Kin discrimination in cooperatively breeding long-tailed tits

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Long-tailed tits *Aegithalos caudatus* are cooperative breeders in which helpers exhibit a kin preference in their cooperative behaviour. We investigated the mechanism through which this preference is achieved by first conducting an experiment for testing whether breeders could recognize the calls of their relatives while controlling for spatial effects. We found that there were significant differences in the responses of breeders to the vocalizations of kin and non-kin, suggesting that vocal cues may be used for kin recognition. We conducted a second experiment in order to investigate whether recognition is achieved on the basis of relatedness *per se* or through association. Nestlings were cross-fostered between unrelated broods in order to create broods composed of true and foster siblings. In subsequent years, survivors from experimental broods did not discriminate between true and fostered siblings when making helping decisions, indicating that recognition is learned and not genetically determined. We discuss the effectiveness of learning through association as an indirect cue to kinship.

Keywords: cooperative breeding; kin discrimination; kin recognition; long-tailed tit

1. INTRODUCTION

Studies of cooperatively breeding vertebrates have suggested that kin selection is a driving force in social evolution (Emlen 1997). Cooperation with close relatives increases the magnitude of indirect fitness gains accrued by helpers (Hamilton 1964), so the ability to recognize kin may be crucial in maximizing fitness. Although kin selection and, hence, discrimination is not universal among cooperatively breeding vertebrates (Cockburn 1998), there is observational evidence for preferential allocation of aid to close kin in some cooperatively breeding birds (Clarke 1984; Curry 1988; Emlen & Wrege 1988; Komdeur 1994; Russell 1999). In such species, there must be an effective mechanism for discrimination of kin from non-kin, i.e. a mechanism of kin recognition. Grafen (1990) used a strict definition of 'true' kin recognition as recognition of genetic relatedness or similarity (e.g. Grosberg & Quinn 1986). Here we use the term in the broader sense to describe any mechanism that permits the successful differentiation of kin from non-kin (Blaustein *et al*. 1987; Hepper 1991; Sherman *et al*. 1997).

How is kin recognition likely to be achieved in social animals? The production component of a recognition system, that is the label or cue, may be of genetic or environmental origin and there is good evidence for the existence of both (Sherman *et al*. 1997). The perception component, that is the sensory detection of cues, entails the matching of perceived phenotypes to some recognition template that may be genetically encoded or learned. There are no unequivocal examples of genetically encoded recognition templates (Sherman *et al*. 1997). In typical cooperative breeders, helpers delay dispersal and act as helpers on their natal territory before dispersing when a breeding opportunity arises (Stacey &

Koenig 1990). In such situations, a decision rule, 'care for young in my natal territory', may function as a reliable discriminator between kin and non-kin. Alternatively, recognition may be based on the phenotypic traits (genetically or environmentally determined) of the recipients, the recognition template being most probably acquired through a learning process (Komdeur & Hatchwell 1999). Vocalizations are the most widespread recognition cues in birds (Halpin 1991) and inheritance and discrimination of vocalizations has been shown in one cooperatively breeding species (Price 1998, 1999). However, no experimental studies have manipulated family membership in order to determine whether helping decisions are based on relatedness *per se*, on association or familiarity or on spatial cues alone (Komdeur & Hatchwell 1999).

In this paper, we describe (i) a playback experiment for testing whether long-tailed tits are able to discriminate between vocalizations of kin and non-kin and (ii) a cross-fostering experiment for investigating whether discrimination is achieved on the basis of relatedness or association. We show that vocalizations do provide information enabling the effective discrimination of kin from non-kin and that kin recognition is learned or acquired because helpers from cross-fostered broods do not discriminate between true and fostered siblings.

