



## Intra-sexual competition alters the relationship between testosterone and ornament expression in a wild territorial bird



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### ABSTRACT

In a reliable signalling system, individual quality is expected to mediate the costs associated with ornamental displays, with relatively lower costs being paid by individuals of higher quality. These relative costs should depend not only on individual quality, but also on levels of intra-sexual competition. We explored the current and delayed effects that testosterone implants have on bird ornamentation in populations with contrasted population densities, as a proxy for intra-sexual competition. In a replicated experiment, we manipulated testosterone in 196 yearling male red grouse *Lagopus lagopus scoticus* in autumn in populations of high and low levels of intra-sexual competition. Males were assigned to one of three exogenous testosterone (T) treatments: empty implants (T0), small T implants (T1) or larger T implants (T2). We monitored subsequent changes in testosterone levels, ornament size and carotenoid-based colouration, carotenoid levels and body condition from autumn to spring. Testosterone implants increased testosterone levels, comb redness and comb size, and decreased body condition but these effects depended on levels of intra-sexual competition. Specifically, T2-implanted birds increased testosterone levels and comb size more, and reduced body condition more, in populations where intra-sexual competition was low. In the following spring, testosterone levels of T2-treated birds kept increasing in populations where intra-sexual competition was high but not in populations where intra-sexual competition was low. Our results highlight that levels of intra-sexual competition alter the relationship between testosterone levels and ornament expression, influencing their condition-dependence; they also indicate that the outcome of standard hormone manipulation conducted in free-living animals vary depending on the population context.

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### Introduction

In many species, males display conspicuous traits considered to be a consequence of inter- and intra-sexual selection processes (Andersson, 1994). Different mechanisms have been proposed to explain the evolution and maintenance of these sexual traits (Maynard Smith and Harper, 2003). Among them, the Handicap Principle suggests that only high quality individuals should be able to afford the costs associated with signal production (Grafen, 1990; Zahavi, 1975). However, males have to compete for resources and the strength of that competition may influence the relative costs associated with the production of sexual traits and therefore the honesty of the signal. Intra-sexual competition is a major selective force in natural populations that strengthens selection on the expression of phenotypic traits (Calsbeek and Cox, 2010). Wild

animals have to adjust their resource allocation according to their surrounding environment (Maynard Smith, 1982; Maynard Smith and Harper, 2003). Thus, it is expected that intra-sexual competition may mediate the expression of secondary sexual traits and their associated costs.

Higher levels of intra-sexual competition have been shown to reduce the expression of secondary sexual traits (Vanpé et al., 2007; Vergara and Martínez-Padilla, 2012), possibly to reduce the behavioural and physiological costs associated with the expression of the trait and allowing individuals to successfully survive and reproduce in more competitive environments (Vergara and Martínez-Padilla, 2012). This individual plasticity in the expression of sexual traits may facilitate individuals in adjusting the production and maintenance costs of sexual traits according to their surrounding environment, as expected with honest sexual signals. The next issue, however, is to understand how those costs are traded-off when levels of intra-sexual competition differ.

Many animal social signals are testosterone-dependent, and for these traits, testosterone may help to disentangle how social context

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mediates the signalling costs. The expression of testosterone-dependent sexual traits imposes a cost on individuals, where only high quality individuals are able to stand the costs associated with the expression of the most elaborate displays according to the Immunocompetence handicap hypothesis (Folstad and Karter, 1992; but see Roberts et al., 2004). Unsurprisingly, testosterone levels in populations increase as intra-sexual competition does, but counter intuitively, testosterone levels of individuals living in more competitive environments are not associated with the expression of secondary sexual traits (Vergara and Martínez-Padilla, 2012) and are poorly linked to individual behaviour (Adkins-Regan, 2005; Fusani, 2008a,b). Thus, it is expected that the costs associated with increased testosterone levels for individuals living in more competitive environments should be higher (Folstad and Karter, 1992; Pérez-Rodríguez et al., 2006). Specifically, when competition for resources increases, individuals might be more constrained and less able to afford testosterone-related costs (Martínez-Padilla et al., 2010). As such, condition-dependence of sexual traits is expected to be stronger in areas of higher competition (Vergara et al., 2012a,b,c). If ornaments are costly to produce or maintain (Zahavi, 1975), the cost of producing a testosterone-dependent signal in less competitive environments is expected to be attenuated. Thus individuals can divert resources to other energetically demanding functions. Surprisingly, however, no study has specifically explored how levels of intra-sexual competition influence the costs of producing testosterone-dependent traits.

