,  $SE = 0.03$ ,  $t = 13.55$ ,  $P < 0.001$ ) corroborate the third  
23 hypothesis (Hypothesis 3, Fig. 4), and reinforce the conclusions of previous studies that this  
24 mechanism in species belonging to the tribe *Caprini* is weak or absent. Our results further  
25 suggested that neither cohort effects ( $\beta = -0.0004$ ,  $SE = 0.0003$ ,  $t = -1.31$ ,  $P = 0.18$ ) nor habitat  
26 differences ( $\beta = -0.05$ ,  $SE = 0.06$ ,  $t = -0.82$ ,  $P = 0.41$ ) promote the occurrence of this mechanism.  
27 The pairwise analyses showed that the length of subsequent annual segments are positively  
28 correlated and therefore no evidences for fine-scale compensatory growth were detected (L3-L2:  
29  $\beta = 0.42$ ,  $P < 0.001$ ; L4-L3:  $\beta = 0.74$ ,  $P < 0.001$ ; L5-L4:  $\beta = 0.71$ ,  $P < 0.001$ ; L6-L5:  $\beta = 0.64$ ,  $P$   
30  $< 0.001$ ).

## 31           **Discussion**

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34           The characteristics of our dataset (*e.g.* large number of yearly-horn segments taken from  
35 many individuals evenly distributed over the study area) provides an excellent opportunity to  
36 explore horn growth patterns and test for compensatory horn growth in male Iberian ibexes. Our  
37 results show that individual characteristics lead to well-differentiated horn growth trajectories and

1 provide statistical support for an evident phenotypic plasticity in horn growth, probably due to  
2 differences in habitat characteristics and quality of food resources. We reported a positive  
3 relationship between L2 and the horn length between the annuli L3-L6, which confirms that  
4 compensatory growth of horns length does not occurs in male ibexes, a pattern already described  
5 in other studies on ungulates (Alpine ibex: Toïgo et al., 1999, Bergeron et al., 2008, Toïgo et al.,  
6 2013; Bighorn rams: Festa-Bianchet et al., 2004). Our study goes one step further suggesting that  
7 the absence of compensatory horn growth in Iberian ibex does not depend on the cohort or habitat  
8 characteristics. The positive correlation between L2 and L3-L6 indicates that L2 could be used as  
9 a reliable proxy of horn size at older ages and suggests that males with fast-growing horns early  
10 in life will probably become large-horned mature males. The absence of compensatory horn  
11 growth may exacerbate individual differences in total horn length among mature males because  
12 small-horned young males will not be able to catch-up large-horned young males later in life  
13 (Bergeron et al., 2008).

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

31       There are some possible explanations, ranging from ontogenetic to environmental, to  
32 explain the effects of temporal and spatial variability of forage quality in alpine ungulates. First,  
33 seasonal and environmental-driven variations in forage availability/quality may lead to poor  
34 maternal cares during prenatal and postnatal stages, which affects offspring mass and survival  
35 (Landete-Castillejos et al., 2009). Second, because the synchrony of parturition time plays an  
36 important role in among-individual variation, too early or too late neonates may mismatch the  
37 peak of vegetation productivity and/or climate mildness (Feder et al., 2008). This seems to be set



1 a vicious circle as early nutritional deficits can have negative effects on the adult survival and its  
2 offspring (Burton and Metcalfe, 2014).

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

32 Our study is correlative which represents an important caveat to our analyses. We do not  
33 control for genetic effects, that may represent an evolutionary constraint to compensatory horn  
34 growth, or for the nutritional value of vegetation units, which hampers the description of the  
35 relationships between differences in habitat characteristics and the possibility of compensatory  
36 horn growth. Experimental long-term studies need to be run in order to shed light about cause-  
37 effect relationships of compensatory horn growth in ungulates. Because trade-offs in relative

