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Exploratory behaviour modulates the relationship between colony familiarity and helping in a cooperative bird

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ABSTRACT

Individuals within animal groups may differ in personality and degree of familiarity raising the question of how this influences their social interactions. In Iberian magpies *Cyanopica cooki*, a portion of first-year males engage in cooperative behaviours and dispersal, allowing addressing this question. In this study, we first investigate the relationship between colony familiarity (native *versus* foreign) and reproductive status (breeding *versus* helping) of males during 21 years. Secondly, we measure the exploratory behaviour and monitor reproductive status of a sample of individuals with different colony familiarity during 2 years. Long-term monitoring revealed that foreign individuals were more likely breeders. The analysis on the subset of individuals in which exploratory behaviour was measured revealed a mediatory effect of exploratory behaviour in the association between colony familiarity and helping behaviour. Specifically, among foreign individuals, higher explorative males were more frequently involved in helping behaviour than lower explorative ones. Conversely, among native males, breeders were more explorative than helpers. Our results suggest that aspects of personality may mediate the value of familiarity in reproductive tasks in social species.

1. Introduction

Animals often show consistent individual differences in the way they cope with environmental and social challenges, what has been termed as "personality traits" (Gosling, 2001; Sih et al., 2004a; Sih et al., 2004b; Dingemanse and Reale, 2005; Réale et al., 2007). Moreover, individual differences in behaviour can be correlated across functional contexts (Dall et al., 2004), giving rise to the existence of behavioural syndromes in a population (Sih et al., 2004a; Sih et al., 2004b). In recent years, aiming to explain the evolutionary consequences of animal personality, evolutionary ecologists have attempted to relate different personality traits with fitness (Dingemanse and Reale, 2005; Smith and Blumstein, 2008), as well as with behavioural aspects that may affect fitness, such as mate choice (Godin and Dugatkin, 1996; Schuett, 2008; Schuett et al., 2010, 2011; David and Cézilly, 2011), dispersal (Dingemanse et al., 2003; Cote et al., 2010a; Cote et al., 2010b) or social behaviour (Cote et al., 2008; Réale and Dingemanse, 2010; Aplin et al., 2013; Favati et al., 2014).

Personality might influence the ability to find mates or mate preferences in social groups (Réale and Dingemanse, 2010). In this context, highly explorative females preferred mating with highly explorative males in zebra finches *Taeniopygia guttata* (Schuett et al., 2011). Also, extra pair paternity rate was higher for female great tits *Parus major* mated with males of the same exploratory behaviour (van Oers et al., 2008). Personality can also affect social relationships between individuals (Cote and Clobert, 2007; Cote et al., 2008; Réale and Dingemanse, 2010), and can ultimately influence the social structure of animal groups (Krause et al., 2010; Colléter and Brown, 2011; Aplin et al., 2013). For instance, shy individuals in sheep flocks are more gregarious than bold ones when they forage (Michelena et al., 2009), and highly explorative territorial male great tits acquire dominant ranks in access to food more frequently than slow explorers (Dingemanse and de Goede, 2004). Also, network analyses have shown that exploratory behaviour was associated with temporal stability of association and patterns of group organization in adult great tits (Aplin et al., 2013).

Animals can show consistent individual differences in their proneness to cooperate with others in social groups (Bergmüler

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et al., 2010; Schürch and Heg, 2010), and therefore, knowing how different personality traits may relate to individual proneness to be cooperative seems critical to reach a better understanding of the evolution of sociality (Bergmuller and Taborsky, 2007). A previous study in the cooperative Lake Tanganyika cichlid fish *Neolamprologus pulcher* has shown that cooperative individuals with highly exploratory behaviour were more aggressive (Bergmuller and Taborsky, 2007). Also a study with the same species has shown that the tendency to help was positively associated with risk proneness (Le Vin et al., 2011). Additionally, a study shows consistent individual differences in cooperative behaviour (i.e. babysitting and provisioning) in wild meerkats *Suricata suricatta* (English et al., 2010). However, studies linking cooperative behaviour to some of the main personality traits in birds are still rare (see however Scheid and Noë, 2010),which precludes a full understanding of sociality in this group.

