Kith or kin? Familiarity as a cue to kinship in social birds

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Abstract

Interacting with relatives provides opportunities for fitness benefits via kin-selected cooperation, but also creates potential costs through kin competition and inbreeding. Therefore, a mechanism for the discrimination of kin from non-kin is likely to be critical for individuals of many social species to maximize their inclusive fitness. Evidence suggests that genetic cues to kinship are rare and that learned or environmental cues offer a more parsimonious explanation for kin recognition in most contexts. This is particularly true among cooperatively breeding birds, where recognition of familiar individuals is usually regarded as the most plausible mechanism for kin discrimination. In this article, we first review the evidence that familiarity provides an effective decision rule for discrimination of kin from non-kin in social birds. We then consider some of the complexities of familiarity as a cue to kinship, especially the problems of how individuals become familiar, and how familiar individuals are recognized. We conclude that while familiarity as a mechanism for kin recognition may be more parsimonious and widespread than genetic mechanisms, its apparent simplicity as a decision rule governing social interactions may be deceptive. Finally, we identify directions for future research on familiarity as a kin recognition mechanism in social birds and other taxa.

Keywords: kin discrimination, kin recognition, cooperation, familiarity, social birds.

Introduction

Kin selection is often invoked to explain the evolution of cooperation among relatives in social animals (Rubenstein & Abbott 2018). Here, we use social to describe species that exhibit cooperative breeding, following the widely used definition of cooperative breeding as a reproductive system in which more than a pair of individuals collectively raise young in a single brood or litter (Emlen & Vehrencamp 1985, Koenig & Dickinson 2016). Hamilton's rule predicts that cooperation confers indirect fitness benefits and will be selected for providing that the coefficient of relatedness between actor and recipient, multiplied by the benefits of cooperation to the recipient exceed the costs to the actor (Hamilton 1964). Therefore, differential treatment of conspecifics that vary in genetic relatedness, i.e. kin discrimination (Sherman *et al.* 1997), is an important consideration in studies of social evolution. In addition to kin-selected fitness benefits, kin discrimination may also play an important role in inbreeding avoidance when passive processes, such as sex-biased dispersal, are insufficient to reduce inbreeding risk (Pusey & Wolf 1996). These functional benefits of discriminating kin from non-kin are well established, but the mechanisms through which this is realized are keenly debated.

Our current framework for understanding kin recognition systems involves three components: the production of external cues; the perception of these cues and formation of recognition templates; and the action taken based on the perceived similarity between a template and an encountered phenotype (Beecher 1982, Gamboa *et al.* 1991, Reeve 1989; Table 1). Both the cue and the template may be either genetically determined or acquired from the biotic or abiotic environment (Sherman *et al.* 1997). Recognition systems will also be prone to errors; in the case of positive discrimination in favor of kin for helping behavior, these will be either rejection errors, in which kin are not recognized as such and rejected as social partners, or acceptance errors in which non-kin are erroneously recognized as kin and accepted as social partners (Reeve 1989; Table 1). The extent to which cues and templates are determined genetically and/or environmentally, and the risk of making rejection/acceptance errors will vary greatly between and within species (Sherman *et al.* 1997, Komdeur *et al.* 2008).

This framework leads to three broad categories of kin recognition mechanism. Recognition may be based on familiarity, in which discriminating individuals learn the recognition cues of relatives (e.g. parents and/or siblings) at a sensitive phase during development (Komdeur & Hatchwell 1999) and discriminate these familiar individuals from unfamiliar ones later in life. Second, recognition may be based on phenotype matching, whereby individuals use their own phenotype and/or those of their familiar kin to form a generalized template with which to compare the phenotypes of other individuals (Lacy & Sherman 1983). Familiarity and phenotype-matching are considered alternative processes (Holmes & Sherman 1983), but both involve matching phenotypes to learned templates; the two mechanisms differ only in the specificity of the template employed (Reeve 1989). Thirdly, it is also possible that both cues and templates are genetically-determined rather than environmentally-acquired or learned, thereby satisfying Grafen’s (1990) definition of kin recognition as requiring discrimination of true genetic relatives, although note that here we use the less restrictive definition of Sherman *et al.* (1997), as stated above.

The ecological and social circumstances in which a recognition system evolves is likely to have a profound effect on the probable mechanism of recognition (Komdeur *et al.* 2008).

Likewise, a species' kin recognition mechanism will have consequences for the accuracy of discrimination and the degree of resolution between different categories of kin. For example, kin recognition that requires prior association for the learning of cues or templates allows individuals to recognize familiar kin only, whereas recognition that is based on phenotype matching may permit recognition of unfamiliar kin (Mateo 2004). Among cooperatively breeding birds, recognition of familiar individuals is usually regarded as the most plausible mechanism for kin recognition (Komdeur & Hatchwell 1999). However, the term familiarity is often ill-defined, the recognition cues are poorly understood, and very little is known about the conditions under which a previous association constitutes familiarity in the context of kin recognition. In this article, we first review the evidence for alternative kin recognition mechanisms in social birds, concluding that recognition based on familiarity is the best-supported decision rule for discrimination of kin from non-kin in most studies. We then consider some of the complexities of familiarity as a cue to kinship, suggesting that while such a mechanism for kin recognition may appear more parsimonious and widespread than phenotype matching, its apparent simplicity is deceptive. Finally, we discuss possible directions for future research on familiarity as a kin recognition mechanism in social birds and other taxa.

