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Dispersal costs set the scene for helping in an atypical avian cooperative breeder

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The ecological constraints hypothesis is suggested to explain the evolution of cooperative breeding in birds. This hypothesis predicts that the scene for cooperative breeding is set when ecological factors constrain offspring from dispersal. This prediction was tested in the atypical cooperative breeding system of the long-tailed tit, *Aegithalos caudatus*, by comparing the degree of philopatry and cooperation in an isolated and a contiguous site whilst experimentally controlling for confounding aspects of reproduction. No difference was found between the two sites in the survival of offspring but a greater proportion were found to remain philopatric in the isolated site. This difference was caused by greater philopatry of normally dispersive females suggesting, as predicted, that dispersal costs were greater from this site. Furthermore, a greater proportion of males and females cooperated following breeding failure in the isolated site than in the contiguous site. Thus, as has been suggested for typical avian cooperative breeders, dispersal costs, relative to philopatric benefits, appear to set the scene for cooperative breeding in long-tailed tits.

Keywords: dispersal costs; helpers; habitat isolation; cooperative breeding; long-tailed tit; ecological constraints

1. INTRODUCTION

Cooperative breeding, a system where individuals other than the breeders carry out parent-like activities (here termed helpers), occurs in a diverse array of animal taxa (Stacey & Koenig 1990; Choe & Crespi 1997; Solomon & French 1997). In most, helpers direct their care towards kin, and dispersal away from kin largely precludes cooperation (Emlen 1995; Komdeur & Hatchwell 1999). The factors that cause individuals to remain associated with kin are therefore likely to hold the key to understanding the evolution of cooperative breeding (Koenig *et al.* 1992; Emlen 1994).

The ecological constraints hypothesis proposes that prolonged associations with kin occur when ecological factors cause dispersal costs to be high (Emlen 1994). However, evidence for this is largely correlational, from which the possibility that dispersal costs are a consequence of philopatry and cooperation rather than a cause cannot always be ruled out (Brown 1987; Zack 1990). In addition, few attempts have been made to test whether dispersal costs directly set the scene for helping in birds, and all those that have have been conducted in typical cooperative breeding systems (see Pruett-Jones & Lewis 1990; DuPlessis 1992; Komdeur 1992; Walters *et al.* 1992). Yet, if the ecological constraints hypothesis is to be used as a unifying theory for the evolution of cooperative breeding, it is essential that direct tests of its predictions are conducted in both typical and atypical systems (Emlen 1990).

Typical avian cooperative breeders live all year round in stable family units that arise when offspring (usually male) delay dispersal for a year or more in response to being constrained from independent breeding (Brown 1987). These constraints on breeding are caused by a combination of paucity of suitable habitat and high adult survivorship causing territory turnover to be low (Arnold & Owens 1999). The aim of this study is to test whether dispersal costs also set the scene for helping in an atypical cooperative breeder, the long-tailed tit, *Aegithalos caudatus*. Long-tailed tits are one of the most atypical avian cooperative breeders as they have no idiosyncratic habitat requirement (Cramp & Perrins 1993), show relatively high levels of annual mortality (Arnold & Owens 1998) and do not face constraints on independent breeding (Hatchwell 1999).

During the non-breeding season, long-tailed tits live in relatively fluid social units that occupy non-exclusive home ranges (Russell 1999). Since these social units comprise immigrants and overlapping generations of kin, they fit the definition of a clan (Emlen 1990). By spring, after considerable death and dispersal, individuals within each clan (including last year's offspring) form socially monogamous pairs and occupy a non-exclusive part of the winter range for breeding. However, 60–90% of all nesting attempts are commonly predated (Cramp & Perrins 1993; Hatchwell *et al.* 1999). Those pairs failing early in the season re-nest, but those failing later abandon breeding and often help by provisioning the nestlings or fledglings of another pair in the same clan (Glen & Perrins 1988; Hatchwell 1999). Most helpers are male, the philopatric sex, and these are virtually always fathers, sons or brothers of the recipient male (Hatchwell & Russell 1996; B. J. Hatchwell, unpublished data).

