



## Evidence for multiple functions in a sexually selected ornament



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In gregarious animals, social interactions frequently take the form of dominance hierarchies that maintain stable relationships between individuals, and settle disputes without extra costs. Traits that function as signals of status can play an important role in mediating interactions among individuals, both in social and in sexual contexts. Carotenoid ornaments are more generally assumed to be sexually selected and not so relevant to general social contexts. However, it is possible for them to function in social contexts if they signal socially relevant aspects. Here we experimentally analysed social dominance and resource control in male groups of a gregarious species, the European serin, *Serinus serinus*, in relation to a sexual ornament. We tested whether yellow carotenoid-based plumage coloration, age, body size and testosterone were predictors of social dominance over a nonsexual resource (i.e. feeding context). We showed that dominance hierarchies were steep and were related to testosterone levels and ornamental coloration, particularly the male yellow carotenoid-based crown patch. Our results suggest that carotenoid-based colour and testosterone levels can be reliable predictors of social status in agonistic encounters in groups of male serins. Moreover, together with previous work on the sexual function of male coloration, this study provides evidence that male serin yellow coloration has a dual function in both sexual and nonsexual contexts. These results raise the possibility that this ornament may have evolved and be maintained via social selection over social competition/cooperation for reproductive opportunities and ecological resources.

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Social relationships in group-living species are an important mechanism for maintaining the balance between gregariousness and conflict between group members. While individuals might increase their fitness by living in groups, they still have to compete over a wide range of limited resources (e.g. food or mating partners), which can lead to increased agonistic interactions between individuals (Alexander, 1974). As aggression can be costly, animals have evolved several strategies to avoid excessive energy expenditure and physical injuries (Parker, 1974), such as the establishment of dominance hierarchies and status signalling. The latter can be an indicator of the opponent's competitive ability, providing decisive information to predict the outcome of a confrontation (Rohwer, 1975) or affect the various stages of agonistic escalation (Chaine & Lyon, 2008; Enquist & Leimar, 1990), which can be particularly relevant in gregarious species, since it can help mediate situations of conflict between members of a group.

The evolution of ornamental traits has commonly been attributed to sexual selection (Andersson, 1994), through either courtship and fighting or mate choice. In contrast, the armament – ornament model predicts that an interaction between contexts can exist, that is, a signal evolved through sexual competition (e.g. weapons) can be co-opted in intersexual choice, since it is a reliable proxy of quality, and occasionally losing its original function (Berglund, Bisazza, & Pilastro, 1996). The concept of social selection considers all socioecological interactions (in both sexual and nonsexual contexts) as selective forces that collectively shape the phenotype (Lyon & Montgomerie, 2012; Tanaka, 1996; West-Eberhard, 1983; but see Clutton-Brock & Huchard, 2013). Thus, the social selection perspective encourages researchers to investigate whether nonsexual contexts are involved in signal evolution (Lyon & Montgomerie, 2012; West-Eberhard, 2014) and, therefore, tests revealing interactions between sexual and nonsexual selection are much needed.

Ornamental traits for social signalling are widespread among vertebrates (Clutton-Brock & Huchard, 2013; Searcy & Nowicki, 2005). Certain traits such as pigment-based coloration can reliably

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signal an individual's fighting ability and, as such, predict the outcome of conflicts or the position of individuals within dominance hierarchies. In contrast to melanin pigmentation, there has been much less research on the function of carotenoid-based traits in status-signalling contexts, but studies suggest they are widespread among taxa such as reptiles (Hamilton, Whiting, & Pryke, 2013), fish (Evans & Norris, 1996) and birds (Griggio, Serra, Licheri, Monti, & Pilastro, 2007). Whether or not they have a sexual function, carotenoid-based signals have the potential to convey information in competitive contexts. Variation in carotenoid coloration is associated with an individual's ability to forage, assimilate and process carotenoids (reviewed in Blount, 2004; Olson & Owens, 1998). Also, since these pigments are vital nutrients, important as immunoenhancers and antioxidants (reviewed in Lozano, 1994; Olson & Owens, 1998; see also Hill & Johnson, 2012), it is often the case that these signals are indicators of individual health condition. In such cases, high-quality individuals should exhibit increased ornamentation and thus advertise their superior competitive ability, irrespective of whether carotenoid coloration is dependent on trade-offs for different functions (Lozano, 1994) or is a direct indicator of both physiological and metabolic capacity, as well as immune condition (Hill & Johnson, 2012).

A positive relation between carotenoid-based plumage and fighting ability has been demonstrated for several bird species, for both red (e.g. widowbirds, *Euplectes ardens* and *Euplectes axillaris*, Pryke, Lawes, & Andersson, 2001; Pryke & Andersson, 2003) and yellow feathers (e.g. rock sparrow, *Petronia petronia*, Griggio et al., 2007; yellow warbler, *Setophaga petechia*, Studd & Robertson, 1985). A recent experimental study with golden-crowned sparrows, *Zonotrichia atricapilla*, has shown that multiple signals of carotenoid and melanin were independently related with social dominance in mixed-sex dominance trials (Chaine, Roth, Shizuka, & Lyon, 2013). In the Gouldian finch, *Erythrura gouldiae*, a genetically based colour-polymorphic species, both red-headed males and females are more aggressive and dominant towards black and yellow colour morphs (Pryke, 2007; Pryke & Griffith, 2006). While all these studies were directed to carotenoid-based status signals, in most cases dominance was only assessed in a sexual competitive context, without considering a social selection perspective.

