

# Effects of season, age and body condition on allocation to testes mass in Iberian ibex

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## Keywords

*Capra pyrenaica*; mating tactic; phenotypic plasticity; sperm competition; testis; ungulate.

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## Abstract

Sperm competition is a powerful evolutionary force, and understanding the factors that regulate testes characteristics may lead to a better understanding of the variability in male reproductive success. We explored the effects of age, body condition and season on relative testes mass in the Iberian ibex *Capra pyrenaica*. We analysed the variability of testes mass from 175 individuals, using a model selection approach based on Akaike's information criterion corrected for a small sample size. The results suggest that season, age and body condition influenced relative testes mass. Allocation to testes mass was greatest in the rutting season (autumn) and at ages that are associated with a subordinate status and a coursing, rather than mate-guarding, reproductive strategy. In addition, males in good condition had relatively heavier testes than those in poor condition. Thus, testes mass in Iberian ibex is governed by multiple factors, and this study leads to a better understanding of gonad plasticity in this polygamous ungulate. The effect of age matches the predictions from theoretical studies on sperm competition, which suggests greater allocation to testes in disadvantaged males.

## Introduction

Testes size is linked to mating strategies (Harcourt *et al.*, 1981; Harcourt, Purvis & Liles, 1995) and reproductive success (Schulte-Hostedde & Millar, 2004) via sperm competition (Birkhead & Møller, 1998). More specifically, multi-male mating systems are associated with relatively larger testes than single-male mating systems (Reynolds & Harvey, 1994; Harcourt *et al.*, 1995). Larger testes provide an advantage in terms of sperm competition (Schärer, Ladurner & Rieger, 2004; Schärer & Vizoso, 2007) and maximize reproductive success (Preston *et al.*, 2003; Schulte-Hostedde & Millar, 2004).

Intra-specific variations in mating tactics may also affect testes (Awata *et al.*, 2006). In seasonal breeding species, testes size (and correlated traits) often vary throughout life (Gupta *et al.*, 2000). In addition, body condition is generally positively correlated with testes size (Schulte-Hostedde, Millar & Hickling, 2003; Schulte-Hostedde & Millar, 2004).

Testes size is positively correlated with male reproductive success (Preston *et al.*, 2003). Ungulates display large variations in sex-specific reproductive success (Vanpé *et al.*,

2008), but few studies have examined the causes and consequences of testes size in wild species (but see Ginsberg & Rubenstein, 1990; Preston *et al.*, 2003).

Like other caprines (Couturier, 1962; Grubb, 1974; Nievergelt, 1974; Schaller, 1977; Habibi, 1994; Preston *et al.*, 2003; Pelletier, Hogg & Festa-Bianchet, 2006), the Iberian ibex *Capra pyrenaica* is a medium-sized polygamous ungulate in which rutting is characterized by direct conflicts over access to females and mate-guarding is a primary tactic (Alados, 1986; Alvarez, 1990). As in closely related species (Couturier, 1962; Grubb, 1974; Nievergelt, 1974; Schaller, 1977; Habibi, 1994; Preston *et al.*, 2003; Pelletier *et al.*, 2006), the most successful tactic, 'tending', involves guarding of a single oestrous female (Couturier, 1962; Pelletier *et al.*, 2006). Subordinate males will attempt to take advantage of any separation between an oestrous female and the dominant male. Separation may occur when the dominant male is in combat with other males, which may lead to rapid male-female chases during which males attempt to force copulation with the oestrous female. This strategy of male-female chases with attempts of forced copulation is called the 'coursing' mating tactic (Couturier, 1962; Pelletier *et al.*, 2006).

In this study, we examined the correlative factors of testes mass in Iberian ibex and tested predictions from different hypotheses.

(1) According to the 'terminal investment' hypothesis (Clutton-Brock, 1984), as males age, their residual reproductive value decreases. Hence, males should increase their investment in reproduction (Williams, 1966; Pianka & Parker, 1975) and their allocation to testes mass.

