

*Review*

# The evolution of cooperative breeding in birds: kinship, dispersal and life history

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The evolution of cooperation among animals has posed a major problem for evolutionary biologists, and despite decades of research into avian cooperative breeding systems, many questions about the evolution of their societies remain unresolved. A review of the kin structure of avian societies shows that a large majority live in kin-based groups. This is consistent with the proposed evolutionary routes to cooperative breeding via delayed dispersal leading to family formation, or limited dispersal leading to kin neighbourhoods. Hypotheses proposed to explain the evolution of cooperative breeding systems have focused on the role of population viscosity, induced by ecological/demographic constraints or benefits of philopatry, in generating this kin structure. However, comparative analyses have failed to generate robust predictions about the nature of those constraints, nor differentiated between the viscosity of social and non-social populations, except at a coarse level. I consider deficiencies in our understanding of how avian dispersal strategies differ between social and non-social species, and suggest that research has focused too narrowly on population viscosity and that a broader perspective that encompasses life history and demographic processes may provide fresh insights into the evolution of avian societies.

**Keywords:** cooperative breeding; helping; avian sociality; ecological constraints; dispersal; avian phylogeny

## 1. INTRODUCTION

The evolution of cooperation has been a fundamental and persistent problem for evolutionary biologists for the past 150 years. Darwin (1859) recognized the paradox of apparently altruistic behaviour among individuals subject to natural selection, but the full extent of the problem of cooperation and its ubiquity in biological systems from the level of genes to our own complex society has been appreciated only recently. Indeed, the last few years have seen a plethora of theoretical studies and synthetic reviews that seek to consolidate the diverse theoretical and empirical approaches and solutions to this long-standing puzzle (West *et al.* 2007).

The cooperative breeding systems of birds have been a fertile testing ground for ideas on the evolution of societies, resulting in some of the most intensive studies of natural populations in ecology (e.g. Stacey & Koenig 1990). As the number of studies has grown, coupled with developments in molecular genetics, so has the realization that vertebrate societies are extremely diverse in their social organization and mating system (Cockburn 2004). This diversity presents significant problems in defining what is meant by 'cooperative breeding'. 'Helper-at-the-nest' systems where grown offspring remain on their natal territory and help their parents to raise subsequent broods are

easily classified, but in many species there are multiple breeders of either sex within social groups, in addition to non-breeding helpers. These 'plural' breeding systems are also universally included as cooperative breeders. More contentious are those species in which all individuals within social groups are potential breeders and there are no non-breeding helpers, e.g. dunnocks *Prunella modularis* (Davies 1992). Cockburn (2006) used a broad definition that considered a species to be cooperative when more than 10 per cent of nests in one or more populations are attended by more than two birds, thereby including such systems. Others have used more restrictive definitions that differentiate between cooperative polygamy and cooperation based on collateral kinship (e.g. Hartley & Davies 1994) or care by non-breeders (Ligon & Burt 2004). However, there is no clear distinction between cooperative polygamy and systems with helpers (Cockburn 1998) and in many cases, it is unknown whether 'helpers' are non-breeders or potential breeders. In this article, I first follow Cockburn's (2006) definition in reviewing the importance of family formation and kinship in avian cooperative breeding systems.

Another problem arises over obligate and facultative cooperation, terms that have been used in various senses by different authors (e.g. DuPlessis *et al.* 1995; Cockburn 1998). In reality, a tiny minority of avian cooperative breeding systems are truly obligate in the sense that successful reproduction is impossible without helpers, e.g. white-winged cough *Corcorax melanorhamphos* (Heinsohn 1992). In principle, at

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least, the facultative nature of the vast majority of their cooperative societies makes birds an ideal group in which to study the conditions that promote cooperative behaviour, but our understanding of the ecological, demographic and phylogenetic factors that have resulted in the evolution of cooperation is still far from comprehensive. In this article, I consider the problems that may have contributed to this failure to fully explain social evolution in birds, and suggest areas of research that may contribute to achieving that goal. First, I consider the phylogenetic distribution of cooperative breeding and describe likely evolutionary routes to cooperative breeding, emphasizing the important role that the kinship of cooperators has played. Next, I discuss the evidence that constraints on dispersal are responsible for the development of kin-structured populations, highlighting our relatively poor knowledge of dispersal strategies in both social and non-social species. Finally, I suggest that explanations have focused too closely on population viscosity, and that a broader perspective on the processes generating kin-structured populations would be profitable.

## 2. PHYLOGENETIC DISTRIBUTION OF COOPERATIVE BREEDING

Cockburn (2006) recently compiled a remarkable dataset that included the breeding systems of 9456 extant bird species, of which 9268 (98%) were assigned to 188 families, the remainder having uncertain affinities. The pattern of parental care has been described, in more or less detail, for over half of these species (5143/9456; 54%) and patterns of parental care for the rest were inferred from phylogenetic relationships. Cockburn (2006) assigned 852 species (9%) as cooperative breeders, which represents a substantial increase on the 2.5–3% recognized in previous studies (Brown 1987; Arnold & Owens 1998; Ligon & Burt 2004). This increase is not simply a consequence of Cockburn's (2006) use of a broad definition of cooperative breeding, but is attributable to the use of phylogenetic inference in the assignment of a breeding system, rather than relying on direct evidence (which is inevitably patchy even for a well-studied taxon, such as the birds) and the assumption of biparental care as the default pattern. Given the lack of detailed studies of the avifaunas of tropical regions, where cooperative breeding is particularly prevalent, this approach is likely to give a closer approximation than previous treatments, despite the likely errors in some assignments (Cockburn 2006).