2. METHODS

(a) *Study species*

We studied a population of 30–49 pairs of long-tailed tits in the Rivelin Valley, Sheffield, UK. The long-tailed tits at our study site spend the non-breeding season (June–February) in flocks, a number of which ($n = 1$–3), augmented by immigrants, usually coalesce during the winter to constitute a clan, each occupying a large non-exclusive range (Russell 1999). The average composition of a clan at the end of the winter is 40% previous breeders, 25% philopatric recruits and 35% unrelated immigrants (Russell 1999). Clans break up in early spring; males occupy part of the clan range for breeding and females

either disperse to other ranges to find a partner or remain within the clan range and pair with a male from that clan. All birds start the season breeding independently in pairs, females laying a clutch of 8 to 11 eggs. Nest failure is frequent (Hatchwell *et al.* 1999) and, if a pair's nesting attempt fails after early May, then those failed breeders may become helpers by moving to help another pair care for their offspring by feeding nestlings and fledglings (Gaston 1973; Glen & Perrins 1988). As a consequence of the large number of failed breeders, *ca.* 50% of the broods in our population have helpers (range 1–3). Helpers allow parents to reduce their provisioning rate (Hatchwell & Russell 1996; Hatchwell 1999) and the presence of helpers at the nest increases the condition and subsequent recruitment of the helped offspring (Glen & Perrins 1988; Russell 1999; B. J. Hatchwell, unpublished data). Helpers usually assist at the nests of relatives and most helpers are brothers of the male breeder whose brood they feed (Glen & Perrins 1988; Russell 1999; B. J. Hatchwell, unpublished data).

(b) *Playback experiment*

In order to conduct the playback experiment, we identified focal male breeders ($n = 8$) with active nests who had first-order male kin (coefficient of relatedness, $r = 0.5$) and male distant/non-kin (hereafter referred to as non-kin) ($r < 0.125$) breeding within the same clan range. The relatedness between birds was initially determined from pedigrees and later verified using microsatellite DNA profiling. The distance between the nests of focal males and the nests of kin and non-kin males did not differ significantly (mean ± s.d. distances, kin 401 ± 263 m and $n = 8$ and non-kin 451 ± 184 m and $n = 8$) (paired *t*-test, $t = 0.74$, d.f. $= 7$ and $p = 0.5$). We recorded the single-note contact calls (Cramp & Perrins 1993) of kin and non-kin males onto metal tapes during the incubation or early nestling period using a Sennheiser MKH416 microphone and Sony Professional Walkman. Calls were then re-recorded onto 1-min continuous loop tapes. Playback experiments were conducted by broadcasting calls of kin or non-kin through Sony speakers from a hide placed 10 m away from a focal pair's nest when nestlings were 11.6 ± 4.6 days old ($n = 8$). The playback protocol mimicked our previous observations of repeated close approaches of potential helpers to nests. These visits occur over a period of one day or more before a helper starts to provision a brood. We observed the behaviour of the focal pair in each of two trials per nest during 5 min with no playback (control period), followed by 5 min of playback, 5 min without playback, 5 min with playback and a final 5 min without playback. We broadcast calls of kin and non-kin (in alternate order for successive focal birds) in two trials with a 1-h interval between trials. An observer stood 25–30 m from the nest in each trial and continuously recorded the distance of each member of the pair from the speaker into a dictaphone. When birds were $\geqslant 30$ m from the speaker they were recorded as absent. The observer also recorded the rates of two vocalizations. The 'churr' call is used in agonistic encounters, while the 'triple' call is a non-aggressive long-distance contact call (Cramp & Perrins 1993). It was not always possible to identify which member of a pair was calling, so the call rate is a property of the focal pair rather than of an individual, while proximity to the speakers was a property of each individual. We played calls of males only and coefficients of relatedness refer to males.

(c) *Cross-fostering experiment*

The nestling cross-fostering experiment, which was conducted in 1996–1998, investigated whether the perception of

recognition cues is genetically determined or learned. Partial broods in experimental nests (mean ± s.d. $= 3.86 \pm 0.66$ nestlings and $n = 14$ broods) were marked by clipping one claw of nestlings and then switched between synchronous unrelated nests (maximum age difference less than one day) when nestlings were four to five days old (nestling period $= 16$–17 days). Partial broods in control nests (mean $= 3.85 \pm 0.56$ nestlings and $n = 13$ broods) were removed, marked and replaced in their own nest after a short interval (removal time, experimental nests 18.2 ± 4.6 min and $n = 14$ and control nests 19.2 ± 5.3 min and $n = 13$) (*t*-test, $t = 0.529$, d.f. $= 25$ and $p = 0.6$). The number of nestlings switched per nest varied slightly according to initial brood size because our aim was to achieve approximately equal numbers of foster and host nestlings per experimental nest. The original brood sizes were unaffected by the experimental or control treatments. Nestlings were weighed (to 0.1 g) and ringed with unique colour ring combinations on day 11 of the nestling period ($n = 9$ broods for the control and experimental treatments due to predation of five experimental and four control nests). The survival of fledglings from control and experimental nests and their breeding and helping behaviour was monitored in later years.