(2) Based on the 'male mating strategy' (Pelletier *et al.*, 2006), the allocation to testes mass should peak in males using the mating tactic with the highest reproductive success (tending in caprines; Couturier, 1962; Nievergelt, 1974; Habibi, 1994; Hogg & Forbes, 1997; Pelletier *et al.*, 2006).

Despite being based on different theoretical concepts, both hypotheses 1 and 2 predict a greater allocation to testes in older males.

(3) Disadvantaged males (due to dominance or female choice) should invest more in ejaculate and testes size compared with favoured males (Parker, 1990; Tazzyman *et al.*, 2009). In caprines, tending males guard females and perform 'retaliatory' copulations after regaining control of an oestrous female that was chased by courting males (Couturier, 1962; Hogg, 1988). Consequently, courting males may be under selective pressure, and, according to theoretical studies of sperm competition (Parker, 1990; Tazzyman *et al.*, 2009), allocation to testes mass should peak in subordinate young males.

(4) As nutrition and body condition are usually positively correlated with testes size (Schulte-Hostedde & Millar, 2004; Schulte-Hostedde, Millar & Hickling, 2005a; Brito *et al.*, 2007), animals in good condition should have larger testes than those in poor condition.

(5) Like other organs (Piersma & Lindström, 1997; Piersma & Drent, 2003), testes show seasonal phenotypic plasticity (Nigi *et al.*, 1980; Glover, D'Occhio & Millar, 1990). Testes are larger during the rut in ungulates (Couturier, 1962) and the Iberian ibex may have a seasonal pattern characterized by greater allocation to testes mass in the autumn.

## Materials and methods

### Study site and population

We analysed testes mass in male Iberian ibex from the Sierra Nevada mountain range (36°00'–37°10'N, 2°34'–3°40'W, southern Spain) in 1995–1998, 2000–2003, 2007 and 2008. This population was intensively monitored (Pérez, Granados & Soriguer, 1994; Pérez *et al.*, 1997), and animals were culled by National Park (Espacio Natural de Sierra Nevada) staff for research and management purposes. We used data from 175 macroscopically healthy males. After culling, each individual was weighed to the nearest 500 g and shoulder height was measured to the nearest 0.5 cm. Age was assessed based on horn segment counts (Fandos, 1991). During necropsy, the testes were removed and weighed to the nearest 0.01 g. The arithmetic mean of the two testicles was used as the overall testicular mass.

## Analysis

Given that age is closely correlated with mating strategy in caprines (Couturier, 1962; Grubb, 1974; Habibi, 1994; Pelletier *et al.*, 2006), we used age as an indicator of mating tactics. Courting is used by subordinate young males and guarding is used by older dominant males (Couturier, 1962; Grubb, 1974; Habibi, 1994; Pelletier *et al.*, 2006).

To examine the relative effects of age, body condition and season, we estimated several residuals (detailed below), and in each case, chose the best-fitting regression between linear and non-linear models based on Akaike's information criterion (AIC – a tool for model selection; Burnham & Anderson, 2002). We log-transformed ( $\log_{10}$ ) body mass and testes mass to normalize the data (Shapiro–Wilk test). Shoulder height is an important growth parameter during the skeletal development of Iberian ibex (Fandos, 1991). We controlled for allometry in testes mass using residuals from linear regression of the log-transformed arithmetic mean of the mass of the two testes on shoulder height (Schulte-Hostedde *et al.*, 2005b) as the dependent variable in all our analyses. We defined seasons as follows: winter (15 December to 5 March), spring (6 March to 15 June), summer (16 June to 15 September) and autumn (16 September to 14 December) (Consejería de Medio Ambiente, 2004). To account for seasonality in body condition, we calculated the residuals of the linear regression of log-transformed body mass on shoulder height (Schulte-Hostedde *et al.*, 2005b) fitted separately for each season. We controlled for expected effects of age on body condition (Harper, 1998; Kojola, *et al.*, 1998; Kyle *et al.*, 2001) and observed a non-linear relationship between the two factors [residual sum of squares of the fitted model (RSS) = 3.799]. Consequently, we used the residuals of the fitted logistic regression of seasonal-specific body condition on age as the body condition index.