As in previous studies, Cockburn (2006) found a patchy phylogenetic distribution of cooperative breeding and evidence that it has evolved multiple times (Russell 1989; Peterson & Burt 1992; Edwards & Naeem 1993; Cockburn 1996). Assuming that biparental care is ancestral, Ligon & Burt (2004) estimated that there had been at least 28 independent transitions to cooperative breeding. Furthermore, although several bird families have cooperative breeding as an ancestral state, and many may have experienced a single transition to cooperation in their evolutionary history, Cockburn (2006) lists 35 bird families in

which there have been multiple transitions to or from cooperative breeding. Of course, the number of evolutionary transitions identified is dependent on phylogenetic relationships and even in a well-studied group like the birds, the affinities of many species remain obscure, with some high-level relationships still a matter of debate (e.g. Hackett *et al.* 2008). Therefore, although the patchy distribution of cooperation within the avian phylogeny and the multiple evolutionary transitions to and from cooperative breeding are robust, the finer details of the phylogenetic distribution and relationships of some cooperative breeders remain to be resolved.

A key point that emerges from this analysis is that avian breeding systems offer an excellent opportunity to understand the evolutionary origins of cooperative behaviour in vertebrates. Three features are important in this regard: (i) our relatively good knowledge of avian breeding systems; (ii) the fact that the great majority of cooperative species exhibit facultative cooperation allowing observational and experimental tests within species; and (iii) the multiple transitions to and from cooperation provide ample opportunity to test evolutionary hypotheses through comparative methods.

## 3. EVOLUTIONARY ROUTES TO COOPERATIVE BREEDING

Ligon & Burt (2004) argued that the evolution of altriciality in birds, which is likely to be an ancestral trait for most extant bird lineages (Ricklefs & Starck 1998), played a key role in the evolution of cooperative breeding because altriciality and the high level of parental investment it requires provides the opportunity of helping as an adaptive strategy. This view is supported by the observation that there have been more transitions to cooperation in altricial lineages than expected if developmental mode and cooperative breeding were randomly associated (Ligon & Burt 2004). Nevertheless, cooperative brood care is found in 4 per cent ( $n = 789$ ) of precocial species, in many of which parental investment may also be high. Therefore, while less frequent than in altricial species (11% of 7698 species), cooperation still occurs in a substantial number of precocial species (Cockburn 2006). It is also important to note that the cooperatively breeding precocial species include helper-at-the-nest systems, such as members of the Psophiidae and Rallidae (del Hoyo *et al.* 1996), although in other precocial families the system is more precisely described as cooperative polygamy, e.g. in the Rheidae and Anseranatidae (del Hoyo *et al.* 1992).

Most treatments propose that helping behaviour evolved as alloparental care within family groups formed through delayed dispersal (Brown 1987; Ligon & Stacey 1991; Ligon & Burt 2004). In this scenario, non-reproductive delayed dispersers might be stimulated to provide care for non-descendant offspring by exposure to the stimulus of begging. This idea is supported by occasional observations of typically non-cooperative bird species feeding conspecific offspring belonging to another pair, or even feeding the offspring of another species (Shy 1982;

Skutch 1987). If the feeding of conspecific offspring confers some form of fitness benefit, either directly or indirectly via kin selection (Hamilton 1964), then adaptive helping behaviour within more or less stable family groups would evolve. This model proposes that helping and independent breeding will generally be sequential; delayed dispersal and a period of helping followed by acquisition of reproductive status (either by dispersal or ascendancy to dominant status within the natal group) and then independent reproduction.

An alternative evolutionary route to cooperation is more opportunistic and has been described as cooperative breeding within kin neighbourhoods rather than within well-defined family groups (Dickinson & Hatchwell 2004; Ligon & Burt 2004). The existence of kin neighbourhoods provides opportunities for helping behaviour beyond the confines of a particular group and also permits greater flexibility in the ordering of helping and independent reproduction. For example, in long-tailed tits *Aegithalos caudatus*, all members of a population breed independently, but failed breeders may become helpers at the nest of close kin towards the end of a temporally constrained breeding season when the prospect of successful independent reproduction is low (MacColl & Hatchwell 2002; Hatchwell & Sharp 2006). Similar behaviour is seen among family members in western bluebirds *Sialia mexicana* (Dickinson *et al.* 1996), and within 'clans' of the colonial white-fronted bee-eater *Merops bullockoides*, where helpers may even be recruited by disruption of relatives' breeding attempts (Emlen & Wrege 1992). More extensive social networks with complex investment patterns occur in the 'coteries' of bell miners *Manorina melanophrys* (Clarke & Fitz-Gerald 1994). This kind of social organization has been neglected because of the focus on the more traditional concept of cooperation within stable nuclear family groups (Ligon & Burt 2004), despite the very substantial fitness consequences that this form of helping may have (e.g. Emlen & Wrege 1991; MacColl & Hatchwell 2004).