The importance of dispersal costs for the incidence of helping in this atypical cooperative breeder is tested in a between-population comparison. Dispersal costs are known to be greater between isolated habitats than within contiguous habitats (see Newton (1998) and references therein). In agreement with this, following extinction, habitat recolonization by long-tailed tits is inversely correlated with the degree of habitat isolation (Hinsley *et al.* 1995). In this study, I compare the degree of

Table 1. *Parameters used to investigate habitat quality*

(Adult body condition was measured by dividing weight by tarsus[3]. Adult and fledgling survivorship was measured as the percentage of each surviving to breed the following year. Lay date and clutch sizes were recorded for first breeding attempts only (sample sizes differ due to depredation). Successful pairs represent the percentage of all pairs giving rise to fledglings. Means are given $\pm$ s.e.m. t, Student's t-test; U, Mann–Whitney U-test; χ^2, chi-squared test.)

measures of habitat quality		isolated site	contiguous site	statistics test	p
mean adult condition	males	1.02 ± 0.01 ($n = 50$)	1.02 ± 0.01 ($n = 38$)	$t_{88} = -0.14$	0.9
	females	1.14 ± 0.02 ($n = 37$)	1.12 ± 0.02 ($n = 30$)	$t_{63} = 0.56$	0.6
annual adult survivorship	1996–1997	56% ($n = 48$)	59% ($n = 22$)	$\chi^2 = 0.05$	0.8
	1997–1998	52% ($n = 48$)	34% ($n = 29$)	$\chi^2 = 2.3$	0.2
mean lay date (day/month)	1996	14 April ± 0.7 ($n = 23$)	16 April ± 0.9 ($n = 22$)	$U = 450$	0.07
	1997	1 April ± 0.9 ($n = 16$)	3 April ± 1.1 ($n = 27$)	$U = 250$	0.4
	1998	26 March ± 1.0 ($n = 22$)	31 March ± 1.0 ($n = 19$)	$U = 343$	0.002
mean clutch size	1996	9.2 ± 0.2 ($n = 17$)	9.9 ± 0.1 ($n = 17$)	$U = 210$	0.001
	1997	9.8 ± 0.2 ($n = 13$)	10.1 ± 0.2 ($n = 15$)	$U = 176$	0.5
	1998	10.1 ± 0.2 ($n = 19$)	10.1 ± 1 ($n = 12$)	$U = 303$	0.9
successful pairs	1996	14.3% ($n = 35$)	15.2 ($n = 33$)	$\chi^2 = 0.01$	0.9
fledgling survival	1997–1998	24% ($n = 113$)	18% ($n = 125$)	$\chi^2 = 1.71$	0.2

philopatry and cooperative breeding in two populations of long-tailed tits, one occupying an isolated site (IS) and the other an equal area of habitat within a 'mainland' or contiguous site (CS). It is predicted that if dispersal costs set the scene for cooperative breeding in long-tailed tits, philopatry and cooperative breeding will be more prevalent in the IS compared within the CS.

2. METHODS

The two sites used in this study were both in South Yorkshire, UK; the IS was Melton Wood (53°31′ N, 1°13′ W; SE 51 01, map 111 of the Landranger Ordnance Survey 1:50 000 series) and the CS was Ecclesall Wood (53°20′ N, 1°30′ W; SK 38 82, map 110). The IS was 1 km^2 and situated in a mosaic of small isolated woodlands and open farmland, with the closest neighbouring sites being 200 m and 600 m away. The CS comprised 3 km^2 of continuous woodland surrounded by a mosaic of gardens, parks and other woodlands, much of which presented suitable habitat for long-tailed tits. To control for the difference in area between the two sites, only the central core of the CS, equal in area to that of the IS, was used in this study. In other words, all site comparisons reported here are between the IS and an equal area (1 km^2) within the CS. Values (± 1 s.d.) are given in the form IS first and CS second. Statistical analyses were conducted using Minitab 12.23 for PCs (Minitab, Inc.).