3. RESULTS

(a) *Playback experiment*

The response of focal pairs to playback of kin and non-kin calls was analysed by paired comparison of the behaviour observed during the 20 min following the start of playback in the kin and non-kin trials (i.e. omitting the initial 5-min control period). There were significant differences in the responses of focal birds to the broadcast calls of kin and non-kin. The speakers were approached more closely during playback of non-kin compared to kin (figure 1*a*), although the time spent close ($\leqslant 15$ m) to the speakers did not differ significantly (figure 1*b*). In seven out of eight of the non-kin playbacks the bird(s) approaching most closely were identified: in five cases it was the male and in the remaining two cases both breeders approached to the same distance. In contrast, closest approaches to kin playbacks were by the female alone ($n = 1$) or by both breeders ($n = 7$), so males were more likely than females to make a close approach during non-kin playback (Fisher's exact test $p = 0.01$).

The focal pairs' vocal responses to playbacks also differed for kin and non-kin trials. We analysed the number of churr and triple calls made when at least one focal bird was $\leqslant 25$ m from the speakers (i.e. when the birds were always within earshot). The rate of churr calling was significantly higher during non-kin playback than during kin playback (figure 1*c*), but there was no significant difference in the rate of triple contact calling during kin and non-kin playbacks (figure 1*d*). Thus, focal birds responded with closer approaches and more aggressive vocalizations to playbacks of non-kin than to playbacks of kin.

The playback protocol also allowed us to compare the behaviour of focal birds during the 5-min control period preceding playback with their behaviour during the playback and post-playback quiet periods. There was no significant difference in the closeness of approach during the control, playback and quiet periods for kin trials, but there was for non-kin trials (figure 2*a*). The duration of
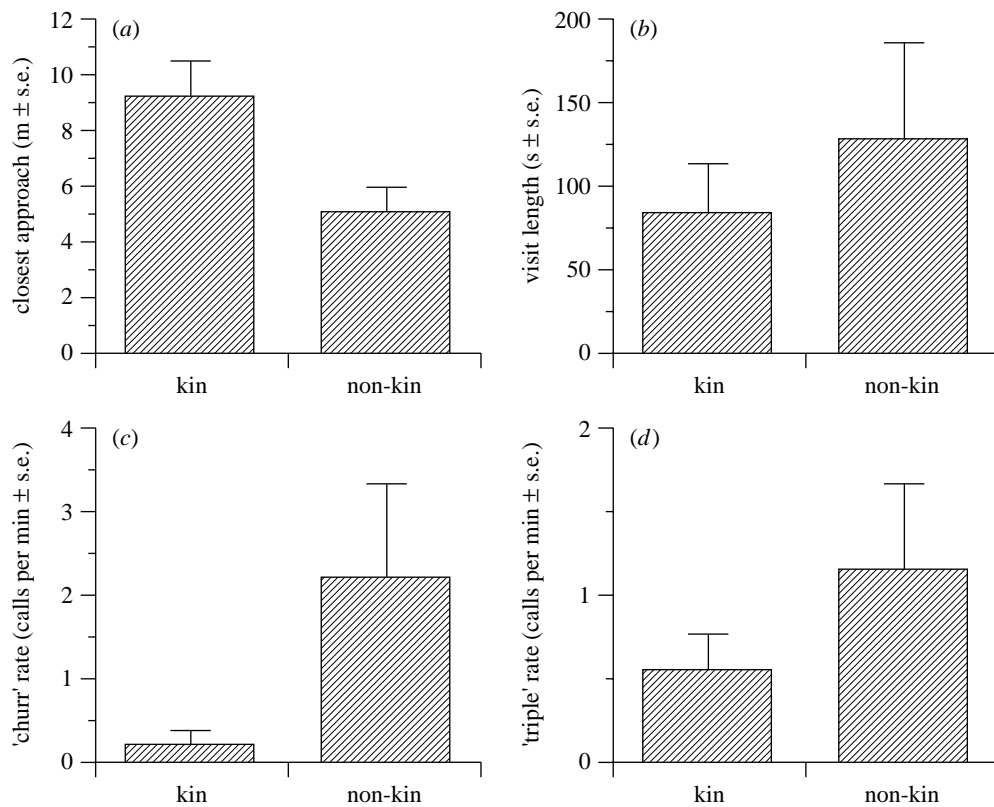
Figure 1. Results of the playback experiments of kin and non-kin calls to long-tailed tit breeders when comparing the responses of focal birds to kin and non-kin trials. (*a*) Closest approach to speakers during playback (paired *t*-test, $t_7 = 3.36$ and $p = 0.01$). (*b*) Mean length of visits spent $\leqslant 15$ m from speakers (paired *t*-test, $t_7 = 0.75$ and $p = 0.5$). (*c*) Rate of aggressive churr vocalizations by focal birds when $\leqslant 25$ m from speakers (Wilcoxon tests, $T = 0$, $n = 7$ and $p = 0.02$) (note that one pair uttered no churrs in response to either playback). (*d*) Rate of non-aggressive triple vocalizations by focal birds when $\leqslant 25$ m from speakers (Wilcoxon tests, $T = 4$, $n = 6$ and $p = 0.2$) (note that two pairs uttered no triple calls in response to either playback).