1 allocation depends on environmental conditions and total resource acquisition (Descamps et al.,  
2 2016), we argue that compensatory horn growth may be adaptive and contingent on region. We  
3 also advocate that future approaches beholding a geographically extensive sampling and the  
4 incorporation of ecologically, epidemiologically and genetically related variables, as well as the  
5 study of others morphological parameters, are increasingly necessary to understand the long-term  
6 consequences of size-selective harvesting and nutritional deficits on horn growth patterns of  
7 *Caprinae* populations. Nevertheless, we demonstrated that habitat characteristics are one of the  
8 key variables that foster significant differences in the males horn length. This information is of  
9 great interest for hunting associations and wildlife managers as it provides scientific support for  
10 design habitat management actions aimed at improving the phenotypic quality of ibex males and  
11 mitigating the impacts of trophy hunting.

### 12

### 13 **Author contributions**

14  
15 JC, JMP, CF, NP and ES conceived the study. OE, JMP and XOB collected the data. JC and ES  
16 analysed the data. JC, JMP, NP and ES wrote the paper. All authors contributed to the  
17 development of ideas and approved the final version of the manuscript.

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

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

7

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

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

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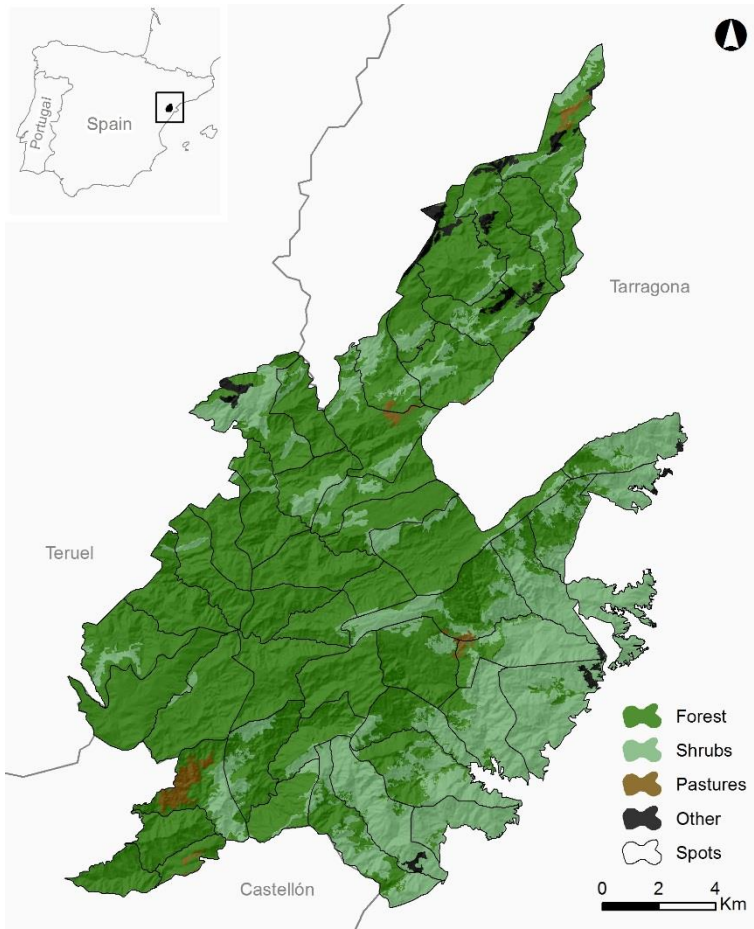
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Figure 1.