Following the initial evolution of helping behaviour via one or other of these routes, variation among species in evolutionary history, ecology and life history would have resulted in the diverse social systems among extant birds. However, despite that adaptive radiation in social organization and complexity, it is clear that the imagined ancestral pattern of cooperative behaviour evolving predominantly among members of family groups still holds among extant cooperative breeders. Among the 9 per cent of bird species that Cockburn (2006) described as cooperative, only a small minority have been described in sufficient detail to characterize their kin structure precisely. The social organization of many species remains completely unstudied, and in some cases only rudimentary information is available on what are likely to be entire families of cooperative species, such as the Galbulidae (del Hoyo *et al.* 2002). However, if social structure is inferred from those species whose kin associations are known to other members of their respective families, then 55/84 (65%) of families with

species that exhibit regular cooperative breeding can be broadly characterized as having cooperative groups composed of kin or not. Of these 55 families, 44 (80%) can be provisionally described as being cooperative within kin groups. If a family's characterization is extrapolated to all the species within that family, then 612/820 (75%, excluding species of uncertain affinity) cooperative species can be characterized, and of these 556/612 (91%) can be provisionally described as being cooperative predominantly within kin groups (appendix A).

The remaining taxa (20% of families, 9% of species), in which cooperation occurs mainly among unrelated individuals, are dominated by cooperative polygamists where all individuals within groups are 'hopeful reproductives'. As explained above, some definitions of cooperative breeding have omitted such systems, regarding them as different in kind from those in which helpers feed broods in which they have no direct reproductive stake (e.g. Ligon & Burt 2004). Instead, it could be argued that they are best considered within conventional mating systems theory (Emlen & Oring 1977), arising from conflict between the sexes over their preferred mating system (e.g. Davies 1992). Therefore, it is important to acknowledge the likelihood that some cooperative polygamous systems have evolved via different routes to the more conventional cooperative breeding systems that are the main focus of this review.

It is also important to note that the dichotomous classification of families as having either kin-based cooperative systems or not, may be perfectly valid in some cases, but less so in others. For example, in the Neosittidae, Corcoracidae, Sturnidae, Sittidae and Mimidae, the breeding systems of many or all of their cooperative species are fairly well known (del Hoyo *et al.* 2005, 2006, 2007, 2008; Woxvold *et al.* 2006; Rubenstein & Lovette 2007; Beck *et al.* 2008), whereas among families such as the Bucconidae, Lybiidae and Dacelonidae, the inference is more speculative (del Hoyo *et al.* 2001, 2002). Furthermore, in a few families, such as the Psittacidae, in which some species are well described, the social structures are sufficiently diverse to defy generalization (del Hoyo *et al.* 1997).

Among those taxa with kin-based cooperative systems, the importance of helping behaviour within kin neighbourhoods has probably been under-estimated (Dickinson & Hatchwell 2004). Using Cockburn's (2006) compilation, I characterized 44 families as having kin-based cooperation (see above), and helping of this sort occurs in at least 18 (41%) of those families (appendix A). Unfortunately, the scant information available prevents the assessment of its significance at the level of species, but it may have been the main route to helping in certain families, such as the Meropidae (del Hoyo *et al.* 2002) and Aegithalidae (del Hoyo *et al.* 2008). An interesting feature of kin neighbourhoods is that the permissive conditions for kin-directed cooperation to evolve may be more frequent than in the more extreme form of family structure that results from delayed dispersal. On the other hand, if the benefits of cooperation are dependent on help being directed towards kin, then for

fitness gains to be maximized some mechanism of kin recognition may be required (Komdeur & Hatchwell 1999; Komdeur *et al.* 2008).

Why should kin association be so important in setting the scene for the evolution of avian societies and cooperation? The obvious answer to this question is that close association of kin creates the opportunity for kin selection to operate (Hamilton 1964). Although the weight of evidence in favour of kin-selected cooperative breeding is debated (e.g. Clutton-Brock 2002; Cockburn 1998), the evidence for kin-selected fitness benefits of cooperative breeding is very strong for many birds (Dickinson & Hatchwell 2004). This is not to say that kin selection is always important: (i) there are many examples of cooperation among non-kin; (ii) there may be various sources of direct fitness benefits for both related and unrelated individuals within cooperative groups, that may have been under-estimated in the past; (iii) the role of indirect fitness benefits may have been over-estimated in some cases by a failure to test whether help in family groups is kin-selected and to take account of confounding effects (for reviews, see Cockburn 1998; Clutton-Brock 2002; Dickinson & Hatchwell 2004). Furthermore, costs of competing with kin are often neglected (Griffin & West 2002). Therefore, although studies have identified various fitness benefits from cooperative breeding, the relative importance of kin selection in the evolution of avian societies is still not fully resolved.