visits to the vicinity of the nest before and during/after playback did not differ significantly for either the kin or non-kin trials (figure 2*b*). There was no significant difference for kin trials between control, playback and post-playback quiet periods for either churr call rates or triple call rates (figure 2*c,d*), but focal birds uttered both vocalizations at significantly higher rates during playbacks of non-kin (figure 2*c,d*). Therefore, these results mirror those of the previous analysis, with the exception of the significant difference in triple call rates during non-kin trials.

(b) Cross-fostering experiment

The mean survival of cross-fostered nestlings in experimental nests from day 5 to day 11 did not differ significantly from that of sham-switched nestlings in control nests (experimental nests = $95.0 \pm 10.0\%$ and $n = 9$ and control nests = $97.2 \pm 8.3\%$ and $n = 9$) (Mann–Whitney *U*-test, $z = 0.54$ and $p = 0.59$) (note that depredated nests were excluded from the analysis). Furthermore, the weight of fostered nestlings on day 11 did not differ from that of host nestlings in experimental broods ($n = 9$ broods) (mean $\pm$ s.d. weight, host chicks 7.61 ± 0.61 g and foster chicks 7.65 ± 0.48 g) (paired *t*-test, $t = 0.22$, d.f. = 6 and $p = 0.8$), nor from that of their true siblings ($n = 7$ broods) (mean weight of siblings in foster nest 7.70 ± 0.47 g and in original nest 7.55 ± 0.36 g) (paired *t*-test, $t = 0.72$, d.f. = 6 and $p = 0.5$). Thus, parents did not

discriminate between their own and fostered nestlings. In addition, there was no difference in local survival to the following breeding season of host fledglings (26.7% and $n = 30$) and foster fledglings (21.2% and $n = 33$) ($\chi^2 = 0.05$, d.f. = 1 and $p = 0.8$) from experimental nests and neither was there a significant difference in the survival of fledglings from control nests (11.8% and $n = 76$) and experimental nests (23.8% and $n = 63$) ($\chi^2 = 2.67$, d.f. = 1 and $p = 0.1$).

