



Social dynamics in nonbreeding flocks of a cooperatively breeding bird: causes and consequences of kin associations



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Kin selection is regarded as a key process in the evolution of avian cooperative breeding, and kinship influences helper decisions in many species. However, the effect of kinship on nonbreeding social organization is still poorly understood despite its potential fitness implications. Here, we investigated the origins and consequences of kin associations in nonbreeding flocks of long-tailed tits, *Aegithalos caudatus*, an atypical cooperative breeder where helpers are failed breeders that redirect care towards relatives living in kin neighbourhoods. We found that kinship is an important factor in initial grouping decisions; all members of a nuclear family initially joined the same flock and failed breeders chose to flock with their relatives. Flocks that merged during the nonbreeding season also contained relatives. In contrast to these findings of positive kin association, when long-tailed tits switched flocks they tended to disperse into flocks with fewer relatives, although such switches often occurred with kin. In a playback experiment, we found no evidence that aggression shown towards members of other flocks was affected by kinship, indicating that kin associations result from a preference to flock with relatives rather than a constraint on flocking with nonrelatives. Finally, using social network analysis, we show that fine-scale nonbreeding associations among individuals were positively related to kinship, and that these nonbreeding associations were reflected in helping decisions in the subsequent breeding season, in addition to the previously reported effects of kinship and proximity. We conclude that long-tailed tits prefer to associate with kin when not breeding, and suggest that by doing so they gain either nepotistic benefits within flocks or future indirect benefits during breeding.

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Cooperatively breeding birds typically live in groups that include close relatives (Hatchwell, 2009; Riehl, 2013) and kin selection is generally regarded as a major driver of helping behaviour (Dickinson & Hatchwell, 2004; West, Griffin, & Gardner, 2007). Indeed, an effect of kinship on the alloparental investment of helpers has been extensively documented (e.g. Curry, 1989; Dickinson, 2004; Wright, McDonald, te Marvelde, Kazem, & Bishop, 2010), but much less is known about the effect of kinship on social interactions in contexts other than breeding, possibly because interactions outside the breeding season are often deemed to be less important in the evolution of sociality. Nevertheless, kin-based winter sociality has been suggested to distinguish species that breed cooperatively from those that do not (Ekman, 1989; Noske, 1991), and to act as an intermediate stage in the transition from asociality to cooperative breeding (Drobnik, Wagner,

Mourocq, & Griesser, 2015). Furthermore, individuals that delay dispersal to associate with close kin during the winter have been shown to derive nepotistic benefits relative to immigrants in western bluebirds, *Sialia mexicana* (Dickinson, Euparadorn, Greenwald, Mitra, & Shizuka, 2009; Dickinson, Ferree, Stern, Swift, & Zuckerberg, 2014) and Siberian jays, *Perisoreus infaustus* (Ekman, Bylin, & Tegelstrom, 2000). However, few other studies have examined the role that relatedness plays in social interactions both within and between groups outside the breeding season, even though such interactions may have important consequences for the cooperative behaviour of individuals during subsequent breeding events.

Most cooperatively breeding bird species spend the nonbreeding season in stable family groups that form when mature offspring delay dispersal and remain on their parents' territory (Covas & Griesser, 2007; Ekman, Hatchwell, Dickinson, & Griesser, 2004; Emlen, 1982). Helping can also occur within extended family networks or 'kin neighbourhoods' (Dickinson & Hatchwell, 2004). In such systems, nonbreeding group membership is often less stable than in typical cooperative breeders, with individuals

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dispersing between groups and groups merging or disbanding. Dispersive behaviour is generally thought to disrupt the kin structure of a population (Emlen, 1997; Gardner & West, 2006; Perrin & Goudet, 2001), raising the question of how kin neighbourhoods develop in dispersive species. Several potential mechanisms exist, the most obvious of which is localized natal dispersal that results in relatives living in close proximity to each other (Dickinson et al., 2009; Preston, Briskie, Burke, & Hatchwell, 2013; Sharp, Simeoni, & Hatchwell, 2008). There is also growing evidence for the coordinated dispersal of kin in cooperative breeders (e.g. Koenig, Hooge, Stanback, & Haydock, 2000; Pollack & Rubenstein, 2015; Ridley, 2012; Williams & Rabenold, 2005), including among species that help within kin neighbourhoods (Sharp, Baker, Hadfield, Simeoni, & Hatchwell, 2008). Of course, there may also be costs of associating with relatives, especially if it entails kin competition over resources (Griffin & West, 2002) or a risk of inbreeding (Pusey, 1987). Therefore, for certain categories of individuals, such as juveniles of one particular sex, there may also be countervailing selection for dispersal away from relatives, resulting in sex-biased natal dispersal (Greenwood, 1980). Alternatively, inbreeding may be avoided via active discrimination against kin as social or sexual partners within kin neighbourhoods that comprise male and female relatives (Dickinson, Akçay, Ferree, & Stern, 2016; Riehl & Stern, 2015).