Mechanisms of kin recognition

Kin recognition may be achieved via a variety of mechanisms that range from simple to complex. In the simplest form of recognition, individuals encountered in a particular area are recognized as kin. As long as relatives are predictably distributed in space, location can correlate reliably with genetic relatedness (Komdeur & Hatchwell 1999). Some researchers suggest this is not a true form of kin recognition, as individuals are responding to location, rather than phenotypic cues (Halpin 1991, Tang-Martinez 2001). However, in many natural populations, it is rare for unrelated individuals to be encountered in the nest for example, and a simple decision rule such as ‘treat anything in my nest as kin’, is an effective and widely used mechanism for offspring recognition in birds (Beecher 1991), despite its potential for exploitation by intra- and inter-specific brood parasites (Davies 2000). Other contextual cues may modify this simple rule; for example, polyandrous male dunnocks *Prunella modularis* are more likely to feed the young of females with which they mated during their fertile period (Burke *et al.* 1989, Davies *et al.* 1992), thereby maximizing their chance of directing their care towards offspring. Spatial cues to offspring recognition may be superseded by individual recognition when fledglings leave the nest (Beecher 1988), but, in most cases, parent-offspring recognition does not persist beyond the period of offspring dependence.

Such simple rules work well in non-social species, in which there is little or weak selective pressure to recognize kin beyond offspring independence. However, in social species there are often indirect fitness benefits to be gained from cooperating with close kin during adulthood or fitness costs of inbreeding, and, consequently, selection for mechanisms of kin recognition that persist beyond the period of parental care (Komdeur & Hatchwell 1999, Cornwallis *et al.* 2009). In this review, we focus on mechanisms in social birds that might permit kin recognition over an individual’s lifetime, or at least the period over which cooperative behavior or the risk of inbreeding exists. Such mechanisms may be based on genetic kin recognition, phenotype matching or familiarity (Table 2).

Genetic recognition

Genetic kin recognition requires discrimination of kin from non-kin based entirely on genetically acquired cues without a period of associative learning. Here, *recognition alleles*, dubbed ‘greenbeard genes’ by Dawkins (1976) or gene complexes encode the production of phenotypic cues, the templates and the perception of the cue and performance of a discriminatory action. Such a system relies on polymorphic recognition genes for reliable discrimination, yet paradoxically, kin-selected fitness benefits are predicted to reduce allelic diversity at these loci. This is because in cooperative contexts, individuals bearing common cues are more likely to encounter equivalent individuals and receive altruistic benefits than those with rare cues. These individuals will gain higher fitness, and eventually the common alleles become fixed and the recognition system breaks down (Crozier 1986). Alternatively, mutation will interfere with genetic kin recognition, and mutant cheats who carry the phenotypic cues but not the associated relatedness, may evolve and spread through the population (Hamilton 1964). Finally, in the case of a gene complex orchestrating recognition, recombination could disrupt kin recognition. In each of these theoretical scenarios, the required correlation between similarity in the inherited phenotypic cue and kinship among pairs of individuals would decrease over time, rendering such a cue useless for kin recognition (Gardner & West 2007). There are no convincing cases of genetic kin recognition in cooperatively breeding birds (Table 3). Indeed, empirical evidence of genetic kin recognition across taxa is scarce, the clear exceptions being the slime mould, *Dictyostelium discoideum* (Queller *et al.* 2003) and fire ant *Solenopsis invicta* (Keller & Ross 1998, Wang *et al*. 2013).

Phenotype matching

The second candidate mechanism for kin recognition is phenotype matching. The distinction between phenotype matching and genetic kin recognition is that template formation requires the learning of phenotypic cues that reliably reflect genetic similarity. However, because individuals can use their own phenotype or the phenotypes of a subset of known kin to learn a generalized 'kin' template, this does not require a period of prior association, or familiarity between matching individuals. Phenotype matching is an attractive potential mechanism for kin recognition, particularly in the context of inbreeding avoidance, because it allows individuals to recognize unfamiliar kin. Phenotype matching has been demonstrated in the decorated cricket *Gryllodes sigillatus* (Capodeanu-Nägler *et al*. 2014) and in several social mammals (e.g. Boyse 1991, Pfefferle *et al.* 2013). Although in some species, such as the Belding’s ground squirrel *Spermophilus beldingi* both phenotype-matching and familiarity seem to play a role (Holmes & Sherman 1982). However, empirical support for phenotype matching in cooperatively breeding birds remains rare and inconclusive (Table 3).

One of the first studies to suggest phenotype matching as a plausible kin recognition mechanism in a cooperative bird was conducted by Price (1998, 1999) on stripe-backed wrens *Campylorhynchus nuchalis.* A series of playback experiments demonstrated that wrens were able to discriminate between vocalisations made by their own group, familiar neighboring groups and unfamiliar groups, consistent with a recognition system based on familiarity (Price 1998). Subsequent experiments showed that the behavioral responses of wrens to calls from patrilineal relatives in the unfamiliar groups did not differ from their responses to calls from patrilineal relatives in their own group, which could indicate phenotype matching (Price 1999). However, patrilineal relatives in unfamiliar groups are dominant males that have dispersed from their natal group, so a period of association between the dominant male in each group cannot be ruled out. As male helpers may follow the dominant male in their behavioral responses to intruders, this result could be achieved through recognition based on familiarity.

A recent study on Siberian jays *Perisoreus infaustus*, a species that exhibits kin-based sociality although not cooperative breeding, has suggested that phenotype matching is used to recognize kin in some contexts. Within family groups, breeders are more aggressive towards immigrants than to their own offspring, but aggression of breeders towards immigrants was negatively associated with the immigrant’s genetic relatedness to the breeding male (Griesser *et al.* 2015). In this study, individuals were considered unfamiliar if they had not interacted between fledging and dispersal, although the possibility that individuals had prior association could not be ruled out unequivocally.