Kinship may also be important in stabilizing and reducing conflict within cooperative groups through inbreeding avoidance, at least within nuclear families. There is good evidence of this in several cooperative breeders, although in others incest is commonplace (Koenig & Haydock 2004). Close kinship between breeders and helpers who are potential breeders may reduce conflict over reproduction, and the scale of this stabilizing effect is illustrated by the intense power struggles that may develop among opposite sex kin when a reproductive vacancy arises through death of a parent in acorn woodpeckers *Melanerpes formicivorus* (Koenig *et al.* 1998). However, the impact of incest avoidance on social birds remains poorly understood (Koenig & Haydock 2004).

In summary, this review of potential routes to cooperative breeding has provided quantitative support for the contention that cooperation typically occurs among relatives. This is not to say that social groups are invariably composed of kin, nor that kin selection has always been a major selective force in the evolution of avian cooperative breeding. Nevertheless, despite these caveats, it is reasonable to conclude that the key to understanding the evolution of cooperative breeding in birds lies in understanding how kin associations develop. In other words, how do we explain the development of kin-structured populations?

#### 4. ECOLOGICAL CONSTRAINTS AND DISPERSAL

Hamilton (1964) proposed that in viscous populations, where dispersal is either delayed or limited, the opportunities to interact with kin increase. This idea has provided the context for all adaptive

hypotheses for the evolution of cooperative breeding. It is not my intention to review the history and development of explanations for the evolution of avian societies in any depth here, because there have been several recent reviews (Cockburn 1998; Hatchwell & Komdeur 2000; Dickinson & Hatchwell 2004), but it is worth briefly summarizing their key features and similarity. Selander (1964) set the ball rolling with the habitat saturation hypothesis, proposing that the opportunities for dispersal and independent breeding are limited in saturated habitats so that offspring remain on their natal territory and wait for suitable reproductive vacancies to appear. Developments of this idea incorporated the merits of delayed dispersal relative to floating (Brown 1969, 1974; Verbeek 1973), the benefits of prolonged parental care (Ekman *et al.* 2001) and the importance of gradients in habitat quality for dispersal decisions (Koenig & Pitelka 1981; Stacey & Ligon 1987, 1991; Zack 1990). These various proposals can be accommodated within the generalized ecological constraints hypothesis of Emlen (1982) and the delayed dispersal threshold model of Koenig *et al.* (1992). These two landmark papers make the common point that the various hypotheses presented above are essentially variants on the same theme: that individuals help when the balance of costs and benefits are weighed against floating, dispersing or attempting to breed independently and in favour of delayed dispersal, deferred reproduction and cooperation. The various hypotheses differ in the emphasis that they place on different components of that cost-benefit equation and the context in which this analysis is made, but they share the same fundamental principles (Emlen 1994). More recently, Covas & Griesser (2007) have proposed the adaptive delayed dispersal hypothesis that treats delayed dispersal as a life-history decision that weighs the relative costs and benefits of dispersal in the long term (i.e. over an individual's lifetime) rather than in the short term (i.e. the chance of filling a breeding vacancy immediately). This hypothesis is important in emphasizing the long-term consequences of decision-making and its recognition of the interplay between parental and offspring decision-making. However, it can be argued that it does not differ in its essentials from previous explanations, simply in the time-span over which costs and benefits of dispersal decisions are weighed.

How strong is the evidence that ecological constraints driving family formation? Again, this issue has been extensively reviewed (Cockburn 1998; Hatchwell & Komdeur 2000; Dickinson & Hatchwell 2004; Covas & Griesser 2007; Hatchwell 2007), so I will present only a brief summary of the evidence here. First, a number of intraspecific studies have investigated the relationship between specific constraints and the prevalence of cooperative breeding either by observation (e.g. Emlen 1984; Russell 2001) or experiment (Pruett-Jones & Lewis 1990; Komdeur 1992; Walters *et al.* 1992; Covas *et al.* 2004), and have provided consistently strong evidence that specific ecological and/or demographic constraints limit dispersal and promote cooperation. By contrast, interspecific comparisons that have sought common ecological factors that drive

family formation and cooperative breeding have proved equivocal (e.g. Ford *et al.* 1988; DuPlessis *et al.* 1995; Cockburn 1996; Arnold & Owens 1999; Rubenstein & Lovette 2007). Therefore, no consensus has emerged about whether cooperatively breeding species share key ecological or demographic traits, and despite its intuitive sense, the notion that constraints drive family formation is less compelling than was once thought because we still lack a predictive framework to explain cooperative breeding (Cockburn 1998; Hatchwell & Komdeur 2000). In the following section I consider in greater detail the processes that lead to kin-structured populations, with the aim of generating insights into the traits that should be examined in such comparisons.