The critical question in the context of kin discrimination by helpers is whether recruits from experimental nests treated foster siblings as true siblings when making helping decisions. A total of 15 birds were recruited into the breeding population from experimental broods. Two of these recruits were the sole survivors from their respective broods and so had neither true or fostered siblings available to help; these birds failed to breed successfully in three bird years but, in the absence of close relatives, none became helpers (row 2 in table 1). Both fostered and host birds ($n = 13$) did recruit from three broods (three foster and two host birds, two foster and four host birds and one foster and one host bird, respectively) and their breeding and helping record was determined in a total of 22 bird years. Successful breeders ($n = 9$ birds in 11 bird years) did not become helpers (row 3 in table 1), but failed breeders ($n = 11$ birds in 11 bird years) had a total of 13 opportunities to become helpers at the nest of a brood-mate (two birds helped at two nests
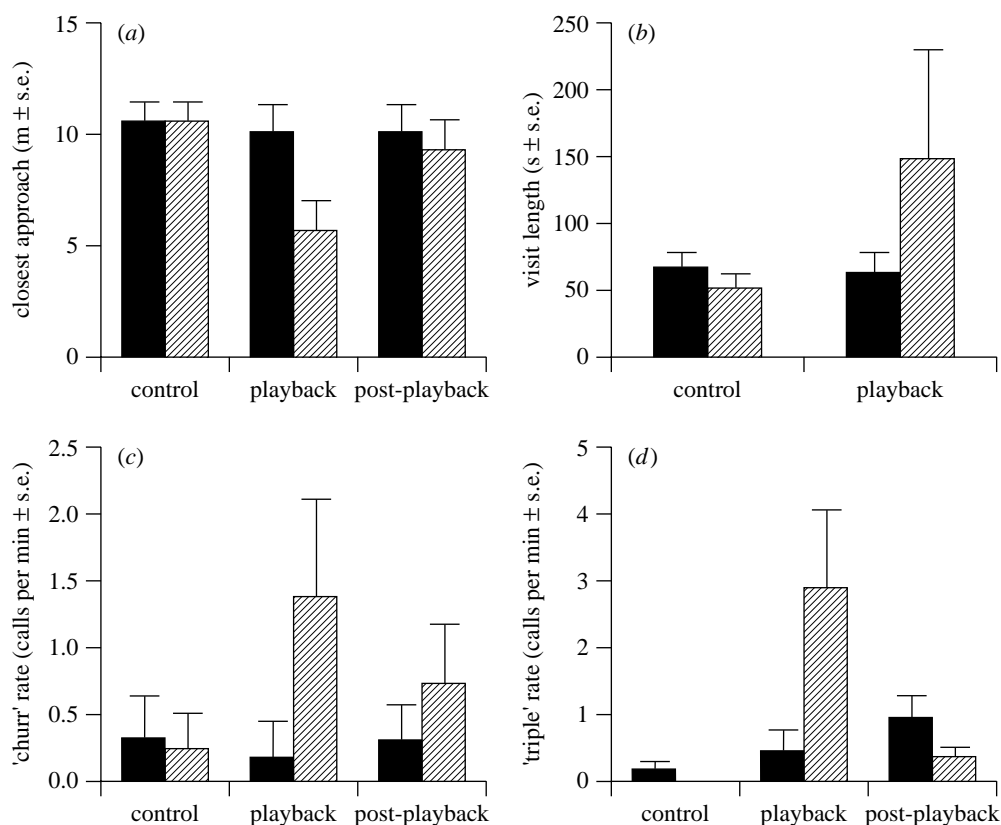
Figure 2. Results of the playback experiments of kin (heavy hatching) and non-kin (light hatching) calls to long-tailed tit breeders when comparing responses during the control, playback and post-playback periods within kin and non-kin trials. (*a*) Closest approach to speakers during the control, playback and post-playback quiet periods (Friedman two-way ANOVA, kin $\chi^2 = 0.67$, d.f. $= 2$ and $p = 0.72$ and non-kin $\chi^2 = 9.24$, d.f. $= 2$ and $p = 0.01$). (*b*) Mean visit duration during the control period and during/after the playback periods (Wilcoxon tests, kin $T = 6$ and $p = 0.50$ and non-kin $T = 3$ and $p = 0.20$) (note that the playback and quiet periods were combined because nest visits overlapped these periods). (*c*) Churr vocalization rate by focal birds during the control, playback and post-playback quiet periods (Friedman two-way ANOVA, kin $\chi^2 = 1.00$, d.f. $= 2$ and $p = 0.61$ and non-kin $\chi^2 = 6.42$, d.f. $= 2$ and $p = 0.04$). (*d*) Triple vocalization rate by focal birds during the control, playback and post-playback quiet periods (Friedman two-way ANOVA, kin $\chi^2 = 4.67$, d.f. $= 2$ and $p = 0.10$ and non-kin $\chi^2 = 9.65$, d.f. $= 2$ and $p = 0.01$). The sample size is six focal pairs in all cases because two pairs did not visit during the control period.

in a year when their first choice failed before fledging). In eight cases failed breeders had either a true sibling or a foster sibling to help and they all helped at a sibling's nest whether the sibling was a true or foster relative (row 4 in table 1). In five instances potential helpers chose between simultaneous broods belonging to true and foster siblings: in three cases the helper chose to help their true sibling and in two cases the choice was for the foster sibling (row 5 in table 1). Thus, in all 13 cases where foster or true siblings were available, failed breeders became helpers and brood-mates were treated as siblings regardless of their true relatedness. This conclusion is based on small sample sizes, but one telling comparison is that none out of three failed breeders without brood-mates became helpers, while seven out of seven failed breeders with only fostered brood-mates became helpers (Fisher's exact test $p = 0.008$) (table 1).