Studies of bell miners *Manorina melanophrys* provide the best evidence for kin recognition via phenotype matching in cooperatively breeding birds (McDonald & Wright 2011). Certain features of the bell miner's social system have important consequences for their recognition systems. They form large colonies, often comprising hundreds of individuals, within which individuals are organized into *coteries* of numerous breeding pairs assisted by non-breeding helpers of varying relatedness that provision multiple nests within their coterie. Like many cooperative breeders, kinship appears to be the most important factor in explaining the patterns of cooperation between breeders and helpers (Wright *et al.* 2010) and the shared provisioning efforts of helpers within social networks (McDonald *et al.* 2016). From an early age, however, young interact with both related and unrelated group members, making spatial or association-based recognition unreliable. Instead, the provisioning effort of helpers correlates with their vocal similarity to the breeding male, an apparently innate signal that also correlates with genetic relatedness (McDonald & Wright 2011). However, whether vocal similarity permits kin recognition on a continuous scale or on a binary scale, whereby conspecifics are categorized as either kin or non-kin based on a threshold of template-phenotype similarity, remains unclear. Furthermore, although no evidence of call learning has been found, a putative association period during which kin may be learned has not been excluded empirically.

In the closely related noisy miner *Manorina melanocephala*, which has a similar social system, helpers direct their help towards genetic relatives (Barati *et al.* 2018), and discriminate between individuals based on acoustic cues (McDonald *et al.* 2012). Still, individuals may also rely on prior association to identify relatives, and whether kin recognition is based on phenotype matching or familiarity remains untested in this species.

The problem with recognition via phenotype matching of inherited cues is that, like genetic kin recognition, it is vulnerable to mutation and recombination, and requires sufficient polymorphism to permit precise discrimination. Another important consideration is that there may be selection for individuals to conceal kinship at certain life stages or in certain situations. For example, when paternity is uncertain, effective kin recognition by parents would be adaptive in order to direct care towards genetic offspring. However, from the offsprings' perspective, it would not be beneficial to display an obvious cue to genetic relatedness, as this could exclude cuckolded care-givers (Beecher 1988, Davies *et al.* 1992). This conflict of interest between parent and offspring may make it difficult for phenotype matching of genetic cues to evolve as a recognition mechanism. Even if recognition cues are learned, the formation of a generalized template may still select for convergence, as individuals with a more common phenotype are more likely to be accepted as social partners than those with rarer cues. On the other hand, theory suggests that genetic diversity at recognition loci may be maintained if rare alleles confer an extrinsic selective advantage, such as resistance to certain parasites (Rousset & Roze 2007). Indeed, the highly polymorphic major histocompatibility complex (MHC), has been implicated as a kinship marker during mate choice in vertebrates, detected through odor cues. MHC diversity affects parasite resistance (Kurtz *et al.* 2004), perhaps explaining how MHC polymorphism is maintained despite its putative role in kin recognition. However, the role of MHC in kin recognition is contested, as disassortative mate preference based on MHC haplotype may arise from the improved immunity associated with heterozygosity at MHC loci itself, rather than MHC haplotype acting as a reliable signal of genetic similarity across the genome (Green *et al.* 2015).

Familiarity

Familiarity is the most widely supported mechanism of kin recognition in cooperatively breeding birds (Komdeur & Hatchwell 1999, Komdeur *et al.* 2008, Riehl & Stern 2015; Table 3). Kin association during extended brood care provides a sensitive period during which reliable recognition templates can form. This period of association also offers an opportunity for learning of cues that are more similar within a family than in the general population, termed a family or kin ‘signature’ (Beecher 1982). Once recognition cues are fixed, individuals are potentially able to recognize familiar kin outside of the association context. When extra-pair paternity (EPP) and brood parasitism is rare, association during this period accurately reflects kinship, and a simple rule such as ‘assist anyone who was present in my natal nest’, can be selected for (Komdeur & Hatchwell 1999). For example, in cooperative contexts, Galápagos mockingbirds *Nesomimus parvulus* and white-fronted bee-eaters *Merops bullockoides* discriminate based on previous association, rather than kinship (Curry 1988, Emlen & Wrege 1988). In complex societies, a more precise rule, such as ‘assist anyone that fed me as a nestling’ may be more reliable (Komdeur 1994). In most cooperatively breeding birds, males are the predominant helping sex, but in the Seychelles warbler *Acrocephalus sechellensis* females are more likely to help than males, and choose to help at nests belonging to female breeders who fed them as nestlings, even if they are not the closest genetic relatives (Komdeur 1994, Richardson *et al.* 2003). This makes evolutionary sense in species with high levels of extra-pair paternity, such as Seychelles warblers, because helpers are often unrelated to the male that fed them (Richardson *et al.* 2003). Cross-fostering experiments confirm that female subordinates base their helping decisions on associative learning and it is unlikely that young can discriminate between their mother and any other female helper (Komdeur *et al.* 2004).

Playback experiments show that cues enabling recognition of familiar individuals beyond the association period are encoded vocally (Table 3). An early study on the splendid fairy-wren

Malurus splendens showed that while fairy-wrens responded aggressively to the songs of fairy-wrens from other social groups, they exhibited a similar response to the songs of both non-kin and unfamiliar close kin (Payne *et al.* 1988). More recent experiments have demonstrated that vocalisations signal group membership in Mexican jays *Aphelocoma wollweberi* (Hopp *et al.* 2001), green woodhoopoes *Phoeniculus purpureus* (Radford 2005) and superb starlings *Lamprotornis superbus* (Keen *et al.* 2013). These studies suggest that vocalisations reflect social association rather than kinship *per se*, as would be expected if cues and templates are learned within groups.