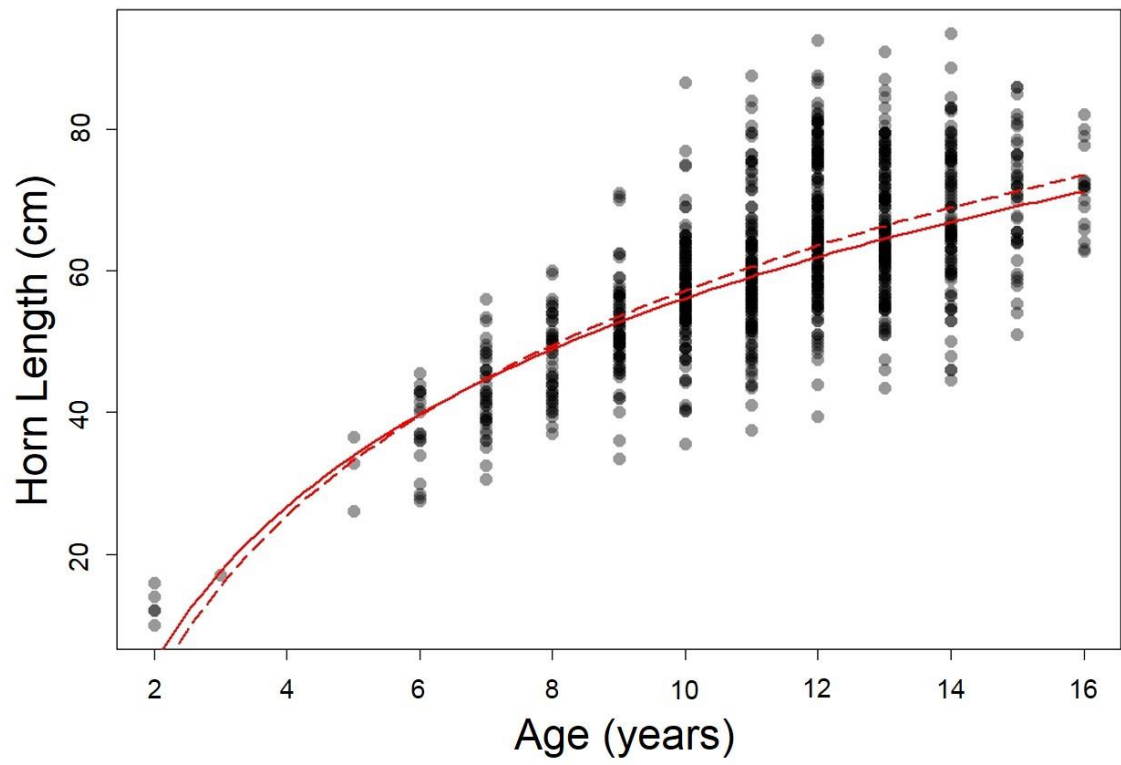
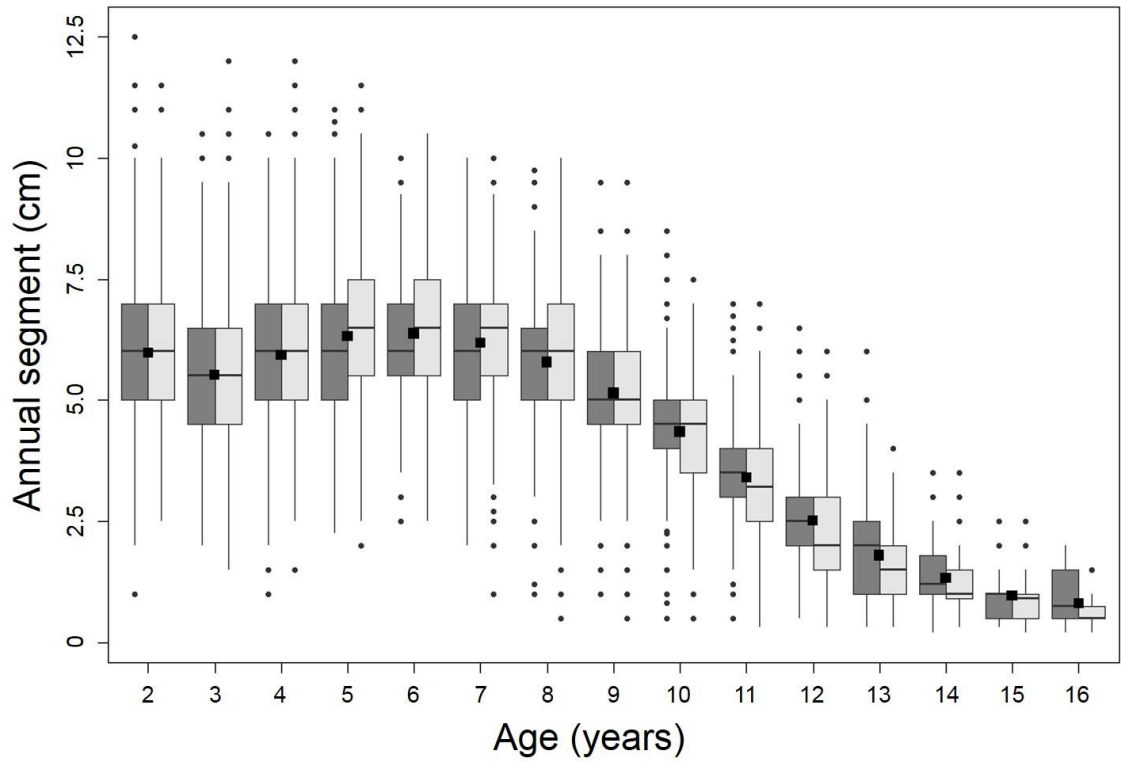