## 5. WHAT FACTORS GENERATE KIN-STRUCTURED POPULATIONS?

Few studies have explored the fine-scale genetic structure of bird populations, and certainly not enough to attempt any systematic comparison of cooperative and non-cooperative species. Among cooperative species, kin structure has been demonstrated in superb fairy wrens *Malurus cyaneus* (Double *et al.* 2005), white-breasted thrashers *Ramphocinclus brachyurus* (Temple *et al.* 2006), apostlebirds *Struthidea cinerea* (Woxvold *et al.* 2006) and white-winged chough (Beck *et al.* 2008), but all these species have retained offspring, so such structure is hardly surprising. Among species that exhibit helping within kin neighbourhoods, population genetic structure has been measured genetically only for the bell miner *Manorina melanophrys* (Painter *et al.* 2000), sociable weaver *Philetairus socius* (Covas *et al.* 2006) and long-tailed tit (S. P. Sharp & B. J. Hatchwell 2009, unpublished data), again revealing significant kin structure, especially among the predominant helping sex.

Among the non-cooperative species whose population structure has been measured, it is notable that many of them also exhibit significant fine-scale kin structure, e.g. Brunnich's guillemots *Uria lomvia* (Friesen *et al.* 1996), manakins *Manacus manacus* (Shorey *et al.* 2000), black grouse *Tetrao tetrix* (Hoglund *et al.* 1999), red grouse *Lagopus lagopus* (Pierrney *et al.* 2008) and blue tits *Cyanistes caeruleus* (Foerster *et al.* 2006). Therefore, even if this is a biased sample of non-cooperative species, it is clear that genetically structured populations are widespread in non-cooperative species as well as cooperative ones.

In addition to direct genetic evidence, indirect methods may also be used. I first consider the evidence that population viscosity (i.e. patterns of natal dispersal) differs in the predicted manner and ask whether dispersal always acts to disrupt kinship ties. Finally, I describe a broader perspective on the processes contributing to the kin structure of populations.

### (a) Population viscosity

Hamilton (1964) and most subsequent workers have identified population viscosity as being the most important process generating the kin structure required for kin-selected cooperation to evolve, leading to the clear prediction that dispersal will be lower in cooperative species than in non-cooperative species. It is patently

true that for those species in which helping occurs within nuclear families formed through philopatry, that dispersal is extremely limited at least during the period of helping. In such species, helping typically occurs prior to natal dispersal from the home territory, and dispersal distance following this period of helping may have no impact on the cooperative system because there is little post-dispersal interaction with kin remaining on the natal territory (Stacey & Koenig 1990). However, cooperative species with nuclear family structure and non-cooperative species are not completely differentiated in this respect because family-living is much more widespread among birds than cooperative breeding is (Ekman *et al.* 2004; Covas & Griesser 2007), although the full extent of family-living without cooperative breeding has not been assessed systematically. Furthermore, among those species that have evolved cooperative breeding within kin neighbourhoods, often with redirected helping following reproductive failure, there must be some natal dispersal prior to breeding (e.g. Dickinson *et al.* 1996; Painter *et al.* 2000; Sharp *et al.* 2008a,b). Dispersal at this stage is likely to generate further overlap in dispersal strategies between cooperative and non-cooperative species, although species in which cooperation occurs within kin neighbourhoods would still be expected to exhibit less dispersal on average than non-cooperative species.

Unfortunately, despite its significance for ecology and evolution, variation among individuals or species in dispersal strategy remains poorly understood (Clobert *et al.* 2001), and there has been no systematic comparison of dispersal distances of cooperative and non-cooperative species beyond broad classifications of species as sedentary, nomadic or migratory (DuPlessis *et al.* 1995; Arnold & Owens 1999). Of those species exhibiting help within kin neighbourhoods, natal dispersal has been determined for long-tailed tits, showing that most males (the more philopatric and predominant helping sex) disperse less than 400 m (Sharp *et al.* 2008a). However, such dispersal distances are not atypical of non-cooperative temperate passerine birds (Paradis *et al.* 1998; figure 1) and detailed studies of many non-cooperative species show very similar dispersal distributions, e.g. great tit *Parus major* (Szulkin & Sheldon 2008), magpie *Pica pica* (Eden 1987) and song sparrow *Melospiza melodia* (Arcese 1989). The measurement of dispersal is fraught with problems (Koenig *et al.* 1996; Nathan 2001), so any comparison across species or populations must be qualified by the recognition of biases in estimating dispersal distances. Russell (1999) conducted a more systematic comparison of dispersal in four non-cooperative and one cooperative species (long-tailed tit) occupying the same habitats, using the recapture rates at the same site of very large samples of ringed juveniles as a measure of philopatry. Recapture rates did not differ, and hence there was no indication that long-tailed tits had unusually limited dispersal. Therefore, despite its intuitive plausibility, at present there is no strong evidence that sedentary species exhibiting cooperation within kin neighbourhoods have an unusual pattern of dispersal relative to non-cooperators.

