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Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate

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The widespread belief that kin selection is necessary for the evolution of cooperative breeding in vertebrates has recently been questioned. These doubts have primarily arisen because of the paucity of unequivocal evidence for kin preferences in cooperative behaviour. Using the cooperative breeding system of long-tailed tits (*Aegithalos caudatus*) in which kin and non-kin breed within each social unit and helpers are failed breeders, we investigated whether helpers preferentially direct their care towards kin following breeding failure. First, using observational data, we show that not all failed breeders actually become helpers, but that those that do help usually do so at the nest of a close relative. Second, we confirm the importance of kinship for helping in this species by conducting a choice experiment. We show that potential helpers do not become helpers in the absence of close kin and, when given a choice between helping equidistant broods belonging to kin and non-kin within the same social unit, virtually all helped at the nest of kin. This study provides strong evidence that kinship plays an essential role in the maintenance of cooperative breeding in this species.

Keywords: cooperation; helpers; indirect fitness; long-tailed tit; kinship

1. INTRODUCTION

Cooperative breeding describes a system where some individuals help with the breeding attempts of others instead of breeding independently (Brown 1987). This behaviour appears to represent an evolutionary paradox because of the apparent altruism expressed by such helpers. However, in most cooperatively breeding species, helpers are constrained from breeding independently and by helping they improve the reproductive success of the recipients, which are usually close relatives (Emlen 1997). Therefore, this apparently paradoxical behaviour may best be explained by kin selection theory (Hamilton 1964; Maynard Smith 1964).

Many vertebrate cooperative breeding systems arise when offspring delay dispersal and help their parents with subsequent breeding attempts (Brown 1987). Typical cooperative breeding systems provide a poor ground for testing the role of kin selection in helping behaviour because helpers, being philopatric offspring, have little opportunity but to help kin. One approach has thus been to compare the levels of helper investment in species where individuals within groups vary in their degree of relatedness. Such studies provide mixed evidence for kin preferences, with some showing variation in helper investment with respect to kinship (Reyer 1984; Curry 1988; Arnold 1990; Komdeur 1994), whilst others show no such variation (Zahavi 1990; Dunn *et al.* 1995; Clutton-Brock *et al.* 2000, 2001). This lack of variation in helper investment with respect to kinship in some species has led to the suggestion that kin selection need not be important for the maintenance of cooperative breeding in vertebrates (Zahavi 1995; Cockburn 1998; Clutton-Brock *et al.* 2001).

Another approach that is used for investigating the role of kin selection in maintaining cooperative breeding systems is to consider whether helpers prefer to help kin versus non-/distant kin when given the choice. Since few cooperative breeding species live in groups where potential helpers have a choice of whom to help in their current group, few studies have considered whether helpers show a kin preference in this respect (but see Emlen & Wrege 1988; Lessells 1990). In this study, we use seven years of pedigree and genetic data from long-tailed tits (*Aegithalos caudatus*) in order to investigate the relatedness of helpers to recipients and describe a choice experiment that attempts to test directly the role of kinship in helping decisions.

Long-tailed tits are small (7.5 g), facultative cooperative breeders of the Palearctic (Cramp & Perrins 1993) that breed in clans of five to eight breeding pairs (Russell 1999). For several reasons they represent an ideal model system in which to test for the importance of kin selection in a cooperatively breeding vertebrate. First, a significant number of males and females found in clans are immigrants (Hatchwell *et al.* 2001*a*; Russell 2001). Second, all individuals initially breed independently in simple pairs, deciding whether and who to help only following breeding failure. Third, individuals are able to discriminate between the calls of relatives and non-relatives (Hatchwell *et al.* 2001*b*). Fourth, helpers have a positive effect on the survival and recruitment of the recipients' offspring (Russell 1999). If kin selection is important in the maintenance of cooperative breeding in this species, we predict that potential helpers should be more likely to help when kin are present and, when given the choice, should be more likely to help kin than non-kin.