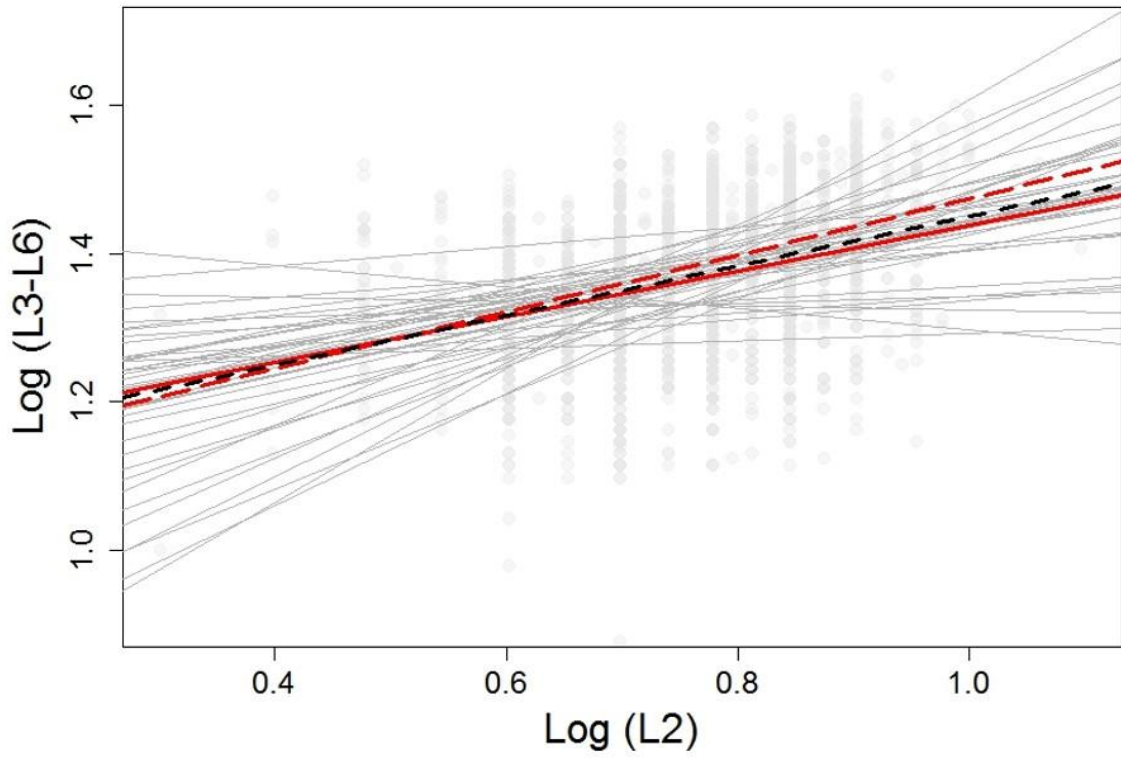


Figure 2.

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2 Figure 4.