To control for the effect of habitat quality on decisions of dispersal and cooperation, the two study sites were selected on the basis of habitat similarity and location. First, long-tailed tits prefer deciduous woodland for feeding (Hartley 1953) and scrub or hedges for nesting (Glen 1985); the two habitats chosen were of similar broad vegetation type: deciduous (74% versus 80%), coniferous (18% versus 8%) and scrub (8% in the IS) or gardens (12% in the CS). Second, at 7.5 g, long-tailed tits are extremely sensitive to cold weather (Perrins 1979); the two sites were unlikely to encounter different weather conditions as they were close (inter-site distance 27 km) and at similar altitude (70–90 m versus 120–150 m).

In the IS there were five clans in each of the three study years comprising 35 pairs in 1996, 30 pairs in 1997 and 33 pairs in 1998. Out of these, I colour ringed 69% of adults and 81% of offspring ($n = 37$ offspring, $n = 5$ broods) in 1996, 80% of adults and 88% of offspring ($n = 94$ offspring, $n = 11$ broods) in 1997 and 95% of adults in 1998. In the CS there were the same number of clans and a similar number of pairs to the IS: 33 pairs in 1996, 30 pairs in 1997 and 31 pairs in 1998. Out of these, I colour ringed 33% of adults and 81% of offspring ($n = 48$ offspring, $n = 5$ broods) in 1996, 47% of adults and 100% of offspring ($n = 88$ offspring, $n = 11$ broods) in 1997 and 69% of adults in 1998.

A number of demographic and breeding parameters known to reflect habitat quality were also compared. These were (i) the number of breeding pairs, (ii) adult body condition (weight/tarsus^3) and annual adult survivorship, (iii) lay date and clutch size, and (iv) breeding success. Few differences were found in these parameters between the two sites and when differences were found they showed no consistent pattern that would suggest that the two sites differed significantly in their quality for long-tailed tits (table 1; Russell 1999). First, the numbers of pairs breeding in the two areas were similar in all three years. Second, no differences were found in the condition of adults between the two sites (1996–1998 combined) or in annual adult survivorship (1996–1997 or 1997–1998). Third, lay date and clutch size differed significantly between sites in only one of the three years, although lay date tended to be earlier in another year. Fourth, natural levels of breeding success (measured in 1996 only) showed no difference in the proportion of pairs giving rise to offspring, no cases of brood reduction and no differences in fledgling survivorship between the two sites.

To control for the effect of breeding success on dispersive and cooperative decisions, breeding success in the two sites was equalized in 1997 by protecting nests. Nest depredation by corvids, the predominant nest predator (Hatchwell *et al.* 1999), can be eliminated by surrounding nests at a distance of 20 cm or more with chicken wire of hole diameter 6 cm. This permits long-tailed tits to pass freely to and from their nests but prevents
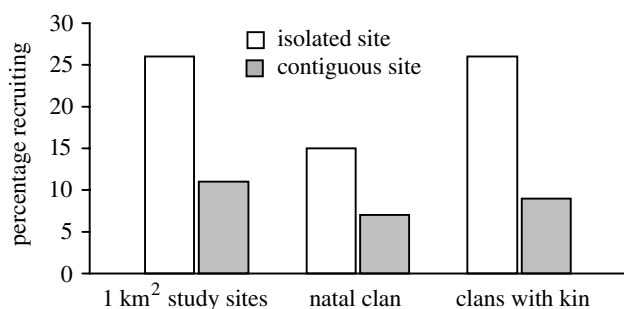
Figure 1. Offspring recruitment: a greater proportion of offspring was recruited in the IS than in the CS (27% versus 11%; $\chi^2 = 6.44$, $p < 0.02$) and, although there was no difference in the proportion of offspring recruited into natal clans between the two sites (14% versus 6%; $\chi^2 = 2.03$, $p = 0.15$), a greater proportion was recruited into the same clan as kin in the IS than in the CS (20% versus 8%; $\chi^2 = 5.56$, $p < 0.02$).