Besides the immediate benefits of living alongside relatives (Ekman et al., 2004), if helping decisions are influenced by familiarity as well as kinship, nonbreeding social associations in kin neighbourhoods may also have important fitness consequences during subsequent breeding events. Within kin neighbourhoods, individuals may interact with both relatives and nonrelatives, so that shared group membership may be insufficient for effective kin discrimination, even though this may be needed for individuals to maximize their inclusive fitness (Cornwallis, West, & Griffin, 2009). The effects of kinship and familiarity on helping behaviour are hard to distinguish in species that live in discrete family groups because helpers are usually both related to and associated with any potential recipients of their help. However, distinguishing the effects of these factors may be more straightforward when helping occurs within kin neighbourhoods comprising both kin and nonkin (e.g. Kraaijeveld & Dickinson, 2001; McGowan, Fowlie, Ross, & Hatchwell, 2007).

We investigated the origins and consequences of kin associations in nonbreeding flocks of long-tailed tits, *Aegithalos caudatus*. Long-tailed tits have a kin-selected cooperative breeding system where redirected helping occurs within kin neighbourhoods. Birds do not delay dispersal or breeding to help; instead, at the beginning of each breeding season all birds attempt to breed in pairs. Helpers are breeders whose own nests have failed and whose care is redirected to the brood of another pair. Helping is typically kin-directed and usually occurs between brothers, although a small minority of helpers are female and a small proportion care at the nests of nonrelatives (Hatchwell, Gullett, & Adams, 2014; Nam, Simeoni, Sharp, & Hatchwell, 2010; Russell & Hatchwell, 2001). Following breeding, long-tailed tits form mixed-sex flocks usually comprising 5–25 birds. Flock members forage together during the day and roost together in linear huddles at night, thereby gaining thermoregulatory benefits (Hatchwell, Sharp, Simeoni, & McGowan, 2009). Flocks occupy large nonexclusive ranges that typically contain both adults and juveniles from multiple families as well as unrelated immigrants that disperse between flocks during their first winter. These immigrants include both sexes, although in our study population the majority are females due to female-biased natal dispersal (Sharp, Simeoni, McGowan, Nam, & Hatchwell, 2011). Most birds flock with at least one close relative ($r \geq 0.25$) during the nonbreeding season (Ezaki, Miyazawa, &

Sakikawa, 1991; Hatchwell, Anderson, Ross, Fowlie, & Blackwell, 2001; McGowan et al., 2007), but how these patterns of kinship arise is not well understood. Likewise, while it is known that the ranges of related flocks overlap more than those of unrelated flocks (Hatchwell, Anderson et al., 2001), and that siblings often disperse together (Sharp, Baker, et al., 2008; Sharp, Simeoni, et al., 2008), flock membership is not fixed with both adults and juveniles switching between flocks, and flocks coalescing or disbanding through the nonbreeding season; the influence of relatedness on these flock mergers and switches has not been examined. Finally, although several factors determining a failed breeder's propensity to help have been described previously, including condition (Meade & Hatchwell, 2010), relatedness (Russell & Hatchwell, 2001) and date (MacColl & Hatchwell, 2002), the potential influence of prior association during the nonbreeding season is unknown.

In this study, we first examined whether flock membership, flock mergers and flock switches were influenced by the relatedness of flock members. We then used a playback experiment to test whether observed kin associations were caused by differential aggression towards unrelated intruders. Third, we used social network analysis to study the effect of kinship on fine-scale social interactions among individual birds. Finally, we investigated the effect of these associations on helping behaviour in the following breeding season.

METHODS

Study System

Field observations

We have studied a population of long-tailed tits occupying a 3 km² site in the Rivelin Valley, Sheffield, U.K. (53°23'N, 1°34'W) since 1994. At the start of each breeding season, pairs (mean = 49 per annum) were located and colour-ringed (>95% of all adults are ringed by the end of each breeding season). Long-tailed tits are single-brooded; their nests were found by following pairs and subsequently monitored closely until they failed or broods fledged. During the nestling period, nests were observed for approximately 1 h every other day and the identities of all provisioning adults (parents and any helpers) recorded. Nestlings in accessible nests were colour-ringed when 11 days old. Flocks were observed during the nonbreeding seasons of 1996–1997 (October–March, 35 observation days), 1997–1998 (May–February, 56 days), 1998–1999 (May–February, 57 days), 2011–2012 (May–March, 87 days) and 2012–2013 (May–March, 80 days). Flocks were followed for up to 4 h, until contact was lost or until all birds in the group were identified. All flock members could rarely be identified in a single observation period, so we assumed that sighting of two or more known flock members was a reliable indicator of flock identity. Flock size was defined as the number of ringed birds in each flock. This is a minimum estimate because most flocks also contained a small number of unringed immigrants that dispersed into our study site in their first winter. Flock position was recorded every 2 min on to large-scale maps (scale 1 cm: 50 m) in 1996–1999, and every minute using a Garmin Geko 201 GPS in 2011–2013. Map registrations were converted to map coordinates for analysis at a resolution of 10 m.

Pedigree construction

We used social pedigrees derived from 19 years of field observations to estimate dyadic relatedness among individuals in our population. Long-tailed tits can use social pedigree information provided by calls that they learn from carers to recognize kin (Sharp, McGowan, Wood, & Hatchwell, 2005), and these cues provide a reliable estimate of genetic relatedness because brood

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