In the context of inbreeding avoidance, good evidence for avoidance of kin as reproductive partners based on familiarity comes from studies of two species of social woodpecker: acorn woodpeckers *Melanerpes formicivorus* and red-cockaded woodpeckers *Picoides borealis*. Acorn woodpeckers exhibit high within-group relatedness, with most individuals being parents, siblings or offspring of everyone else within the group (Koenig & Haydock 2004). Acorn woodpecker females do not breed in their natal group when the reproductive male in their natal group at the time of their birth (their assumed father) is still present (Koenig & Pitelka 1979). Furthermore, when a dominant male or female dies, reproductive vacancies remain unfilled when nonbreeding helpers of the missing sex are present, and breeding does not usually occur until the vacancy is filled by immigrants from outside the group (Koenig *et al.* 1999). Similarly, red-cockaded woodpecker females will abdicate a breeding position following the death of their mate when the remaining males are their sons, but will remain when they are unrelated to the male helpers (Walters *et al.* 1988). The mechanism behind these decisions has not been examined experimentally in either species.

The most compelling cases of kin recognition based on familiarity come from cooperative breeders in which helping occurs within kin neighbourhoods (Dickinson & Hatchwell 2004), where individuals routinely interact socially with both kin and non-kin so that selection for effective kin discrimination is likely to be strong (Cornwallis *et al*. 2009). In western bluebirds *Sialia mexicana* there is a strong kin preference in helping behavior (Dickinson *et al.* 1996) and active kin avoidance during mate choice (Dickinson *et al.* 2016). However, males do not reduce their provisioning effort in response to behavioral cues to paternity loss, such as extra-pair male intrusion or witnessing female acceptance of extra-pair copulations (Dickinson 2003). This suggests, along with earlier studies (Leonard *et al.* 1995), that males do not recognize their own offspring, and that discrimination by both parents and offspring is based on social experience in the nest, rather than genetic relatedness (Dickinson 2003). Playback experiments have shown that individuals discriminate kin based on vocal cues (Akçay *et al.* 2013) even though these vocalizations are poor indicators of genetic relatedness, because they are most similar among neighbours, regardless of kinship (Akçay *et al.* 2014). These findings collectively suggest that western bluebirds recognize familiar individuals, rather than kin, using vocal cues.

Kin recognition has also been extensively studied in another species that helps within kin neighbourhoods, the long-tailed tit *Aegithalos caudatus.* Long-tailed tits have a kin-selected cooperative breeding system in which failed breeders preferentially redirect their care to help relatives (Russell & Hatchwell 2001, Hatchwell *et al.* 2014). Playback experiments show that long-tailed tits are able to discriminate between the calls of close kin and non-kin (Hatchwell *et al.* 2001, Sharp *et al.* 2005), and the calls thought to be used as recognition cues are individually distinctive, repeatable and more similar among close kin than among non-kin (Sharp & Hatchwell 2005, Leedale *et al.* in press). Cross-fostering experiments showed that nestlings and/or fledglings acquire their recognition templates from familiar kin during an associative learning period, when the cues themselves develop (Sharp *et al.* 2005), and that cross-fostered offspring subsequently help at the nest of foster siblings (Hatchwell *et al.* 2001). Moreover, there is strong evidence for effective discrimination of first-order kin, but not second-order kin, both in the context of helping behavior and mate choice (Leedale *et al.* in press, Leedale 2018). These results are all consistent with the idea that long-tailed tits categorize conspecifics as either kin or non-kin based on early association in the context of brood care (Sharp *et al.* 2005). On the other hand, Nam *et al.* (2010) and Leedale *et al.* (in press) both found that long-tailed tit helpers modified their effort according to their relatedness to the helped brood, suggesting that assessment of kinship is not based on a simple dichotomous rule of familiar (kin) versus unfamiliar (non-kin) birds. Indeed, this suggests a mechanism of phenotype matching, with a gradation of similarity in vocalizations providing a fine-grained, continuous estimation of kinship. However, bioacoustic analysis did not support this suggestion (Leedale *et al.* in press), so even in this relatively well-studied system, the mechanism underlying graded discrimination remains unknown.

This review focuses on kin recognition, but familiarity also provides a potential mechanism by which individual recognition may be achieved; for example, some cooperative bird species, such as the chestnut-crowned babbler *Pomatostomus ruficeps* have individually distinct vocalisations (Crane *et al.* 2014). However, although individual recognition has been identified in several social mammals, including chacma baboons *Papio hamadryas* (Bergman 2003) and golden hamsters *Mesocricetus auratus* (Johnston & Bullock 2001), there are no conclusive examples of individual recognition in cooperatively breeding birds (Table 3). The difference between individual and group recognition depends on the specificity of the templates acquired during the association period, which in turn depends on the nature of the interactions that occur between individuals during that time. In practice, this makes distinguishing individual from kin or group recognition difficult (Tibbets & Dale 2007). We discuss this in more detail in the following section.