access by corvids (Glen 1985). Using this method, three important aspects of breeding could be made similar in the two sites: the number of pairs breeding successfully ($n = 11$ in each); the number of clans with successful breeding attempts ($n = 5$ in each); and the mean fledge date (23 May ± 17 d versus 21 May ± 13 d: Mann–Whitney U-test, $U = 125$, $p = 0.90$).

(a) Degree of philopatry

Measures of philopatry were based on observations of offspring that were born in 1997 and re-sighted in the breeding season of 1998. In both sites, 11 broods (mean size, 8.27 ± 1.10 versus 8.0 ± 1.79; Mann–Whitney U-test, $U = 133$, $p = 0.68$) were raised successfully (totalling 94 versus 88 offspring), out of which 95% were colour ringed from ten broods in the IS ($n = 83$) and 100% from 11 broods in the CS ($n = 88$).

In 1998, systematic searches were made of the two sites and 2 km² of the most suitable surrounding habitat (totalling 3 km² in each site). The main sites were visited every second day from the onset of breeding (March) until the end (mid-May), except for six days in March and April when the surrounding areas were visited instead. The identities of all colour-ringed birds and the clans in which they were found were recorded. In addition, the nests of all pairs within the two sites and those of colour-ringed birds in the surrounding areas were located. Individuals were defined as having survived if they were found breeding within the total areas searched in the two sites (3 km²). Philopatry was measured as the proportion of offspring recruiting into one of the five clans in each site and their natal clan.

(b) Extent of cooperation

The extent of cooperative breeding was investigated by determining the proportion of pairs with helpers, the proportion of individuals that became helpers following breeding failure, and the number of helpers per nest. In 1997, the same number of pairs bred successfully ($n = 11$) and unsuccessfully ($n = 19$) in the two sites and fledge date did not differ significantly (see § 2). A similar proportion of individuals could therefore potentially act as helpers in the two sites ($n = 38$ in each). Only data from 1997 were included in the analyses because the numbers of potential helpers and recipients were not controlled between sites in the other years. The presence and identities of helpers at the 11 successful nests in each site were determined during hour-long nest observations, conducted on approximately alternate days

Table 2. *Percentage of breeders in 1998 comprising adults from the previous year and recruits and immigrants from the current year*

(Since not every adult or offspring was ringed in 1997, the values below represent estimations based on extrapolations of adult survival and offspring recruitment levels (1997–1998) and breeding numbers (1998).)

	isolated site	contiguous site	χ^2	p
percentage breeders comprising				
surviving adults	47	34	2.3	0.13
recruits	33	16	5.0	0.02
immigrants	20	50	13.0	< 0.001
percentage first-order relatives in clans				
	30	15	4.6	0.03

during the 16-day chick-rearing period. Observations were carried out from a hide placed 5–10 m from the nests.

3. RESULTS

(a) Degree of philopatry

The proportions of those offspring colour ringed in 1997 that survived to breed in 1998 did not differ significantly between the two sites (table 1), nor did the sex of those surviving (45% versus 44% female, $\chi^2 = 0.011$, $p = 0.92$). However, a greater proportion of offspring was recruited into the IS than into the CS and, although there was no difference in the degree of natal-clan recruitment between the sites, a significantly greater proportion was recruited into clans with relatives in the IS compared with in the CS (figure 1). Thus, in 1998, clans in the two sites comprised a similar number of adults remaining from the previous year, but out of the other breeders, most in the IS were recruits, whilst most in the CS were immigrants. As a consequence, clans in the IS contained twice as many kin as those in the CS (table 2).