2. METHODS

(a) *Observations of kin-biased helping*

We studied a colour-ringed population of 30–49 breeding pairs of long-tailed tits in the Rivelin Valley, Sheffield, UK

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(53°23′ N 1°34′ W) from 1994 to 2000. The breeding attempts of all pairs were closely monitored throughout the breeding season (February–June) in each year of study. Nests were located by following pairs during nest building and were checked at regular intervals in order to monitor their progress. During the nestling period we identified all carers from hour-long hide observations conducted every two to three days.

The relatedness of helpers to breeders was determined from pedigrees and through DNA profiling a subset of helpers using eight polymorphic microsatellite loci (B. J. Hatchwell, unpublished data). In order to estimate relatedness, we used the frequency distributions of mismatched loci for 19 helper/breeder pairs of known first-order relatedness through pedigree data and male and female members from 30 breeding pairs (which were assumed to be non-relatives) (figure 1). Although all individuals with three or fewer mismatches are probably non-relatives, there is clearly some overlap in the two distributions. Just 32% of each social unit in this population were close relatives (Hatchwell *et al.* 2001*a*), so by weighting the relative frequencies of mismatches for first-order relatives and non-relatives accordingly, we estimated that, for zero, one, two and three mismatches, the probabilities of two birds being close kin are 85, 77, 15 and 0%, respectively. Therefore, we assumed that individuals with zero or one mismatch are close relatives ($r = 0.5$) and that all others are non-relatives ($r < 0.5$). There is clearly a margin of error in these estimates, but it is unlikely to make a substantial difference to our overall estimate of relatedness and, since second-order relatives will be considered as non-kin, our estimates are conservative.

(b) *Kin preference experiment*

Observations of kin preferences in cooperative behaviour might be confounded by differences in the distance between, and availability of, the nests of kin and non-kin. Therefore, in 1998 we conducted a choice experiment in order to investigate whether helpers prefer kin to non-kin when controlling for their spatial distributions and availability. The experiment was carried out in two populations (total = 82 pairs) of long-tailed tits in South Yorkshire, UK: at Ecclesall and Melton Woods (see Russell 2001 for details). The experiment involved selecting trios of nests during egg laying, two belonging to close relatives ($r = 0.5$) (sibling or parent, hereafter referred to as kin) and one to a distant/non-relative ($r < 0.25$) (hereafter referred to as non-kin). One of the relatives was assigned as the potential helper, whilst the other relative and the non-relative were assigned as the potential recipients of help. The trios of nests were selected on the basis that the distances between the nests of the potential helpers and the nests of the potential recipients were similar and that the potential recipients bred within 14 days of each other (see below).

Depending on the distance that individuals disperse before breeding, potential recipients may or may not breed in the same clan as their potential helpers. For those trios where the potential recipients and helpers were members of the same clan, trios were chosen on the basis that the distances from the potential helpers to their two potential recipients did not differ by more than 100 m (median difference = 22 m). For those trios where the potential helpers were in a different clan from the potential recipients, trios were only selected for the experiment if the distance between the two potential recipients and the potential helpers did not differ by more than 200 m (median difference = 45 m) (see figure 2 for details). Fourteen days was chosen as the maximum difference in the timing of breeding by the potential recipients since this meant that they would overlap for at least 2 days in their 16–18 day chick rearing periods. Potential recipients were not exclusive to each potential helper. Thirty-one trios were identified where the above criteria were met. Since all helpers are failed breeders that begin helping during the chick provisioning period, a final requirement was that the nesting attempts of the potential helpers had to fail prior to the fledging dates of either of the potential recipients' broods.

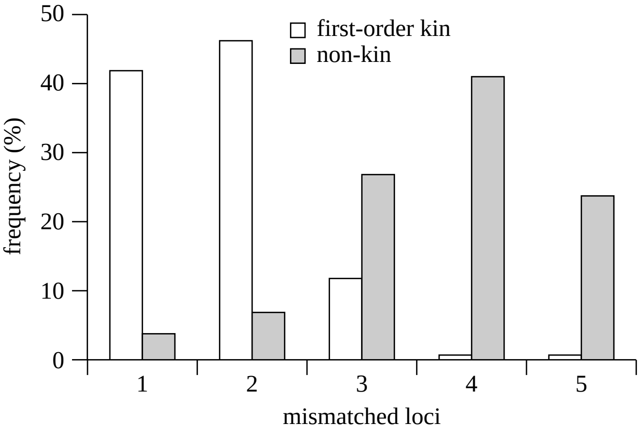

Figure 1. Frequency distribution of the number of mismatches at eight polymorphic loci for 19 helper/breeder pairs known from pedigrees to be close kin and for 30 male and female breeding pair members that were assumed to be non-kin.