Overall, there is substantial evidence that familiarity is a widespread kin recognition mechanism in cooperatively breeding birds. The limitation of familiarity is that non-kin will be considered kin if they are encountered during the putative associative learning stage, and kin not encountered during this period will not be recognized as such. However, in most cases, proximity at certain life stages is a reliable indicator of kinship. This is particularly true of birds, which have a prolonged period of parental care at the nest where encountered individuals are likely to be close kin. A second assumed limitation of recognition based on familiarity is that it may result in a binary recognition rule, in which individuals are categorized as either kin or non-kin. A more sophisticated mechanism that permits relatedness to be assessed on a continuous scale would be adaptive, in accordance with Hamilton's rule (Hamilton 1964), although, as already discussed, such mechanisms may be evolutionarily unstable. Kin recognition through familiarity or prior association is also considered the most likely mechanism of kin recognition in social birds because it is simpler to evolve and arguably less cognitively demanding than an assessment of genetic relatedness based on phenotypic similarity. Yet, while a recognition system based on familiarity may be more parsimonious and widespread than phenotype matching and genetic mechanisms, we argue below that its apparent simplicity is deceptive.

The complexities of familiarity as a cue to kinship

Despite the general acceptance of familiarity as an important means of kin recognition and discrimination, much remains unknown about how associating individuals are categorized as kin and how familiar individuals are recognized after the associative learning period. Here, we suggest that progress will be made in understanding familiarity as a mechanism of kin recognition only when certain gaps in knowledge can be addressed: (i) the meaning of 'familiarity', (ii) the sensitive period for association; (iii) the cues used for recognition; and (iv) the distinction between familiarity and phenotype matching.

(i) What is 'familiarity'?

Familiarity in the context of kin recognition is difficult to define and to quantify. What is the specific series of events during which an individual learns who is familiar? In the kin recognition literature, familiarity generally refers to some previous social association among individuals, usually during early life stages (Hepper 1986, Komdeur & Hatchwell 1999), but the nature of this association is often vague. For instance, is spatial proximity sufficient, or do individuals need to interact in specific ways in order to become familiar? In studies of social birds, such as long-tailed tits, spatial proximity of nestlings may provide the basis for future helping among siblings, but helping also occurs across generations indicating that association when provisioning a brood or when being provisioned also provides the basis for future helping (Sharp *et al*. 2005, Nam *et al*. 2010). Precisely when the interactions took place, how many interactions there were, their duration, and the specific behavior and information transfer that took place during these interactions may influence how individuals are recognized and treated later in life. A critical issue here is that individuals often become familiar with and recognize many conspecifics through their lifetime, including mates (Blumenrath *et al*. 2007), territorial neighbours (Stoddard 1996) or flock mates (Nowicki 1983), so is it the timing, frequency or nature of the social interaction that results in some individuals being treated as kin and others not? A particularly nice example of such context-specificity in kin recognition is suggested by Komdeur *et al*.'s (2004) finding that Seychelles warbler helpers assist in the rearing of half-siblings that are the offspring of their mother but not those of their father, even though both parents would have provisioned the helper when it was young.

It may also be possible for individuals to acquire cues to kinship based on observations of the behaviour of their familiar relatives towards other individuals. For example, unfamiliar individuals observed engaging in positive interactions with one's parents could be treated as kin. Indeed, such 'indirect familiarity' could provide a kin recognition mechanism through which individuals recognize their younger siblings, despite not being reared together. Although we are not aware of any evidence for indirect familiarity among cooperative breeders, this idea parallels the social interaction expected under indirect reciprocity, in which help is directed towards an individual who has been observed providing help to others (Nowak & Sigmund 2005). However, indirect cues to kinship are likely to be more error-prone than those learned through direct association because the link between kinship and familiarity will tend to be diluted. For example, in the case of direct association among parents, offspring and siblings during rearing, kinship of familiar individuals will usually be consistently high. But, if an offspring observes their parent interacting positively with an uncle, say, its relatedness to the 'indirectly familiar' individual is lower than that between directly familiar individuals. If the offspring subsequently helps its uncle, and this is observed by their offspring, the relatedness between such 'indirectly familiar' individuals is further reduced. As with direct familiarity, the frequency and nature of the interactions observed must also be considered, which, overall, may make the behaviour of others a noisy and unstable cue to kinship.

Social network analysis is being used increasingly to quantify the strength of association between individuals and can be applied at different life history stages (Kurvers *et al.* 2013, McDonald *et al.* 2016). A social network inevitably reflects the nature of the behavior used to construct it (Madden *et al.* 2012), and they do not necessarily reflect genetic relatedness alone (Godfrey *et al.* 2014). For example, Napper & Hatchwell (2016) found that helping decisions in long-tailed tits reflected not only kinship, but also individuals' spatial distribution and their social associations during the previous winter. More work is needed to evaluate how prior association affects kin-directed behaviors using precisely quantified social networks in different contexts and life history stages.

(ii) When is the sensitive period?

There is good evidence that kin recognition requires a period of learning, but when is this critical period? Many vocal learners have a sensory learning phase or window when they learn songs that they sing during adulthood (Kroodsma 1978). Once this window closes, most songbirds are unable to learn new songs, although their repertoire may later be modified in some species (Mooney *et al.* 2008). Studies of songbirds show that that the window can be very short with a long delay between the sensory learning phase and the sensorimotor phase, during which the song is rehearsed and perfected, e.g. swamp sparrows *Melospiza georgiana* (Marler & Peters 1982). Likewise, offspring that imprint on parents have a sensitive imprinting period (Bateson 1964), and it has been suggested that learning of parental calls may even precede hatching, resulting in a parent-specific password, in superb fairy-wrens *Malurus cyaneus* (Colombelli-Negrel *et al*. 2012). This is interpreted as defense against inter-specific brood parasitism, but selection for early parent-offspring recognition would also be expected whenever there is a substantial risk of mis-directed parental care. For example, parents in colonial bank swallows *Riparia riparia* accept any offspring in their nest before 15 days, then recognize their own offspring at 15-17 days, i.e. just before fledging (Beecher 1982, 1988, 1991).