To test the effects of age, body condition and season on the allocation to testes mass, we used generalized additive mixed models (Wood, 2006; Zuur, Ieno & Smith, 2007), using an information-theoretic approach based on AIC corrected for a small sample size (AIC<sub>c</sub>; Burnham & Anderson, 2002). The sampling period was introduced into models as the month at which each individual was culled (coded as 12 months). Year was also included as a random factor (Wood, 2006). The analysis identified the most parsimonious model (lowest AIC<sub>c</sub>) of all possible subsets, ranging from the null model (MO, intercept only) to a model with explanatory variables and two-order interactions. The relative importance (RI) of the explanatory variables was examined to highlight evidence for the importance of each variable within the set of models (Anderson, Burnham & Thompson, 2000; Anderson *et al.*, 2001; Burnham & Anderson, 2002). Adjusted  $R^2$  values, providing an estimate of the model fit (Wood, 2006), are also presented.

## Results

Season (S), age (A) and body condition (BC) were found to influence allocation to testes mass in Iberian ibex. According to our model selection procedure, the best model was

**Table 1** Model selection for determining factors of relative testes mass in Iberian ibex *Capra pyrenaica*

Model	Sample size	<i>K</i>	AIC <sub>c</sub>	$\Delta i$	$L(gil/x)$	<i>W<sub>i</sub></i>	<i>R</i> <sup>2</sup> (adj)	RI	
S+A+BC+S*A	175	9	-89.75	0	1	0.41	0.82	S	1
S+A+BC+S*BC	175	9	-87.86	1.89	0.39	0.16	0.82	BC	1
S+A+BC+S*A+A*BC	175	10	-87.52	2.24	0.33	0.14	0.82	A	1
S+A+BC+S*A+S*BC	175	10	-87.50	2.25	0.32	0.13	0.82	S*A	0.84
S+A+BC+S*BC+A*BC	175	10	-86.75	3.00	0.22	0.09	0.82	S*BC	0.60
S+A+BC+S*A+S*BC+A*BC	175	11	-85.24	4.52	0.10	0.04	0.82	A*BC	0.28
S+A+BC	175	7	-82.89	6.86	0.03	0.01	0.83		
S+A+BC+A*BC	175	8	-81.44	8.31	0.02	0.01	0.83		
S+BC+S*BC	175	8	-67.89	21.87	0	0	0.76		
S+A+S*A	175	7	-63.63	26.12	0	0	0.79		

Relative testes mass is corrected for allometry.

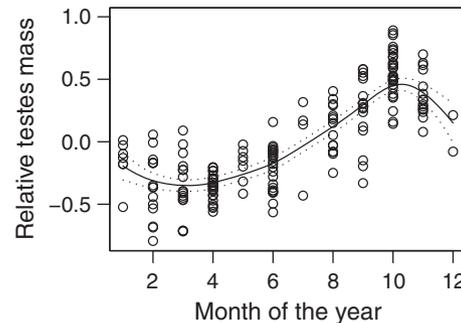
S, season; A, age; BC, body condition; \*, interaction; MO, null model; *K*, number of estimated parameters; AIC<sub>c</sub>, Akaike's Information Criterion corrected for small sample size;  $\Delta$ AIC<sub>c</sub>, difference of AIC<sub>c</sub> between the model and the most-parsimonious model;  $L(gil/x)$ , probability of the model being the Kullback–Leibler best model given the dataset; *W<sub>i</sub>*, Akaike weight of the model; *R*<sup>2</sup> (adj), adjusted *R*<sup>2</sup> of the fitted model; RI, relative importance of factors. Only the 10 best models are reported; see Burnham & Anderson (2002) and Wood (2006).