Studies of sexual selection have mainly focussed on ornament size or colour, but a deeper comprehension of the costs associated with ornamental displays requires a focus on different characteristics of the same trait. In birds, most yellow-red sexual traits are pigmented by carotenoids and can be testosterone-dependent (Alonso-Alvarez et al., 2009; Hill and McGraw, 2006; Kurtz et al., 2007; Martínez-Padilla et al., 2010; Mougeot et al., 2007). Carotenoids have immunostimulant and antioxidant properties and can be deposited in ornaments or used to enhance immune responsiveness (Lozano, 1994; von Schantz et al., 1999), playing a key role in the trade-off between self-maintenance and ornamentation. Testosterone can up-regulate levels of circulating carotenoids, which could buffer testosterone-mediated immunosuppression (Blas et al., 2006; McGraw and Ardia, 2007). However, the testosterone-dependent size and carotenoid colouration of the same ornament do not always provide information on the same individual qualities, possibly due to different allocation priorities (Martínez-Padilla et al., 2010). Moreover, individuals could change their carotenoid allocation priorities depending on conspecific density (Gautier et al., 2008; Martínez-Padilla et al., 2010). Therefore, if individuals can adjust their testosterone levels to the current social context, and if carotenoid allocation is testosterone-dependent, it is expected that the social context mediates the effect of testosterone on carotenoid allocation priorities (Martínez-Padilla et al., 2010).

In this paper, we explore how intra-sexual competition levels influence current and delayed effects that testosterone has on ornamental displays. We use red grouse (*Lagopus lagopus scoticus*) as a study species, and their supra-orbital combs (size and carotenoid-based colouration) as the focus sexual trait. Male red grouse display red supra-orbital red combs whose size and redness are testosterone and carotenoid-dependent, respectively (Martínez-Padilla et al., 2010; Mougeot et al., 2007, 2010). These combs are displayed during intra- and inter-sexual interactions and influence both dominance and mate choice (Redpath et al., 2006a). Red grouse populations cycle, with population density varying from 4- to more than 10-fold during the course of a population cycle and intra-sexual competition has been suggested as a leading hypothesis at explaining red grouse population cycles (Mougeot et al., 2003a). Changes in population density are associated with changes in the social structure of male populations (Mougeot et al., 2005c; Piertney et al., 2008) and changes in the levels of intra-sexual competition between males in autumn (Mougeot et al., 2003a,b; Watson, 1985). In fact, it has been shown that intra-sexual

competition in male red grouse increases with density with one year as a time lag (Mougeot et al., 2003a,b; Piertney et al., 2008). Specifically, as population density increases, competition between males for holding a territory in autumn increases, and successful territory owners have greater survival rates overwinter and breeding outcomes the following spring (Mougeot et al., 2003b; Redpath et al., 2006a; Watson and Moss, 2008). The association between male grouse density and aggressiveness has been consistently reported throughout the range of the species and has been suggested as a proximal factor causing population cycles in red grouse (Martínez-Padilla et al., 2014b).

We manipulated the levels of testosterone in young male grouse in autumn in 5 populations, which were all increasing and characterized by different densities, and therefore different levels of intra-sexual competition. Wild males were assigned to one of three exogenous testosterone (T) treatments: empty implants; small testosterone implants or larger testosterone implants. We then explored the current (during autumn, i.e. when implants were delivering the exogenous testosterone) and delayed effects (the following spring, i.e. after the implants were exhausted) of T-treatments on circulating testosterone levels, comb size, comb colour, circulating carotenoids and body condition. Adult males are dominant and more aggressive than yearlings (Mougeot et al., 2005b). In addition, adult and yearling red grouse differ in their survival prospects, breeding success, mating success, parasite levels, body mass and comb size (Mougeot et al., 2006; Redpath et al., 2006a; Seivwright et al., 2005; Vergara et al., 2012a,b). Thus, we studied only wild yearlings at their time of independence to avoid age-mediated biases (Mougeot et al., 2005a). We initially purged all males of their main parasite to avoid potential confounding effects, because parasites may influence aggressiveness and ornament expression (Martínez-Padilla et al., 2007, 2010; Mougeot et al., 2005b, 2007). We predicted that 1) levels of intra-sexual selection should influence the associations between ornament expression and testosterone levels, with birds in populations of high levels of intra-sexual competition being more constrained, and less able to translate increases in testosterone levels into enhanced ornament expression; 2) levels of intra-sexual competition should alter the effect of testosterone on carotenoid allocation to coloured ornamental traits. Specifically, we expected a weaker link between ornament colouration and circulating levels of carotenoids under more competitive populations, because carotenoids would be more likely to be used for alternative demanding functions. Finally, we predicted that 3) the expected negative effect of testosterone on individual condition would be less pronounced in populations where intra-sexual competition is low, as males would have more resources to counteract this effect.

## Material and methods

### General procedures

The experiment was conducted in autumn 2007 in 5 grouse populations (or moors) in the UK: Edinglassie and Invermark (north-east Scotland) and Catterick, Moorhouse and Geltsdale (North Yorkshire, England). Further details of the experimental manipulation of testosterone are given elsewhere (Martínez-Padilla et al., 2014a). In autumn, red grouse males start establishing their territories, keeping them overwinter in order to survive and breed in the next spring (Watson and Moss, 2008). The highest mortality rate occurs at the time young male red grouse become independent, in autumn, accounting for around 60% of mortality (Martínez-Padilla et al., 2014a). Holding a territory increases the probability of surviving overwinter for young males (Watson and Moss, 2008). In September 2007 (first capture or R1, Fig. 1 – see Appendix A), we caught young wild male red grouse (all born in summer 2007) by lamping and netting them at night. Birds were individually ringed and fitted with a radio collar with a unique frequency (TW3-necklace radio tags, Biotrack) to facilitate relocation and recapture in the field.

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