Our study species, the European serin, *Serinus serinus*, is a gregarious, nonterritorial, socially monogamous finch that exhibits male mate-guarding behaviour (Mota & Hoi-Leitner, 2003). Male European serins display a sexually dichromatic yellow carotenoid-based breast and crown, resulting from a single annual moult 6–8 months before breeding. Male coloration has been shown to be a sexually selected trait preferred by females (Leitão, Monteiro, & Mota, 2014). In this study, we investigated whether male serin yellow carotenoid-based coloration plays a role in male social dominance over nonmating resources. Since testosterone is known to modulate a set of behaviours such as courtship, parental and aggressive behaviours (Adkins-Regan, 2005), we also measured testosterone levels in order to determine its relation to male dominance, and to assess whether it was related to male ornamentation.

We established male groups under laboratory conditions to determine whether male yellow ornamentation was related to aggressive interactions and social dominance, testing the possibility that social competition over nonreproductive resources also influences the evolution of this trait.

## METHODS

### *Housing and Morphological Measurements*

We captured 28 male European serins, using mist nets, in the surroundings of Coimbra (40°11'25" N 8°33'35" W, Portugal), in the

winter (February) of 2012, after moult and before breeding. Individuals were housed in an indoor aviary in the Laboratory of Ethology at the University of Coimbra (40°12'26"N 8°25'21"W, Portugal), where we divided them into seven groups of four males, and housed them in cages (118 × 50 cm and 50 cm high) with ambient temperature of 20 ± 2 °C and natural lighting. Birds had ad libitum access to a commercial seed mixture (canary seed 46%, rapeseed 22%, niger seed 7%, linseed 7%, peeled oats 6%, hempseed 5%, wild seeds 5%, radish seed 1% and spinach seed 1%; European Finches Prestige, Versele-Laga, Deinze, Belgium), tap water and mixed grit with crushed oyster shell. We minimized the opportunity for dominant males to monopolize food resources in the groups by placing multiple food and water receptacles in each cage.

We ringed birds with numbered black plastic rings (A. C. Hughes, Hampton Hill, U.K.), which were replaced by plastic colour rings just before the experiments to allow visual identification during video analysis. Ring colour was not related to any variables analysed (Pearson correlations:  $P > 0.10$  for all tests). We also aged birds (first year or adult birds) using plumage marks according to Svensson (1992). We measured morphological parameters including wing (±1 mm), tarsus (±0.01 mm) and mass (±0.5 g) immediately before the experiments. Body size was estimated from the PC1 of a principal component analysis using these variables, which explained 50.8% of variance, had high loadings for tarsus (0.80) and mass (0.88) and a medium loading for wing (0.31). The crown and breast yellow patches were measured by the same person (S. T.) by overlaying a transparent grid on these areas and estimating the number of squares they covered, as described by Hill (1992).

### *Spectral Analysis*

During the month of capture, we performed spectral analysis of males' plumage reflectance, taking into account the passerine bird vision perception range (320–700 nm), using an Ocean Optics USB4000 spectrophotometer, a MikropackMini-DT-2-GS light source (Ocean Optics, Dunedin, FL, U.S.A.) and an optical fibre reflectance probe (Ocean Optics R400-7 UV/VIS), held vertically, attached to a rigid black holder to standardize the distance between probe and sample (distance of 3 mm, providing a sampling area of 28 mm<sup>2</sup>). All measurements were standardized using white (Ocean Optics, WS-1-SS) and dark standards. We measured the crown, throat, breast and belly of each male by taking three readings from each area, which were then averaged for each region. We then quantified coloration as perceived by birds, by applying avian visual models (Vorobyev & Osorio, 1998; Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998). We calculated cone quantum catches for each of the five cone types present in the avian retina (Bowmaker, Heath, Wilkie, & Hunt, 1997), four single cones and the double cone (using equation 1 in Vorobyev et al., 1998), integrating cone sensitivity, irradiance light and reflectance spectrum of the plumage. Since cone sensitivity data are unavailable for our species, we considered the cone sensitivities of another ultraviolet-sensitive (UVS) representative species, the blue tit, *Cyanistes caeruleus*, for single and double cones (Hart, Partridge, Cuthill, & Bennett, 2000). As a measure of irradiance we used D65, the spectrum of standard daylight. Plumage coloration was quantified using the short-wavelength-sensitive (SWS) ratio and the double cone, representing chromatic and achromatic indices of plumage reflectance (Evans, Hinks, Wilkin, & Sheldon, 2010). We assumed double cones are responsible for achromatic discrimination, since experimental data suggest that they are responsible for luminance vision (Hart, 2001; Jones & Osorio, 2004; Vorobyev & Osorio, 1998). As carotenoid-based plumage coloration results from the pigment absorption of wavelengths otherwise typical of white feathers

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