'S+A+BC+S\*A' ( $W_{S+A+BC+S*A} = 0.41$ , see Table 1;  $W_i$  = Akaike weight of the model), followed by 'S+A+BC+S\*BC' ( $W_{S+A+BC+S*BC} = 0.16$ , see Table 1). Allocation to testes mass was season dependent, peaking in the month before rutting (October) and reaching its lowest point in spring (Fig. 1). Size-corrected testes mass also varied with age, but with season-dependent trends as suggested by the interaction between season and age in the best model (Fig. 2). From winter to summer, relative testes mass was positively correlated with age, whereas in autumn (the rutting season) allocation to testes peaked in males that were near their asymptotic skeletal development (4–6 years old; Couturier, 1962; Fandos, 1991; Serrano, Gállego & Pérez, 2004). Body condition was positively correlated with relative testes mass, although the slope of this relationship may be season dependent, as suggested by the second model ( $\Delta$ AIC<sub>c</sub><sub>S+A+BC+S\*BC</sub> = 1.89; Fig. 3).

All the best-ranked models included all explanatory variables. Thus, season, body condition and age had an RI equal to 1. By contrast, the RIs of the interactions between season and age (S\*A) and between season and body condition (S\*BC) were higher than the RI of the interaction between age and body condition (A\*BC) (Table 1). Finally, estimates of the adjusted *R*<sup>2</sup> of the fitted models were high (Table 1), and thus the factors explained a great proportion of the variability in testes mass (about 80%). Data on mean testes and body mass provide a comparison with other species (Appendix S1).

## Discussion

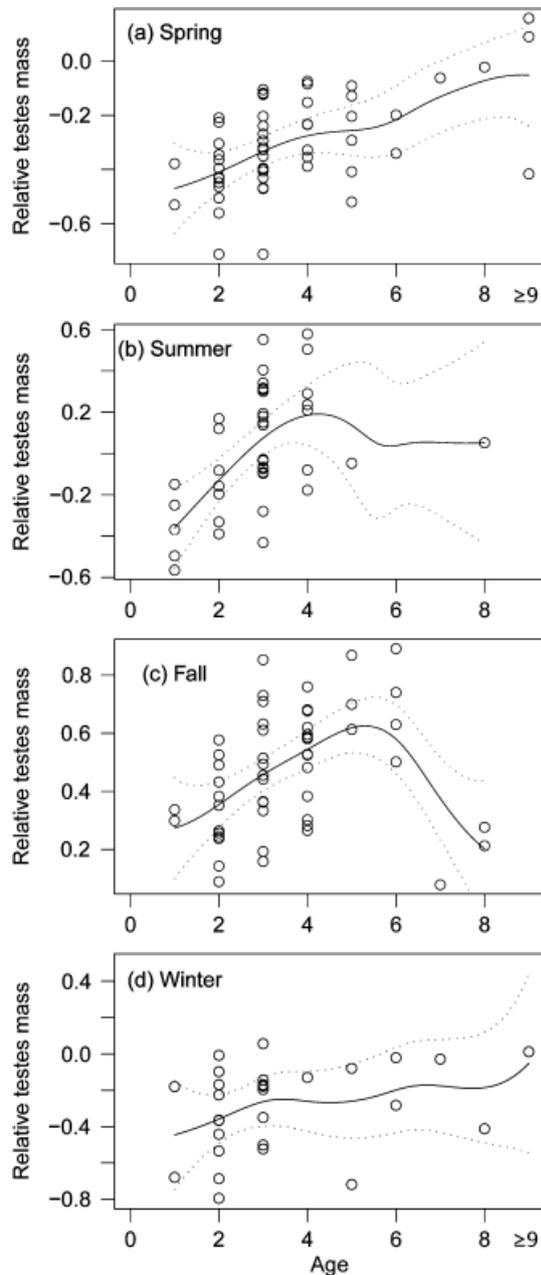
The present results provide evidence that testes mass varies with the season, age and body condition in Iberian ibex. Previous studies of sperm competition and evolution of testes size in ungulates examined behavioural traits that optimize sperm deposition in relation to mating tactics (Hogg, 1988; Ginsberg & Rubenstein, 1990) or the relationship between testes size and reproductive success (Preston *et al.*, 2003).