Moreover, familiarity is another factor that might influence the outcome of social interactions because native individuals may benefit more than foreign ones from their knowledge of physical and social environments at their natal sites (Beletsky and Orians, 1989; Ekman, 2006; Chiarati et al., 2011; Piper, 2011; Grabowska-Zhang et al., 2012). Familiarity, for instance, plays a key role in mate choice (Cheetham et al., 2008). Females may prefer to mate non-familiar males (Zajitschek and Brooks, 2008; Vega-Trejo et al., 2014; Graber et al., 2015) to avoid inbreeding (Pusey and Wolf, 1996; Johnson et al., 2010). Also, a recent study by Kurvers et al. (2013) showed a significant role of early life familiarity on mate choice in the barnacle geese *Branta leucopsis* with females mating preferentially with unfamiliar males, although no effect of personality on social behaviour was found. However, others studies have found that females may prefer familiar males (i.e. in birds and flies) (Senar et al., 2013; Tan et al., 2013), even when they were less ornamented than non-familiar males (Senar et al., 2013), suggesting in any case a role of familiarity in shaping mate preferences. The influence of familiarity can be relevant when social groups in cooperative species involve individuals from different origins. In particular, whenever dispersal occurs, groups are formed by both native (i.e. not dispersing individuals who live in their natal environment) and foreign individuals (i.e. dispersing individuals coming from outside). Familiarity can benefit native over foreign individuals because the former obtain a preferential access to resources of the territory, as shown in the carrion crown *Corvus corone* (Chiarati et al., 2011). In Siberian jay *Perisoreus infaustus* philopatric offspring survive better than immigrants (Ekman et al., 2000; Griesser et al., 2006) because they are less attacked by breeders (Ekman et al., 1994) and benefit from the group's protection toward predators (Griesser, 2003; Griesser and Ekman, 2004, 2005).

The Iberian magpie *Cyanopica cooki* is a small colonial corvid (Cramp and Perrins, 1994), with a cooperative socially monogamous breeding system (Valencia et al., 2003). Each year, about 50% of breeding pairs in a colony have helpers (i.e. individuals cooperating in provisioning offspring and removing faecal sacs with the breeding pair (Brown, 1987)). Genetic benefits of helping have not been yet studied in this system, although behavioural observations show that helping might not necessarily be associated to relatives (De la Cruz et al., 2003, unpublished data). Intensive trapping of individuals across years reveals an imbalance in the sex-ratio (more males than females) in the Iberian magpie (Cruz and Valencia, 2012) but despite the shortage of females, male helping behaviour is not always determined by a mating impossibility. Helpers can be differentiated into first (i.e. sexually mature individuals that cooperate although may reproduce and that are invariably males) and second option helpers (i.e. individuals, mainly males, who collaborate with other breeders after their failed or successful reproduction) (Valencia et al., 2003). First option helpers are exclusively males, and first-year Iberian magpie are more likely to help than older ones (Valencia et al., 2003). At fledging time (July) all young females are engaged in post-juvenile dispersal whereas juvenile males may either disperse from or remain in their natal colony (Cruz and Valencia, 2012). As a consequence, young males may have two different origins in a colony: first, foreign individuals that come from other colonies (i.e. non-familiar with the colony), and, second, native individuals that have not dispersed (i.e. familiar with the colony) and, therefore, may have some close relatives in the colony. Hence, Iberian magpie cooperative behaviour with partially delayed male dispersal provides an ideal system to test for a role of social familiarity, estimated through population origin, on the relationship between reproductive and exploratory behaviour in the wild.

The main aim of this study is testing whether differences in a classic personality trait (exploratory behaviour) may modify the value of colony familiarity in a social context in the Iberian magpie. In a first stage we evaluate how colony familiarity is linked to reproductive status (i.e. breeder *versus* helper) of Iberian magpie males based on long-term monitoring of ringed birds in one population. Given that native males may benefit from their knowledge of their natal sites whereas immigrants cannot (see above), we predict i) that native individuals were more likely breeders and less likely helpers than foreign males in the colony. In a second stage we study how differences in personality, here measured as exploratory behaviour (i.e. number of hops and flights), might influence the relationship between colony familiarity and reproductive status. Our expectation regarding the mediatory effect of exploratory behaviour on colony familiarity is not clear because no previous study has analysed how the interplay between these two aspects may relate to social behaviour in this species. However, based on previous studies in birds reporting female preference by either familiar (Senar et al., 2013; Tan et al., 2013) or more exploratory males (Schuett et al., 2010) we can tentatively predict ii) that the proportion of breeders was the largest among natives with high exploratory behaviour and the smallest among foreigners with low exploratory behaviour.

2. Material and methods

2.1. Study area

We studied Iberian magpies in an area located at 22 km north of the city of Badajoz (39° 03′ N, 6° 48′ W), Spain. This area has a typical Mediterranean climate, i.e. dry-hot summers and mild-wet winters, where the dehesa, i.e. open holm oak *Quercus ilex* woodland, is the predominant habitat. Since 1992, Iberian magpies have been captured and ringed for individual identification, allowing the study of different aspects of their biology (e.g., De la Cruz et al., 2003; Valencia et al., 2003, 2006; Avilés et al., 2008; Solís et al., 2008).

2.2. Data collection

The relationship between familiarity and reproductive status of Iberian magpie males was investigated by using data from 21 years (1995–2015) on reproductive status and familiarity collected at all nests in our study site. Age was determined by differences in moult extension at the time of capture following De la Cruz et al. (1992). Sex and reproductive status (breeder or helper) were determined by 1 h behavioural observations made from a hidden position near each nest in the colony twice a week from incubation until fledging. Sex assignment was based on the fact that only females are engaged in incubation and brooding duties (Cramp and Perrins, 1994), and beg to males (Cruz and Valencia, 2012). On the other hand, helpers usually join the breeding group after the chicks have