A fundamental assumption of the argument that population viscosity increases the opportunity for the

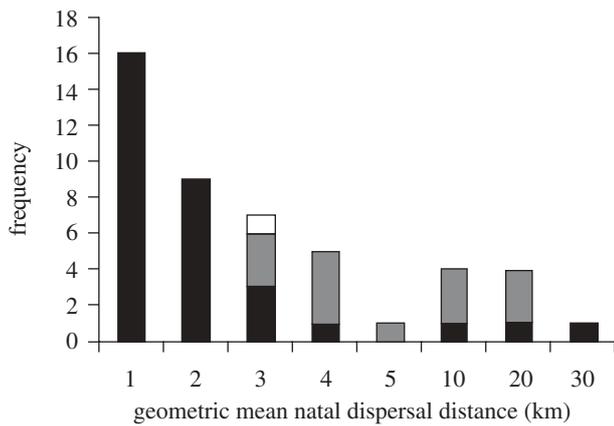


Figure 1. Geometric mean natal dispersal distances for 47 UK passerine species. Black and grey bars represent resident and migratory species, respectively; the only UK species exhibiting kin-directed cooperative breeding, the long-tailed tit, is represented by the white bar. Data from Paradis *et al.* (1998).

evolution of kin-selected cooperation is that dispersal is a largely random process with respect to kinship (Hamilton 1964; Perrin & Goudet 2001; Gardner & West 2006). However, kin association during natal dispersal has been recorded in both social (Heinsohn *et al.* 2000; Koenig *et al.* 2000; Williams & Rabenold 2005; Sharp *et al.* 2008b) and non-social birds (e.g. Shutler & Clark 2003; Matthysen *et al.* 2005). Kin association during dispersive movements may also occur at a much larger scale, serving to maintain kin structure in populations despite the occurrence of long-distance migration. The observation that cooperative breeding is not expected to occur in migratory species because of the disruptive effect of large-scale movements on kinship has been made frequently (Brown 1987; Russell 1989; Cockburn 1996, 1998; Kokko & Lundberg 2001). However, kin-directed cooperative breeding has evolved in migratory bee-eaters (Lessells *et al.* 1994; Boland 2004), dusky woodswallows *Artamus cyanopterus* (Sims 2007) and long-tailed tits (B. K. Woodward 2008, personal communication). Indeed, figure 1 illustrates that the natal dispersal distances of migrants overlap considerably with those of resident species.

To summarize, the difference between the population viscosity of cooperative and non-cooperative species appears less clear-cut than is generally assumed. In particular, the limited evidence available suggests that there is much overlap in dispersal strategies of non-social species and those social species where helping occurs within kin neighbourhoods. Furthermore, even when dispersal does occur it does not preclude the evolution of kin-directed cooperation. It is also clear that our understanding of the role of dispersal in generating the permissive conditions for the evolution of cooperative breeding is generally poor and would benefit greatly from more systematic study.

#### (b) *Life history and demography*

Life-history traits have been formally included as a potential influence on the evolution of society in the life-history hypothesis (Brown 1987; Arnold &

Owens 1998). Life-history traits are highly conserved in avian evolution (Owens & Bennett 1995), so the strong phylogenetic signal in cooperative behaviour fits well with this hypothesis. However, the results of comparative analyses are again inconsistent (Yom-Tov *et al.* 1992; Poiani & Jermiin 1994; Arnold & Owens 1998), although the most extensive of them concluded that low adult mortality was the key factor predisposing certain avian lineages to cooperate (Arnold & Owens 1998). In these comparative studies, consideration of life-history traits as factors influencing the evolution of cooperative breeding has been in the context of population viscosity, and their influence on the rate at which breeding vacancies arise and to which helpers can disperse. Therefore, Hatchwell & Komdeur (2000) argued that the life-history hypothesis is complementary to the ecological constraints hypothesis rather than an alternative, because ecological factors and life-history traits will act in concert to influence dispersal decisions.

However, life-history traits and demographic processes might affect the opportunity for cooperation to evolve in ways that have been neglected hitherto. A recent theoretical study indicates that rather than focusing solely on population viscosity, a broader perspective on factors influencing the kin structure of populations would be worthwhile. Beckerman *et al.* (submitted) used a demographic model to explore the consequences of variation in population size, adult longevity and recruitment, as well as dispersal, on the emergent kin structure of a population. In addition, the model demonstrates that the pattern of offspring mortality plays a critical role in determining the probability of a kin neighbourhood developing among adults. The model is based on the redirected helping system of long-tailed tits and similar species, and formalizes the verbal arguments of Riehm (1970) and Russell (1999). Mortality occurs either at the nestling phase, removing whole families from the pool of potential recruits, or at the post-fledging stage, when individuals rather than whole families will be lost. This simple difference in the timing of offspring mortality has a substantial impact on the size and relatedness of the pool of juveniles from which recruits must be drawn, and hence has a profound effect on the genetic structure of the population in the following year, even when all other variables are held constant. Thus, the kin structure of two populations may be strikingly different even though dispersal does not differ between them. The model can be generalized to predict the combinations of life history and demographic traits that generate kin structure in the absence of variation in dispersal, and the outcome has particular relevance for those cooperative systems where helping occurs within kin neighbourhoods (Beckerman *et al.* submitted).