These conditions were met in 26 of the trios. Nest failure through depredation was common in the study sites (Russell 1999) and 20 out of the 26 potential helpers' nests failed naturally. Failure of the nesting attempts of the remaining six potential helpers was induced (under licence) by fostering their clutches and broods with other pairs ($n = 3$ each). The nests of the potential recipients were protected from depredation using chicken wire (hole diameter 6cm), which allows long-tailed tits to pass freely, but prevents access by large nest predators such as corvids (Glen 1985).

All potential helpers that were used in the experiment ($n = 26$) were first-year recruits, 12 of which (10 males and 2 females) were recruited into their natal clan and 14 of which (4 males and 10 females) were recruited into a non-natal clan. Those recruiting into their natal clan were paired with a relative and non-relative within their natal clan ($n = 12$). Those recruiting into non-natal clans with kin ($n = 5$) were paired with a relative and a non-relative in their adopted clan and a relative and a non-relative in their natal clan. Individuals that dispersed to non-natal clans without kin ($n = 9$) were paired with a relative and a non-relative in their natal clan, but they also had the option of helping non-kin within their adopted clan. The distance that potential helpers would have to travel in order to help the relative and the non-relative when in the same clan did not differ significantly (figure 2) (Wilcoxon's test = 72.5, $n = 17$ and $p = 0.9$). The distance that helpers would have to travel in order to help relatives and non-relatives in different clans was greater, but again there was no difference in the distances between recipients (figure 2) (Wilcoxon's test = 40.0, $n = 14$ and $p = 0.7$).

Nests were monitored every five days of the incubation period and every three days of the chick rearing period. Broods of related and non-related recipients overlapped by an average of 11 ±4.4 days and there was no difference between the recipients

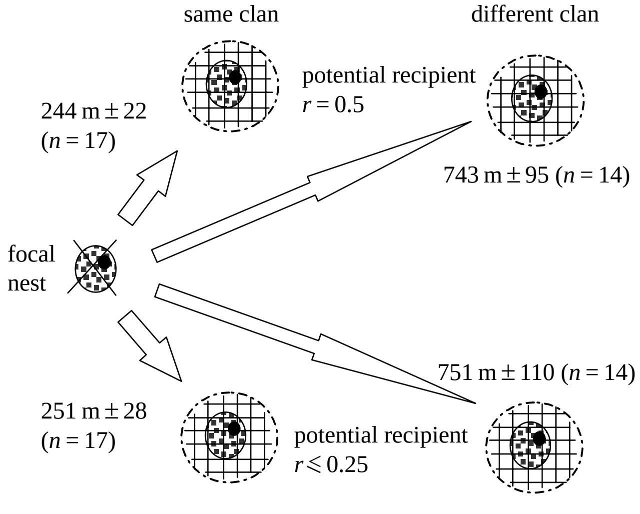

Figure 2. Design of the kin preference experiment showing the mean distances (± s.d.) from the unprotected nests of potential helpers to the protected nests of potential recipients. Potential helpers could help kin by remaining in their natal clan ($n = 12$), by either remaining in their non-natal clan or dispersing to their natal clan ($n = 5$) or by dispersing to their natal clan only ($n = 9$). Kin and non-kin did not differ in their distances from potential helpers, either when in the same clan ($n = 17$) or when in a different clan ($n = 14$).

in the age of their offspring when potential helpers failed (mean age difference of broods in the same clan for kin versus non-kin $= -2.88 \pm 7.25$ days ($n = 17$) and mean age difference of broods in a different clan for kin versus non-kin $= -1.64 \pm 7.07$ days ($n = 14$)) (one-sample t-test against a difference of 0 days, $t_{16} = 1.64$ and $p = 0.12$ and $t_{13} = 0.87$ and $p = 0.40$, respectively). The identity of helpers at nests was determined through hour-long hide observations conducted every three days of the nestling period (helpers do not arrive prior to this period).