**Figure 1** Effect of season on relative testes mass (corrected for body size) in Iberian ibex *Capra pyrenaica* (Sierra Nevada, Spain), according to the selected generalized additive mixed model (the solid line represents the estimated pattern and the dotted lines indicate 95% confidence intervals; Wood, 2006).

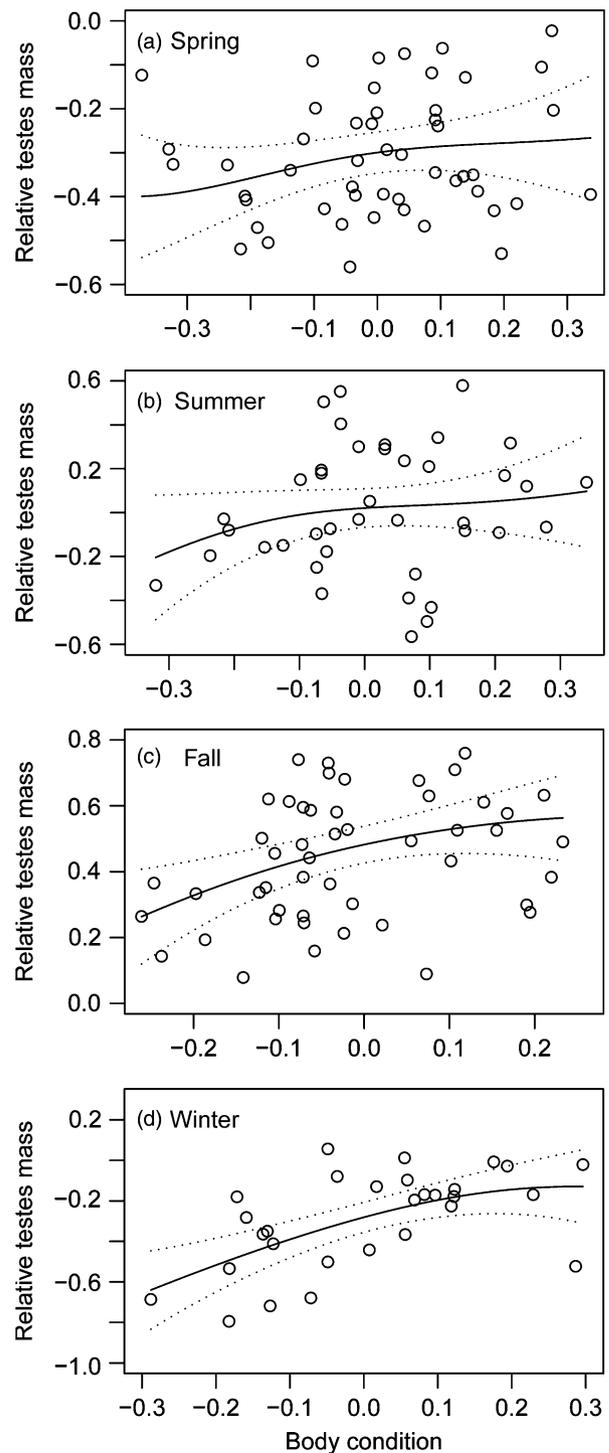
## Testes mass, age and mating tactics

In several caprids, including the Iberian ibex, mate-guarding (tending) is the primary mating tactic (Couturier, 1962; Pelletier *et al.*, 2006). The use of this tactic increases with rank (Pelletier *et al.*, 2006), which is also positively correlated with age (Couturier, 1962; Grubb, 1974; Habibi, 1994; Pelletier & Festa-Bianchet, 2006). Relative testes mass in autumn peaked in males that were near their asymptotic skeletal development. This result contradicts predictions based on 'terminal investment' (Clutton-Brock, 1984) and the 'male mating strategy' (Pelletier *et al.*, 2006), but matches predictions from theoretical studies on sperm competition games (Parker, 1990; Tazzyman *et al.*, 2009). In Iberian ibex, allocation to testes mass was higher at ages linked to subordinate status. In subordinate males, the courting mating tactic prevails in caprines (Couturier, 1962; Grubb, 1974; Habibi, 1994; Pelletier & Festa-Bianchet, 2006). Theoretical studies on sperm competition predict that disadvantaged males should invest more in ejaculate and testes size compared with favoured males