## 6. CONCLUSION

In summary, despite several decades of research into cooperatively breeding birds, including some of the most detailed ecological and behavioural studies of any vertebrate species, we are still some way from understanding the evolution of avian societies. In this

review, my first aim has been to build on the important compilation of Cockburn (2006) to emphasize the importance of the development of kin associations for the subsequent evolution of cooperation. These associations are not necessarily stable nuclear families, but in a surprisingly large number of taxa are better described as kin neighbourhoods (Dickinson & Hatchwell 2004), often characterized by a more flexible or opportunistic system of helping. Second, I have sought to highlight the deficiencies in our understanding of the key demographic process thought to be responsible for the development of families, i.e. dispersal. Measurement of dispersal is a challenge in both social and non-social systems but it is clear that there is considerable overlap in dispersal strategy between the two, with family-living more common than cooperative breeding, and helping frequently occurring following natal dispersal. Finally, I suggest that consideration of the factors influencing the kin structure of populations, and hence generating the permissive conditions for the evolution of kin-directed cooperation have been too narrowly focused on population viscosity, and that a broader perspective that encompasses life history and demographic processes may provide fresh insights into the circumstances in which avian societies have evolved.

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## APPENDIX A

Occurrence of kin-based groups and kin neighbourhoods among avian families that contain cooperative species (table 1).

Table 1. Avian taxa (family level) containing cooperative species (from Cockburn 2006), showing the number of species in the taxon (*n*), the number of cooperative species (CB), whether cooperative groups in most of those cooperative species are composed of kin (kin) and whether cooperative species within that taxon includes systems where cooperation occurs within kin neighbourhoods (KN) (Dickinson & Hatchwell 2004).

family <sup>a</sup>	<i>n</i>	CB	kin <sup>b</sup>	KN <sup>c</sup>	reference
Rheidae	2	1	0	0	del Hoyo <i>et al.</i> (1992)
Apterygidae	5	1	?	?	del Hoyo <i>et al.</i> (1992)
Anseranatidae	1	1	0	0	del Hoyo <i>et al.</i> (1992)
Galbulidae	18	18	?	?	del Hoyo <i>et al.</i> (2002)

(Continued.)

Table 1. (Continued.)

family <sup>a</sup>	<i>n</i>	CB	kin <sup>b</sup>	KN <sup>c</sup>	reference
Bucconidae	33	5	1	0	del Hoyo <i>et al.</i> (2002)
Lybiidae	41	26	1	0	del Hoyo <i>et al.</i> (2002)
Ramphastidae	48	11	?	?	del Hoyo <i>et al.</i> (2002)
Picidae	214	18	1	0	del Hoyo <i>et al.</i> (2002)
Bucerotidae	51	20	1	0	del Hoyo <i>et al.</i> (2001)
Bucorvidae	2	2	1	0	del Hoyo <i>et al.</i> (2001)
Upupidae	2	2	0	0	del Hoyo <i>et al.</i> (2001)
Phoeniculidae	5	5	1	0	del Hoyo <i>et al.</i> 2001
Coraciidae	12	1	?	?	del Hoyo <i>et al.</i> (2001)
Meropidae	25	20	1	1	del Hoyo <i>et al.</i> (2001)
Cerylidae	9	1	1	0	del Hoyo <i>et al.</i> (2001)
Dacelonidae	59	14	1	0	del Hoyo <i>et al.</i> (2001)
Todidae	5	5	?	?	del Hoyo <i>et al.</i> (2001)
Coliidae	6	6	1	0	del Hoyo <i>et al.</i> (2001)
Cuculidae	140	4	0	0	del Hoyo <i>et al.</i> (1997)
Opisthocomidae	1	1	1	0	del Hoyo <i>et al.</i> (1996)
Psittacidae	347	19	?	?	del Hoyo <i>et al.</i> (1997)
Apodidae	91	12	?	?	del Hoyo <i>et al.</i> (1999)
Musophagidae	23	5	?	?	del Hoyo <i>et al.</i> (1997)
Psophiidae	3	3	0	0	del Hoyo <i>et al.</i> (1996)
Rallidae	132	18	1	1	del Hoyo <i>et al.</i> (1996)
Rhynchocetidae	1	1	1	0	del Hoyo <i>et al.</i> (1996)
Mesitornithidae	3	2	1	0	del Hoyo <i>et al.</i> (1996)
Stercorariidae	8	1	0	0	del Hoyo <i>et al.</i> (1996)
Charadriidae	65	1	?	?	del Hoyo <i>et al.</i> (1996)
Haematopodidae	10	1	0	0	del Hoyo <i>et al.</i> (1996)
Accipitridae	235	14	0	0	Kimball <i>et al.</i> (2003)
Falconidae	62	15	0	0	Kimball <i>et al.</i> (2003)
Scopidae	1	1	?	?	del Hoyo <i>et al.</i> (1992)
Acanthisittidae	2	1	1	1	del Hoyo <i>et al.</i> (2004)
Eurylamiidae	15	3	?	?	del Hoyo <i>et al.</i> (2003)
Thamnophilidae	188	2	?	?	del Hoyo <i>et al.</i> (2003)

(Continued.)

