

Evolution of phenotypic sex differences in cooperative species: is competition an opposing force?

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Abstract. Sexual selection is generally thought to be weak in cooperative breeding species, largely because polygamous mating patterns that drive sexual selection can erode the kin-selected benefits of cooperation. Social selection, on the other hand, is expected to be strong among cooperative species especially because of the intense competition over status and resource access. In support of this view, several studies have shown monogamous mating and little sex difference in cooperative species. However, most previous studies have focused on species with relatively simple social systems and few studies have examined how mating patterns, social organization and ecological attributes have influenced the evolution of ornamentation in cooperative species. Here I used secondary data to examine several hypotheses and shed some light on how social and sexual selection influenced the evolution of phenotypic sex traits in cooperatively breeding birds. Despite the broad assumption that cooperative breeding species are monomorphic, results demonstrate that sex differences and the presence of ornamentation are widely spread in the group. Stable environments with higher precipitation are associated to the strongest differences between sexes. Results indicate that although extrapair matings and environment attributes are determinant to the evolution of sex differences, males and females of cooperative species seem to be more alike than their non-cooperative counterparts. The extent of mutual ornamentation found in cooperative species indicates that the combination of both sexual and social selection are imperative to determine how evolution has shaped phenotypic attributes in cooperative species.

Key words: dimorphism, dichromatism, epigamic selection, joint-nesting, mutual ornamentation, ornaments

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INTRODUCTION

Sexual reproduction and its inevitable dilution of relatedness between parent and offspring sets the stage for genetic conflicts of interest among interacting individuals, which led Wilson (1975) to assert that “sex is an antisocial force in evolution”. Accordingly, animal societies represent a balance between competition and cooperation influenced by underlying genetic conflicts of interest (Emlen 1982). Social competition is likely to be particularly acute in cooperative breeding species, as in such species some individuals invest in raising offspring that are not their own (Grinsted & Bilde 2013, Lutermann et al. 2013, Nelson-Flower & Ridley 2015). The study of cooperative species therefore has been a focal point of interest for behavioral ecologists since the late 1950s and early 1960s (e.g., Skutch 1959, 1961, Orians 1961, Brown 1963, Rowley 1965, 1968), and these first case studies were associated with early theoretical models

of inclusive fitness theory that attempted to explain helping behavior in animals as a result of kin selection (Hamilton 1964).

Species that breed cooperatively are taxonomically diverse, exhibit different mating and social systems (Ligon 1999). Among them, cooperative breeding birds are particularly well studied (Emlen 1991, Mumme 1992, Arnold & Owens 1998, Blackmore & Heinsohn 2008, Preston et al. 2016). Yet most such studies have focused on the costs and benefits of helping, both direct and indirect, to reproducers and helpers alike (Russell 2001, McGowan et al. 2003, Dias et al. 2015), and relatively few studies have examined competition for mates (or resources needed for breeding) in such species (Brouwer et al. 2011, Cockburn et al. 2013, Aranzamendi et al. 2016). Particularly, in addition to mate choice, sexual selection was traditionally defined as an evolutionary force that derives explicitly from competition among individuals for mating access to individuals of the