3. RESULTS

(a) *Observations of kin-biased helping*

A total of 90 helpers were observed, of which 77 (85.6%) were male and 13 (14.4%) were female. The relatedness of 37 helpers (all male) was determined unequivocally from pedigrees: 35 out of 37 helpers (95%) helped a first-order relative (eight sons, 26 brothers and one father of a breeder) and two out of 37 helpers (5%) helped a second-order relative (both uncles of a breeder) (see also table 1). Using genetic criteria from DNA profiling alone, 69% of 39 helpers were closely related ($r = 0.5$) to at least one of the breeders whose brood they helped to feed (table 1). Combining information from pedigrees and DNA profiling enabled us to determine the relatedness of 52 helpers; 41 out of 52 helpers (79%) were closely related to either the male breeder, the female breeder or to both (table 1). Thus, the majority of helpers assisted relatives in rearing their offspring.

Kin-biased helping might arise simply through spatial effects if failed breeders choose to help at nearby nests that happen to belong to relatives because of limited natal dispersal. Two pieces of evidence contradict this interpretation. First, not all failed breeders become helpers. The median distance travelled by helpers between their failed nest and a helped nest was 300 m and the maximum distance was 1100 m. However, just 39.1% ($n = 69$) of males and 4.8% ($n = 62$) of females with active nests $\leqslant 300$ m away from their last failed attempt became helpers and just 47.1% ($n = 104$) of males and 10.8% ($n = 93$) of females with active nests < 1100 m away became helpers. Thus, failed breeders do not always become helpers even when active nests are available close to their last breeding attempt. Second, those failed breeders that do become helpers do not always help at the closest active nest (figure 3). These results suggest that potential helpers make a choice of whether or not to become helpers and do not choose which pair of breeders to help based solely on the distance to their nest.

Table 1. Percentage of failed breeders helping at a nest where either, both or neither of the breeding recipients were estimated to be first-order relatives.

(The pedigree data ($n = 37$) show the number of individuals helping first-order kin as determined from colour ringing. The genetic data ($n = 39$) show the number of individuals helping first-order kin for which both breeders were profiled. The combined data include all the genetic data and data from 13 pedigrees for which genetic data were not available but the identity and origin of both parents were known.)

	helper is a first-order relative of breeders			
	male only	female only	both	neither
pedigree data	25 (68%)	9 (24%)	1 (3%)	2 (5%)
genetic data	15 (38%)	8 (21%)	3 (8%)	13 (33%)
combined data	25 (48%)	11 (21%)	5 (10%)	11 (21%)

(b) *Kin preference experiment*

The above results were confirmed in an experiment designed for investigating whether the presence of kin is necessary for cooperation and whether, whilst controlling for spatial effects, kin are preferred to non-kin when given the choice. Potential helpers (failed breeders) only helped within their current clans. All of the 17 individuals that had the opportunity to help either kin or non-kin within the same clan elected to help, irrespective of whether that clan was natal ($n = 12$) or adopted ($n = 5$) or whether they were male ($n = 12$) or female ($n = 5$). In contrast, none of the nine failed breeders with only non-kin available within their current clan helped those non-kin ($n = 2$ males and $n = 7$ females) (figure 4*a*). Of the 17 individuals that helped within their current clans, 94% ($n = 16$) helped at the nest of the relative in their clan (figure 4*b*): 11 out of 12 helpers in natal clans and five out of five helpers in adopted clans. Thus, failed breeders became helpers only when kin were present in the same clan and, when they had a choice of helping kin and non-kin, they preferred to help kin.