Table 1. (Continued.)

family <sup>a</sup>	<i>n</i>	CB	kin <sup>b</sup>	KN <sup>c</sup>	reference
Furnariidae	213	7	1	0	del Hoyo <i>et al.</i> (2003)
Cotingidae	67	1	?	?	del Hoyo <i>et al.</i> (2004)
Tyrannidae	337	6	?	?	del Hoyo <i>et al.</i> (2004)
Climacteridae	7	5	1	1	del Hoyo <i>et al.</i> (2007)
Maluridae	28	28	1	0	del Hoyo <i>et al.</i> (2007)
Meliphagidae	174	22	1	1	del Hoyo <i>et al.</i> (2008)
Pardalotidae	67	29	1	1	del Hoyo <i>et al.</i> (2008)
Pomatostomidae	5	5	1	1	del Hoyo <i>et al.</i> (2007)
Neosittidae	2	2	1	1	del Hoyo <i>et al.</i> (2007)
Vireonidae	53	1	?	?	Cockburn (2006)
Campephagidae	80	5	1	0	del Hoyo <i>et al.</i> (2005)
Falcunculidae	2	2	1	0	del Hoyo <i>et al.</i> (2007)
Oriolidae	28	2	?	?	del Hoyo <i>et al.</i> (2008)
Artamidae	24	17	1	1	Sims (2007)
Malaconotidae	101	23	1	0	Urban <i>et al.</i> (1997)
Dicruridae	23	1	?	?	Thangamani <i>et al.</i> (1981)
Corcoracidae	2	2	1	1	Heinsohn (2000); A. F. Russell (2009), unpublished data
Monarchidae	90	1	1	0	del Hoyo <i>et al.</i> (2006)
Laniidae	30	6	1	0	del Hoyo <i>et al.</i> (2008)
Corvidae	116	47	1	1	Madge & Burn (1994)
Corvoidea <i>incertae sedis</i>	24	12	—	—	— <sup>d</sup>
Picathartidae	3	1	1	0	del Hoyo <i>et al.</i> (2007)
Petroicidae	43	12	?	?	del Hoyo <i>et al.</i> (2007)
Paridae	62	20	1	0	del Hoyo <i>et al.</i> (2007)
Stenostiridae	10	2	1	0	Urban <i>et al.</i> (1997)
Alaudidae	86	2	?	?	del Hoyo <i>et al.</i> (2004)
Aegithalidae	10	4	1	1	del Hoyo <i>et al.</i> (2008)
Pycnonotidae	121	20	?	?	del Hoyo <i>et al.</i> (2005)
Cisticolidae	116	12	?	?	del Hoyo <i>et al.</i> (2006)
Timaliidae	385	84	1	1	del Hoyo <i>et al.</i> (2007)
Acrocephalidae	42	4	1	0	del Hoyo <i>et al.</i> (2006)

(Continued.)

Table 1. (Continued.)

family <sup>a</sup>	<i>n</i>	CB	kin <sup>b</sup>	KN <sup>c</sup>	reference
Cettidae	27	3	?	?	del Hoyo <i>et al.</i> (2006)
Malagasy warblers	10	4	?	?	del Hoyo <i>et al.</i> (2006)
Passerida <i>incertae sedis</i>	72	20	—	—	— <sup>d</sup>
Troglodytidae	74	16	1	0	del Hoyo <i>et al.</i> (2005)
Sittidae	25	2	1	0	del Hoyo <i>et al.</i> (2008)
Sturnidae	112	18	1	1	Rubenstein & Lovette (2007)
Mimidae	34	6	1	1	del Hoyo <i>et al.</i> (2005)
Muscicapidae	291	23	1	0	del Hoyo <i>et al.</i> (2005)
Turdidae	143	4	1	1	del Hoyo <i>et al.</i> (2005)
Promeropidae	4	1	?	?	del Hoyo <i>et al.</i> (2008)
Nectariniidae	123	3	?	?	del Hoyo <i>et al.</i> (2008)
Prunellidae	13	13	0	0	del Hoyo <i>et al.</i> (2005)
Ploceidae	268	19	1	1	Fry & Keith (2004)
Passeridae	36	2	?	?	Fry & Keith (2004)
Fringillidae	159	5	?	?	Pratt (2005)
Passeroidea: Calcarius	6	1	0	0	Briskie <i>et al.</i> (1998)
Emberizidae	603	53	?	?	Alves (1990); Skutch (1987)
Parulidae	115	1	?	?	King <i>et al.</i> (2000)
Icteridae	96	12	1	1	Fraga (1991)

<sup>a</sup>Phylogeny and categorization of species as cooperative or non-cooperative followed Cockburn (2006).<sup>b</sup>Taxa were categorized as having groups composed predominantly of kin (1), non-kin (0) or unknown (?). In most families, species have similar social structures, but where they do not (e.g. Acciptridae and Falconidae), they were assigned to the category most prevalent within the taxon. One taxon, Psittacidae, has several well-described species, but no prevalent classification was possible due to the diversity of social organization.<sup>c</sup>Taxa with kin-directed cooperation were categorized as having helpers operating within kin neighbourhoods (1) if helpers in at least one species redirected their care to a relative's brood following failure of their own breeding attempt, or if helping occurred at multiple nests within clans, coterie, etc. If taxa were composed of species in which cooperative groups were not kin-based or helping occurred only within stable nuclear family groups, they were categorized as not having kin neighbourhoods (0).<sup>d</sup>Taxa of uncertain affinity were not assigned family-level characteristics.

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