**Figure 2** Effect of age on relative testes mass (corrected for body size) in Iberian ibex *Capra pyrenaica* (Sierra Nevada, Spain), in (a) spring, (b) summer, (c) autumn and (d) winter (the solid line represents the estimated pattern and the dotted lines indicate 95% confidence intervals; Wood, 2006).

(Parker, 1990; Tazzyman *et al.*, 2009). This is supported by our study of Iberian ibex. Couraging males may compensate for lower access to females (Couturier, 1962; Hogg & Forbes, 1997) by increasing testis investment. This age-dependent testis investment may explain the significant number of paternities assigned to young and subordinate males (Coltman *et al.*, 1999, 2002; Wroblewski *et al.*, 2009).



**Figure 3** Effect of body condition on relative testes mass (corrected for body size) in Iberian ibex *Capra pyrenaica* (Sierra Nevada, Spain), in (a) spring, (b) summer, (c) autumn and (d) winter (the solid line represents the estimated pattern and the dotted lines indicate 95% confidence intervals; Wood, 2006).

Larger testes are probably advantageous when dominant males cannot control access to all oestrous females (Preston *et al.*, 2003).

Once males reached their asymptotic mass, social rank, which also depends on the phenotypic quality and on the fine-scale age structure of the population, is more closely correlated with mating tactics than age (Pelletier *et al.*, 2006). Hence, further analysis of the determining factors of testes mass should include this behavioural dimension. A role for senescence might explain the decrease in relative testes mass in older animals. However, only one male in our sample was over 10 years old, and senescence only becomes evident in ibexes at about 10–12 years of age (Couturier, 1962; Schaller, 1977; Toïgo *et al.*, 2007).

### Testes mass, seasonality and phenotypic plasticity

Caprids are seasonal breeders (Couturier, 1962; Nievergelt, 1974; Schaller, 1977) and, as expected on the basis of testicular activity and plasma testosterone concentrations (Toledano-Díaz *et al.*, 2007), allocation to testes mass was the highest in the autumn in Iberian ibex and declined considerably thereafter. Testes investment and increased testosterone levels may favour muscular mass (Schulte-Hostedde *et al.*, 2003) and aggressiveness (Muller & Wrangham, 2004; Archer, 2006). Increased muscular mass, aggressiveness, testes size and testosterone levels probably improve male reproductive success in social species with limited mate access (Couturier, 1962; Grubb, 1974; Habibi, 1994; Pelletier *et al.*, 2006) and high intra-group competition (Krause & Ruxton, 2002). Investing earlier in testes and then maintaining larger testes might confer preferential access to precocious oestrous females or to food during periods of seasonal scarcity. The interaction between body condition and season in Iberian ibex suggests that males in good condition might invest earlier and then maintain testis investment. This inter-individual variability in testes investment is likely to affect the temporal variation in reproductive effort and in siring success (Preston *et al.*, 2001; Mysterud *et al.*, 2008) and might be relevant for inter-individual heterogeneity in testosterone-linked immunodepression and reproductive costs (Zuk, 1996; Klein, 2000; Sinervo & Clobert, 2008; Grear, Perkins & Hudson, 2009).

The present results suggest that testis investment in Iberian ibex is controlled by several factors, and we provide empirical evidence supporting predictions from theoretical studies on sperm competition games (Parker, 1990; Tazzyman *et al.*, 2009).

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Data on testes and body mass in Iberian ibex (Sierra Nevada, Spain).

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