4. DISCUSSION

Long-tailed tits responded differently to the broadcast calls of kin and non-kin while controlling for spatial effects. This discriminatory ability could be used in the context of helping decisions, although we have not shown

that it is vocal recognition *per se* that determines whether a potential helper actually becomes a helper at a particular nest. There have been two previous studies of kin recognition cues in other cooperative bird species. Price (1999) showed that stripe-backed wrens *Campylorhynchus nuchalis* discriminated between the calls of different patrilines rather than on the basis of group membership. Conversely, Payne *et al.* (1988) found that splendid fairy wrens *Malurus splendens* discriminated between the songs of group and non-group members, but not between kin and non-kin in other groups. However, it should be noted that social relationships offer very unreliable cues to genetic relationships in fairy wrens because of their extraordinarily high level of extra-group paternity (Brooker *et al.* 1990). Kinship and association in long-tailed tits are closely correlated at the nestling and fledgling stage because extra-pair paternity and intraspecific brood parasitism are infrequent (B. J. Hatchwell, unpublished data). The absence of discrimination by parents of fostered and true offspring at this stage was unsurprising because there is abundant evidence that parent birds do not discriminate related from unrelated brood-mates (Kempenaers & Sheldon 1996). Thus, spatial cues must offer an effective mechanism of kin recognition at the

Table 1. *The breeding and helping records for recruits from cross-fostered broods of long-tailed tits*

(The frequencies of helping true siblings, helping foster siblings or not helping are expressed as fractions of the number of opportunities to do so. Successful breeders had no opportunity to become helpers because they were rearing their own broods during the time that other broods might be available. For recruits without brood-mates, none became helpers because failed breeders usually become helpers only if close relatives have active nests available for them to help at (Russell 1999). For recruits with brood-mates, recruits failed in their own breeding attempt and had either a true sibling ($n=1$) or a foster sibling ($n=7$) available to be helped (failed breeder 1) or they failed in their own breeding attempt and had both a true sibling and a foster sibling ($n=5$) available to be helped (failed breeder 2).)

recruits	helped at the nest of true sibling	helped at the nest of foster sibling	did not help
recruits without brood-mates ($n=2$ birds)			
successful breeder ($n=1$ bird year)	—	—	1/1
failed breeder ($n=3$ bird years)	—	—	3/3
recruits with brood-mates ($n=13$ birds)			
successful breeder ($n=11$ bird years)	—	—	11/11
failed breeder 1 ($n=7$ bird years)	1/1	7/7	0/8
failed breeder 2 ($n=4$ bird years)	3/5	2/5	0/5

nestling stage. However, we can dismiss the possibility that potential helpers use spatial cues for recognizing kin when making helping decisions. Russell (1999) showed that helpers with a choice of kin and non-kin nests exhibited a kin preference when they were in their natal clan range and also when they had dispersed to neighbouring clan ranges. Furthermore, in our cross-fostering experiment, the small number of recruits without close kin did not become helpers even though they remained within their natal area and even though there were non-kin broods available to be helped. In fact, spatial cues offer unreliable information on kinship for helpers because there is considerable dispersal of non-kin among clans during the non-breeding period (Russell 1999; B. J. Hatchwell, unpublished data).

The helping behaviour of cross-fostered siblings showed that there was no discrimination between related and unrelated brood-mates, indicating a recognition mechanism of learning through association. A process in which the recognition cues of probable relatives are learned is the likely mechanism for the expression of kin preferences in birds (Sherman *et al.* 1997; Price 1998, 1999; Komdeur & Hatchwell 1999) and mammals (Clarke & Faulkes 1999). For example, in Galapagos mockingbirds *Nesomimus parvulus*, the care of helpers is predicted better by prior association than by kinship *per se* (Curry & Grant 1990). The long period of kin association in long-tailed tits is a general characteristic of avian cooperative breeding systems (Langen 2000) and provides an opportunity for vocal signals to be learned, thereby offering an indirect cue to kinship in avian societies. We know of no instances among cooperative breeders where kin-directed helping occurs in the absence of opportunities for learning the phenotypic traits of kin, but this does not mean that this is the only possible mechanism. Self-referent phenotype matching has recently been invoked in explaining kin discrimination in peafowl *Pavo cristatus* (Petrie *et al.* 1999) and may also operate in other species.