Based on these parallels between bird song learning and associative learning of kin, we postulate that the critical period for learning the template for recognition of kin through familiarity is similar to the sensory learning phase in many vocal learners. Thus, individuals could discriminate kin from non-kin even though they also associate with non-kin before they start vocalizing (Radford 2005) or cooperating, and any associations that occur after the sensory learning phase (but before the sensorimotor phase) might result in non-kin being disregarded as social partners (i.e. associated but not ‘familiar’). Cross-fostering experiments provide strong empirical support for this putative learning period (Hatchwell *et al.* 2001, Komdeur *et al.* 2004, Sharp *et al.* 2005). However, although the time of call development is known in some species (e.g. Sharp *et al.* 2005), the precise timing of kin recognition template formation has not been identified in any cooperatively breeding species. Furthermore, while this mechanism may be effective as a rule for reliably directing care towards kin when mature offspring help their parents or siblings to raise subsequent broods, as is typical of many cooperatively breeding birds (Cockburn *et al.* 2016), there are species in which helpers care for the offspring of a younger generation of breeders (e.g. Richardson *et al.* 2007, Nam *et al.* 2010), suggesting that older birds can learn the identity of younger relatives, a process that must occur outside the putative critical learning period. A similar conclusion must be drawn when parents avoid breeding with younger relatives, as in acorn woodpeckers (Koenig *et al.* 1999).

Therefore, while the parallels with song-learning are intuitive and appealing, there are clearly situations in which a single sensitive period for learning kin identity do not apply. Cross-fostering experiments targeted at different life history stages and social network analysis across lifetimes provide invaluable tools with which to address this problem, but there remain formidable challenges to achieving a better understanding of the putative learning phase in natural populations.

(iii) What are the recognition cues?

Another challenge when determining the role of familiarity is determining the cues used in kin recognition. Vocal cues are the most likely mechanism in birds (Table 3), but this has been the default sensory modality in all of the cited studies, so visual and olfactory cues cannot be ruled out. Kin recognition mechanisms in several non-cooperatively breeding birds, particularly in the context of inbreeding avoidance, have focused on odor cues (Coffin *et al.* 2011, Krause *et al.* 2012). Storm petrels *Hydrobates pelagicus* prefer non-kin odors when choosing mates (Bonadonna & Sanz-Aguilar 2012) and odor has also been suggested as a recognition cue in zebra finches *Taenopygia guttata* (Caspers *et al.* 2013, but see Ihle & Forstmeier 2013). These studies should encourage future work on olfactory kin recognition in cooperatively breeding birds for two reasons. First, most recent evidence of odor-based kin recognition comes from species with enclosed nests, which may retain odor more readily than open nests, thereby promoting the learning and familiarization of nest odors. Many cooperative breeders nest in domed nests or cavities (Price & Griffith 2017), suggesting that olfactory cues to kinship are plausible. Second, most species in which odor-based kin recognition has been identified live in flocks or breed in colonies, even though they do not breed cooperatively, suggesting that there might be common selection pressures for odor-based kin recognition to evolve. Interestingly, the finding that preen gland secretion chemicals are positively correlated with MHC relatedness in black-legged kittiwakes *Rissa tridactyla* (Leclaire *et al.* 2014) suggests that phenotype-matching of odor cues is a feasible recognition mechanism, just as in mammals (Green *et al.* 2015). However, it should also be noted that even less is known about the timing of development, individuality and repeatability of odor profiles than is known about vocal cues.

For any kin recognition cue, whether vocal or odor, to be effective it must carry either an individual or family signature and be individually repeatable from its initial development to the time of discrimination; the same logic applies to a recognition template. Signal convergence therefore presents a significant problem for the stability of any recognition system. Frequent interactions may lead to an increase in phenotypic similarity among individuals. Vocal convergence can be adaptive for coordinated foraging (Bradbury & Balsby 2016), particularly when birds forage in annual winter flocks that disband each spring. For example, black-capped chickadees *Parus atricapillus,* exhibit vocal plasticity throughout adulthood and vocal convergence can occur within a week of winter flock formation (Nowicki 1989). However, such species do not breed cooperatively and individuals do not gain indirect fitness benefits from associating with kin. In kin-selected systems, kin recognition cues must be fixed during early development and cannot be updated during adulthood, even when interactions with non-kin are frequent (Keen *et al.* 2013, Radford 2005). In long-tailed tits, vocalisations do not change significantly over an individual's lifetime once learned (Sharp & Hatchwell 2005), but more studies that investigate the plasticity of putative recognition cues are needed. In addition, while the idea of a *signature system*, a specific profile of phenotypic components that vary in their combination from individual to individual, is well-established (Beecher 1982), most studies continue to focus on a single recognition modality, rather than recognizing that familiarity is likely to be based on a combination of cues, which may minimize convergence and maintain recognition cue diversity and integrity.