4. DISCUSSION

Our observations indicate that potential helpers make choices about when and who to help in long-tailed tits. First, less than half of all failed breeders became helpers even though active nests were available within their clans. Second, less than half of all helpers chose to become a

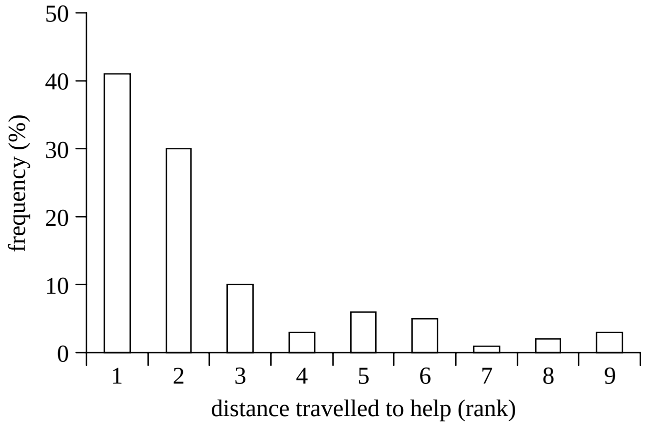

Figure 3. Frequency distribution of the rank order of nest distances from the nest of a helper's last breeding attempt to the nest at which it became a helper (i.e. 1 indicates the nearest nest, 2 indicates the second nearest nest and so on).

helper at the closest available nest, some moving a considerable distance. Pedigree and genetic data indicated that relatedness was involved in these choices because most helpers assisted at the nests of relatives. The key role of kinship in helping was confirmed in an experiment that showed that failed breeders not only refrain from helping in the absence of kin but, in their presence, they are virtually always helped in preference to non-kin.

Two results from the kin preference experiment suggest that kinship is key to the maintenance of cooperative breeding in long-tailed tits. First, all failed breeders cooperated when kin were present in the same clan and virtually all helped kin rather than non-kin. Second, failed breeders did not help in the absence of kin. This suggests that direct fitness benefits are insufficient for maintaining cooperative breeding in this species and that helping non-kin may largely result from recognition errors. Long-tailed tits have a kin recognition mechanism of learning through association (Hatchwell *et al.* 2001*b*) that does not permit kin recognition in the strict sense (Grafen 1990), but rather the discrimination of familiar from unfamiliar individuals. The extensive mixing of families, which occurs during the non-breeding season in long-tailed tits (Russell 1999; Hatchwell *et al.* 2001*a*), may increase the probability of recognition errors arising. A more detailed knowledge of the kin recognition mechanism is required in order to resolve the question of how much non-kin helping might be expected through errors.

Failed breeders never returned to their natal clan to become helpers at the nests of relatives, even when no relatives were available in their current clan. There are three possible reasons for this.

(i) Having dispersed and become established in a new clan, there may be little marginal benefit in returning home to assist relatives that may or may not have bred successfully.

(ii) If inbreeding avoidance drives the initial dispersal then it may not pay to return to the natal area if there is a risk of inbreeding in future breeding attempts (Johnson & Gaines 1990; Hatchwell *et al.* 2000).

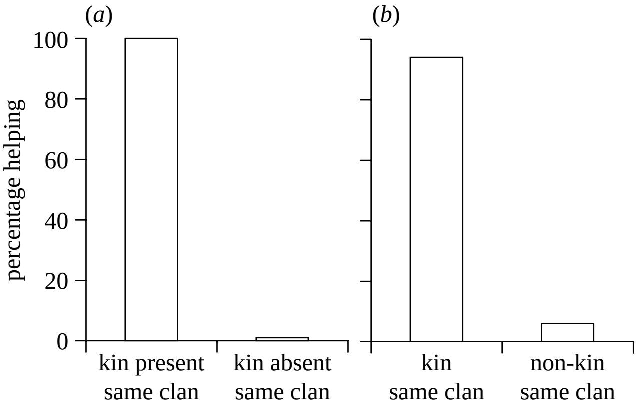

Figure 4. The kin preferences of and helping decisions taken by failed breeders. (*a*) The proportion of potential helpers that helped when kin were present within the same clan ($n = 17$) and absent from the same clan ($n = 9$) (one-tailed binomial test, $p < 0.005$). (*b*) The proportion of potential helpers that helped at the nests of kin and non-kin when both were available in the same clan ($n = 17$) (one-tailed binomial test, $p < 0.001$).

(iii) The ability to discriminate kin from non-kin may diminish during a period of separation so that birds that have dispersed and subsequently returned have a higher error rate in their identification of kin (Sherman *et al.* 1997; Komdeur & Hatchwell 1999).