A kin recognition mechanism of learning through association implies a learning period during which the recognition template is established. The contact calls of long-tailed tits used in our playback experiment developed towards the end of the 16–17 day nestling period (A. MacColl, personal communication), which was well after the time when nestlings were cross-fostered. However, there may be further development of these calls during the post-fledging period. It is unlikely that the putative kin-learning period extends throughout the non-breeding period because our playback experiment showed that breeders were able to discriminate between kin and non-kin from within the same clan despite the dispersal of non-kin between clans during the autumn and winter. Furthermore, helpers exhibit a kin preference even when the choice is between kin and non-kin nests from the same clan (Russell 1999). Thus, the kin recognition label and template must be established before the movement of non-relatives between clan ranges.

There are limitations to the use of indirect 'rules of thumb', such as learning through association, as a recognition mechanism. First, they are vulnerable to errors resulting from brood parasitism, extra-pair paternity or accidental association. Second, cheats may exploit a learning mechanism in order to procure the care of unrelated helpers, a phenomenon that was dubbed 'kinship deceit' by Connor & Curry (1995). For example, in white-winged chough *Corcorax melanorhamphos*, groups may kidnap unrelated offspring who subsequently become helpers in their adoptive group (Heinsohn 1991). The frequency of errors in identification will also depend on the degree of overlap between calls of relatives and non-relatives (Reeve 1989). Although long-tailed tits can recognize the calls of kin, we do not yet know which characteristics of calls are recognized, nor whether vocalizations provide information regarding family-specific or individual-specific identity. Furthermore, these calls could be either genetically encoded or environmentally acquired through learning. If offspring learn calls from their parents, members of a particular family will share a common call type (Price 1998, 1999). Provided that vocal characteristics are relatively fixed through life, a family-typical call acquired during a period of family association could provide effective kinship cues. Alternatively, 'signature' calls may enable individual recognition resulting in a library of calls recognized as belonging to familiar

individuals that are likely to be kin. These possibilities remain to be explored, but they do have important implications for other aspects of avian cooperative breeding systems, such as the investment rules used by helpers. Family-specific calls may result in an all-or-nothing investment strategy such that helpers do not help individuals perceived as non-family, but feed at a certain rate when individuals are perceived as family, subject to other factors such as brood size and number of carers (Hatchwell 1999). In contrast, individual-specific calls may permit fine adjustments in helper investment, as occurs in some cooperative species (Curry 1988; Emlen & Wrege 1988; Komdeur 1994), according to a perceived degree of relatedness.

REFERENCES

Blaustein, A. R., Bekoff, M. & Daniels, T. J. 1987 Kin recognition in vertebrates (excluding primates): empirical evidence. In *Kin recognition in animals* (ed. D. J. C. Fletcher & C. D. Michener), pp. 287–331. Chichester, UK: Wiley.

Brooker, M. G., Rowley, I., Adams, M. & Baverstock, P. R. 1990 Promiscuity: an inbreeding avoidance mechanism in a socially monogamous species? *Behav. Ecol. Sociobiol.* **26**, 191–200.

Clarke, F. M. & Faulkes, C. G. 1999 Kin discrimination and female mate choice in the naked mole-rat *Heterocephalus glaber*. *Proc. R. Soc. Lond.* B **266**, 1995–2002.

Clarke, M. F. 1984 Cooperative breeding by the Australian bell miner, *Manorina melanophrys* Latham: a test of kin selection theory. *Behav. Ecol. Sociobiol.* **14**, 137–146.

Cockburn, A. 1998 Evolution of helping behaviour in cooperatively breeding birds. *A. Rev. Ecol. Syst.* **29**, 141–177.

Connor, R. C. & Curry, R. L. 1995 Helping non-relatives: a role for deceit? *Anim. Behav.* **49**, 389–393.

Cramp, S. & Perrins, C. M. (ed.) 1993 *The birds of the western Palearctic*, vol. VII. Oxford University Press.