(iv) Familiarity versus phenotype matching

Although in principle the mechanisms of familiarity and phenotype matching are readily distinguished, in practice this may often not be the case. The two mechanisms differ in the predictions they make about whether the ability to discriminate requires prior association and about the resolution of discrimination. First, familiarity is explicitly dependent on social partners having prior knowledge of each other, whereas phenotype-matching allows recognition of unfamiliar kin. In practice, it is extremely difficult to rule out prior association in most field studies, even in cross-fostering experiments where there is often a period of association between parents and offspring prior to separation (e.g. Hatchwell *et al.* 2001). Kin recognition cues may even develop during gestation (e.g. Hepper 1987) or incubation (e.g. Colombelli-Negrel *et al.* 2012, Dowling *et al.* 2016). Secondly, familiarity is generally assumed to result in dichotomous classification of conspecifics into familiar (kin) and unfamiliar (non-kin) individuals, while cue-template similarity under phenotype-matching is assumed to be continuous. However, if the recognition system involves a threshold for acceptance/rejection of social partners (Reeve 1989), then discrimination based on phenotype-matching and familiarity may appear very similar in practice. Equally, it is possible that familiarity could be assessed as a continuous trait, with conspecifics discriminated according to their degree of familiarity.

Thus, the extent to which recognition cues permit kinship to be perceived on a continuous or binary scale is an important aspect of the kin recognition mechanism. When group membership is used to categorize relatives, as in Arabian babblers *Turdoides squamiceps* (Wright 1999), kin discrimination is binary. When recognition is based on phenotype, e.g. white-fronted bee eaters *Merops bullockoides* (Emlen & Wrege 1988), it may be binary or continuous, depending on the algorithm used to assess kinship. Binary or threshold kin discrimination will be effective in most cooperative breeders living on stable territories that, at least with regard to the helping sex, are mostly made up of first-order relatives, facilitating a decision rule based on prior association (Curry 1988, Payne *et al.* 1988, Komdeur *et al.* 2004). In contrast, a recognition cue that permits individuals to discriminate kin varying in relatedness has been identified only in the bell miner (Wright *et al.* 2010), even though such fine-scale discrimination has been reported in at least one other species (Nam *et al*. 2010, Leedale *et al*. in press).

The ability of helpers to assess the relatedness of conspecifics continuously may have been overlooked in some cases because of the way in which cooperative behavior is measured. For example, some studies focus on the probability of helping (Curry 1988, Creel *et al.* 1991, Dickinson *et al.* 1996), whereas others measure the amount of help given (Wright *et al.* 1999, Dunn *et al.* 1995, Clutton-Brock *et al.* 2001), and both have been measured in just a few (Emlen & Wrege 1988, Komdeur 1994, Russell & Hatchwell 2001, Nam *et al.* 2010). Moreover, consideration must also be given to how relatedness is assessed by helpers, especially the possibility of error and degree of resolution achievable (Leedale *et al.* in press).

These problems pose formidable challenges to empiricists, with more sophisticated observations and experiments required to determine how relatedness is perceived.

Conclusions

Familiarity is an intuitively plausible mechanism of kin recognition in social birds that, at first sight, appears more parsimonious than alternatives. However, we think that this apparent parsimony is deceptive, so that although most empirical studies support familiarity as the most likely mechanism, we argue that there is a great deal we do not understand about this process. In particular, we have identified four specific issues that would benefit from further investigation, although in making these recommendations, we acknowledge the difficulty of addressing them in natural populations.

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Author Contributions

AEL, BJH and JL collated research and wrote the manuscript.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Data Availability Statement

No datasets were generated for this study.

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Table 1. Key terms in kin recognition research

Term	**Definition**
Kin discrimination	The differential treatment of conspecifics within a population that differ in their genetic relatedness (Sherman *et al.* 1997).
Kin recognition	The mechanism by which kin discrimination is achieved. A discriminating individual, or *actor*, acquires *cues* to kinship from a *referent* (itself, a subset of kin, or the local environment) and uses these cues to form a *template* (Reeve 1989). This template is compared with the phenotype of an encountered conspecific, or *recipient*, and an assessment about kinship is made based on the perceived similarity between the template and the recipient's phenotype (Lacy & Sherman 1983). A specific action is then taken, based on this assessment.
Recognition cue	A phenotypic trait expressed by a individual that acts as a reliable signal of kinship, whereby within populations, similarity at the phenotypic trait is correlated with genetic similarity across the genome.
Recognition template	An internal representation of kin traits with which the phenotypes of encountered conspecifics can be compared. Templates are usually formed by learning the recognition cues of putative kin, or ones own cues. Templates may also conceivably be genetically determined.
Recognition errors	*Desirable* recipients are those which, following acceptance, provide greater fitness pay-offs to the actor than *undesirable* recipients (Reeve 1989). Within populations, recognition templates are matched against a finite set of cues which overlap in *desirable* and *undesirable* recipients due to individual variation (Lacy & Sherman 1983). Therefore, any recognition system will involve a certain amount of *acceptance errors*, where undesirable recipients are accepted, and *rejection errors*, where desirable recipients are rejected (Reeve 1989).

Table 2. Mechanisms of kin recognition

Mechanism	**Definition**
Genetic kin recognition	All three components of the recognition system are determined by a specific allele or gene complex (Mateo 2004). Genetic kin recognition does not require a period of learning in order for templates to form.
Phenotype matching	Individuals use their own phenotype and/or those of their familiar kin to form a generalized template with which to compare the phenotypes of other individuals (Greenberg 1979; Holmes & Sherman 1982). Because learned templates are generalized, a period of previous association is not required for kin to recognize one another. Instead, a positive correlation between cue similarity and level of genetic relatedness is required, so the recipients with phenotypes that most closely match the actor's general template are its closest kin (Tang-Martinez 2001).
Familiarity	The recognition cues of putative relatives are learned and used to form templates during a sensitive phase during development (Komdeur & Hatchwell 1999), within which associating individuals are likely to be kin. Individuals are subsequently able to discriminate these familiar individuals from unfamiliar ones outside of the association period. Recognition based on familiarity therefore requires a period of prior association for individuals to be categorized as kin.