We have interpreted our results showing kin-directed care as being evidence for a kin preference by helpers. An alternative interpretation is that breeders only tolerate familiar birds as helpers and that familiar birds are more likely to be relatives. Hatchwell *et al.* (2001*b*) showed that breeders react more aggressively to the playback calls of non-kin, and we have observed some instances of aggression between breeders and potential helpers. However, we have no evidence to suggest that helpers have detrimental effects on their recipients either in terms of mate competition (Hatchwell *et al.* 2000), survival, or breeding success (Russell 1999; B. J. Hatchwell, unpublished data). Indeed, helpers allow breeders to reduce their rate of chick provisioning (Hatchwell & Russell 1996), to be heavier (Glen & Perrins 1988) and to increase their survival probability to the following year (Russell 1999). In addition, helpers can have a positive effect on overall chick provisioning frequency, chick weight and their subsequent recruitment (Russell 1999; B. J. Hatchwell, unpublished data). Therefore, we have not identified any obvious cost to breeders of having helpers and so there is no obvious selective advantage in being intolerant of unfamiliar helpers. Moreover, the fact that helpers improve the condition and reproductive success of recipients to which they are usually related provides strong evidence for the importance of kin selection in the maintenance of cooperative breeding in this species.

Only two other studies, to our knowledge, in a cooperative vertebrate have provided evidence for kin preferences in helping while taking into account differences in the spatial distribution of kin and non-kin. Emlen & Wrege (1988) showed that, in the colonially nesting white-fronted bee eater (*Merops bullockoides*), failed breeders do not always help at the nest of the closest neighbour, but at the nest of the most related individual. Similarly, Lessells (1990) showed that, in European bee eaters (*Merops apiaster*), failed breeders provision kin more often than would be expected by chance based on spatial distributions alone. More commonly, studies have tested the significance of kin selection in cooperative breeding by focusing on whether helpers invest differentially in offspring according to relatedness. Although some studies suggest that helpers invest with respect to kinship (Reyer 1984; Curry 1988; Arnold 1990; Komdeur 1994), others suggest that this need not be universal among cooperative breeders (Brown & Brown 1990; Zahavi 1990; Wright *et al.* 1999; Clutton-Brock *et al.* 2000, 2001; Cant 2001). In addition, some studies show that helpers are often unrelated or only distantly related to their recipients (Reyer 1984; Dunn *et al.* 1995). Such findings have led to the conclusion that kin selection may either be inadequate or unimportant in the maintenance of vertebrate cooperative breeding societies (Zahavi 1995; Cockburn 1998; Clutton-Brock *et al.* 2001).

However, this conclusion may be premature, at least for some species. First, kin discrimination requires an effective mechanism of kin recognition and, if there is no mechanism through which varying degrees of relatedness can be determined by helpers, then evidence for indiscriminate help need not be evidence against the importance of kin selection (Komdeur & Hatchwell 1999; Wright *et al.* 1999). For instance, in banded mongooses (*Mungos mungo*), where multiple females give birth synchronously, it is unlikely that potential helpers can effectively discriminate between different degrees of relatedness (J. Gilchrist, personal communication). Second, indiscriminate help within a social unit may still be kin selected provided that the mean relatedness of the recipients is sufficiently high to satisfy Hamilton's (1964) rule (Keller 1997). Moreover, cooperation with distant relatives need not provide evidence against the importance of kin selection, as in long-tailed tits helpers only rarely help to raise full siblings because adult mortality is high and divorce is common following a successful breeding attempt (Hatchwell *et al.* 2000). Despite this, we have shown that kinship is important for this species' cooperative breeding system.

Therefore, while there are undoubtedly a few species where kin selection must play at best a minor role in the maintenance of cooperative breeding (see Cockburn 1998), we have shown that kin selection is likely to play a key role in the cooperative breeding system of long-tailed tits. In addition, we support Keller's (1997) contention that a lack of variation in the levels of investment with respect to kinship can result when there is no mechanism for effective discrimination among different orders of kin and need not negate the importance of kin-selected benefits. Furthermore, it may be that occasional helping by non-kin in some cooperative systems can be explained by recognition errors or as a simple consequence of being physiologically primed to carry out parent-like activities (*sensu* Jamieson 1989).

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