Curry, R. L. 1988 Influence of kinship on helping decisions in Galapagos mockingbirds. *Behav. Ecol. Sociobiol.* **22**, 141–152.

Curry, R. L. & Grant, P. R. 1990 Galapagos mockingbirds: territorial cooperative breeding in a climatically variable environment. In *Cooperative breeding in birds: long-term studies of ecology and behavior* (ed. P. B. Stacey & W. D. Koenig), pp. 289–332. Cambridge University Press.

Emlen, S. T. 1997 Predicting family dynamics in social vertebrates. In *Behavioural ecology: an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 228–253. Oxford, UK: Blackwell Science.

Emlen, S. T. & Wrege, P. H. 1988 The role of kinship in helping decisions among white-fronted bee-eaters. *Behav. Ecol. Sociobiol.* **23**, 305–315.

Gaston, A. J. 1973 The ecology and behaviour of the long-tailed tit. *Ibis* **115**, 330–351.

Glen, N. W. & Perrins, C. M. 1988 Cooperative breeding by long-tailed tits. *Br. Birds* **81**, 630–641.

Grafen, A. 1990 Do animals really recognize kin? *Anim. Behav.* **39**, 42–54.

Grosberg, R. K. & Quinn, J. F. 1986 The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. *Nature* **322**, 457–459.

Halpin, Z. T. 1991 Kin recognition cues of vertebrates. In *Kin recognition* (ed. P. G. Hepper), pp. 220–258. Cambridge University Press.

Hamilton, W. D. 1964 The genetical evolution of social behaviour I. *J. Theor. Biol.* **7**, 1–16.

Hatchwell, B. J. 1999 Investment strategies of breeders in avian cooperative breeding systems. *Am. Nat.* **154**, 205–219.

Hatchwell, B. J. & Russell, A. F. 1996 Provisioning rules in cooperatively breeding long-tailed tits *Aegithalos caudatus*: an experimental study. *Proc. R. Soc. Lond.* B **263**, 83–88.

Hatchwell, B. J., Russell, A. F., Fowlie, M. K. & Ross, D. J. 1999 Reproductive success and nest site selection in a cooperative breeder: effect of experience and a direct benefit from helping. *Auk* **116**, 355–363.

Heinsohn, R. G. 1991 Kidnapping and reciprocity in cooperatively breeding white-winged chough. *Anim. Behav.* **41**, 1097–1100.

Hepper, P. G. 1991 *Kin recognition*. Cambridge University Press.

Kempenaers, B. & Sheldon, B. C. 1996 Why do male birds not discriminate between their own and extra-pair offspring? *Anim. Behav.* **51**, 1165–1173.

Komdeur, J. 1994 The effect of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). *Proc. R. Soc. Lond.* B **256**, 47–52.

Komdeur, J. & Hatchwell, B. J. 1999 Kin recognition: function and mechanisms in avian societies. *Trends Ecol. Evol.* **14**, 237–241.

Langen, T. A. 2000 Prolonged offspring dependence and cooperative breeding in birds. *Behav. Ecol.* **11**, 367–377.

Payne, R. B., Payne, L. L. & Rowley, I. 1988 Kin and social relationships in splendid fairy wrens: recognition by song in a cooperative bird. *Anim. Behav.* **36**, 1341–1351.

Petrie, M., Krupa, A. & Burke, T. 1999 Peacocks lek with relatives, even in the absence of social or environmental cues. *Nature* **401**, 155–157.

Price, J. J. 1998 Family- and sex-specific vocal traditions in a cooperatively breeding songbird. *Proc. R. Soc. Lond.* B **265**, 497–502.

Price, J. J. 1999 Recognition of family-specific calls in stripe-backed wrens. *Anim. Behav.* **57**, 483–492.

Reeve, H. K. 1989 The evolution of conspecific acceptance thresholds. *Am. Nat.* **133**, 407–435.

Russell, A. F. 1999 Ecological constraints and the cooperative breeding system of long-tailed tits *Aegithalos caudatus*. PhD thesis, University of Sheffield, UK.

Sherman, P. W., Reeve, H. K. & Pfennig, D. W. 1997 Recognition systems. In *Behavioural ecology: an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 69–96. Oxford, UK: Blackwell Science.

Stacey, P. B. & Koenig, W. D. (ed.) 1990 *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press.