Table 3. Summary of empirical field studies of cooperatively breeding birds in which kin or group discrimination has been identified.

Species	**Cue**	**Origin**	**Recognition mechanism**	**Protocol**	**Evidence**	**Reference**
Acorn woodpecker *Melanerpes formicivorus*			Familiarity	Field observations	Females do not breed in their natal group as long as their known or presumed father is still present. Reproductive vacancies remain unfilled by related nonbreeding helpers of the missing sex.	Koenig & Pitelka 1979, Koenig *et al.* 1999
Apostlebird *Struthidea cinerea*	Vocal			Call similarity analysis and playback experiments	Individuals can differentiate between different group members by call, but there is no relationship between call similarity and genetic relatedness.	Warrington *et al.* 2014, 2015
Arabian babbler *Turdoides squamiceps*	Spatial		Spatial information	Field observations	All nestlings present in the territory are fed at a similar rate, regardless of kinship or genetic similarity.	Wright *et al.* 1999
Bell miner *Manorina melanophrys*	Vocal	Genetic	Phenotype matching	Call similarity analysis	Vocal similarity correlates with genetic similarity and helper effort. The relationship between call similarity and helper effort persists after exclusion of known first-order kin.	Wright *et al.* 2010, McDonald & Wright 2011, McDonald *et al.* 2015
Chestnut-crowned babbler *Pomatostomus rifuceps*	Vocal		Familiarity	Playback experiments	Groups react more strongly to the playback of familiar group members than unfamiliar individuals from other groups.	Crane *et al.* 2014
Galápagos mockingbird *Nesomimus parvulus*			Familiarity	Field observations, cross-fostering experiments	More birds help at nests where both breeders fed the potential helper as a nestling than where one or both breeders have not. Nestling swaps do not affect behavior, so preferences	Curry 1988

					are based on the identity of breeders. Helper rates do not vary with relatedness.	
Green woodhoopoe *Phoeniculus purpureus*	Vocal		Familiarity of group members or recognition of a converged group-signature	Call similarity analysis, playback experiments	Groups have acoustically distinct rallies. Groups respond differently to rallies of neighbor groups than to stranger groups.	Radford 2005
Long-tailed tit *Aegithalos caudatus*	Vocal	Learned	Familiarity	Call similarity analysis, playback experiments, cross-fostering, Field observations	Individuals recognize familiar kin using calls learned during development. Helping and mate choice models show strong discrimination of first order kin but not second order kin.	Russell & Hatchwell 2001, Sharp *et al.* 2005, Nam *et al.* 2010, Leedale *et al.* in press, Leedale 2018
Mexican jay *Aphelocoma wollweberi*	Vocal		Familiarity of group members or recognition of a converged group-signature	Playback experiments	Jays respond more strongly individuals from other groups than to group members.	Hopp *et al.* 2001
Noisy miner *Manorina melanocephala*	Vocal			Field observations, playback experiments	Related helpers provision offspring more often than unrelated helpers. Noisy miners can differentiate individuals based on vocal cues.	McDonald *et al.* 2012, Barati *et al.* 2018
Red-cockaded woodpecker *Leuconotopicus borealis*			Familiarity	Field observations	Female breeders abdicate following the death of their mate when remaining males are sons, but remain when male helpers are unrelated.	Walters *et al.* 1988
Seychelles warbler *Acrocephalus*			Familiarity	Cross-fostering	Birds become helpers at nests belonging to individuals who fed them as nestlings, even if they are not always the most genetically	Komdeur 1994, 2004, Richardson

sechellensis				related. Females are more likely to help than males, and the decision to help is based on whether the breeding female previously fed the helper.	2003
Siberian jay *Perisoreus infaustus*		Familiarity and phenotype matching?	Cross-fostering, field observations	Cross-fostering experiments demonstrate equal tolerance towards genetic and foster offspring. Aggression of male breeders towards immigrants is negatively associated with genetic relatedness.	Griesser *et al.* 2015
Splendid fairy-wren *Malurus splendens*	Vocal	Familiarity	Playback experiments	Wrens respond aggressively to songs of wrens from other social groups. Wrens respond similarly to songs of non-kin and unfamiliar close kin.	Payne *et al.* 1988
Stripe-backed wren *Campylorhynchus nuchalis*	Vocal	Familiarity and phenotype matching?	Playback experiments	Wrens discriminate between the calls of unrelated neighboring groups and unfamiliar groups, and they discriminate both of these from calls of their own groups. Responses to calls from presumably unfamiliar patrilineal relatives in other groups do not differ from responses to those in own groups. Calls are likely to be learned during development.	Price 1998, 1999
Superb starling *Lamprotornis superbus*	Vocal	Familiarity	Call similarity analysis, playback experiments	Flight calls are more similar within groups than within the larger population. Call similarity is uncorrelated with genetic relatedness.	Keen *et al.* 2013
Western bluebird *Sialia mexicana*	Vocal	Familiarity	Playback experiments, field experiments	Familiar kin are actively avoided as mates when pairing occurs in winter groups. Males respond more aggressively towards songs of nonkin than songs of kin, but call similarity does not indicate kinship.	Açkay *et al.* 2013, 2014, Dickinson *et al.* 2016

White-fronted bee eater *Merops bullockoides*		Familiarity	Field observations	Helpers preferentially help kin; the probability of helping decreases with relatedness between helper and potential recipient. Recognition is based on early associations formed during nestling or fledgling development.	Emlen & Wrege 1988