These results were mediated by differences in recruitment of normally dispersive females in the two sites. Out of those offspring that survived, there was no difference in the proportions of males that were recruited to the two sites (100% versus 89%; Fisher's exact test, $p = 0.86$) but a greater proportion of females was recruited into the IS (100% versus 29%; Fisher's exact test, $p < 0.001$). Similarly, there was no difference between the two sites in the proportion of males that was recruited into clans with kin (100% versus 78%; Fisher's exact test, $p = 0.34$) but there was a trend for greater recruitment into clans with kin among females in the IS (50% versus 0%; Fisher's exact test, $p = 0.081$).

(b) Extent of cooperation

The incidence of cooperative breeding was similar in the two sites, as a similar number of pairs that bred successfully had helpers in each (45% versus 55%). Out of these helped pairs, all were assisted by males but a significantly greater proportion were also assisted by females in the IS (36% versus 0%; Fisher's exact test, $p = 0.030$). Furthermore, a greater proportion of individuals (male and female) became helpers following
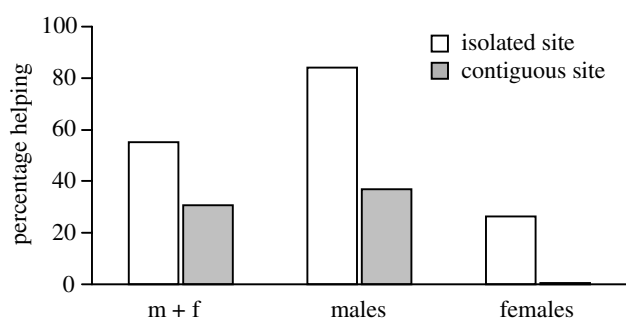
Figure 2. Proportion of individuals cooperating following breeding failure in the IS and the CS: males and females (m + f) (55% versus 31%; $\chi^2 = 11.08$, $p = 0.001$); males (84% versus 37%; $\chi^2 = 17.26$, $p < 0.001$); and females (26% versus 0%; Fisher's exact test, $p < 0.05$).

breeding failure in the IS (figure 2). As a consequence, a greater number of helpers were present at helped nests in the IS (4.6 ±1.14) than in the CS (1.17 ±0.41) (Mann–Whitney U-test, $U = 45$, $p < 0.006$).

4. DISCUSSION

Most studies investigating the factors that set the scene for cooperative breeding in birds have suggested ecologically mediated dispersal costs to be the causal factor (Koenig *et al*. 1992; Emlen 1994). However, most such studies have been correlational and conducted on co-operative breeders where dispersal costs and breeding constraints appear to be positively coupled. It has therefore proved difficult in many studies to determine unequivocally whether dispersal costs are a consequence or a cause of philopatry and whether philopatry is a consequence or a cause of cooperative breeding (Brown 1987; Zack 1990). This study attempts to avert both problems.

First, since dispersal costs vary positively with habitat isolation (Newton 1998), it was possible to predict the expected pattern of philopatry and cooperative breeding if dispersal costs set the scene for cooperative breeding, by using a between-population approach. Second, by selecting two study sites differing in their isolation but similar in their habitat, and by experimentally equalizing breeding success, most of the important confounding variables could be controlled. Third, by using the long-tailed tit, a species in which all offspring breed independently from their first year, the degree of philopatry observed is more likely to be a function of dispersal costs *per se* rather than of the fact that they are cooperative breeders.

As predicted, a greater proportion of offspring was recruited into the IS than into the CS and, consequently, offspring were more likely to be recruited into clans with relatives in the IS. In addition, a greater proportion of individuals cooperated following breeding failure in the IS and more helpers were present per nest in this site. These results suggest that dispersal costs set the scene for cooperative breeding in long-tailed tits. However, it should be pointed out that helper number has been shown to influence offspring survival in long-tailed tits (Hatchwell 1999) and therefore it could be argued that the greater degree of philopatry in the IS was caused by differences in helper number. In this study, however,

there was no difference in offspring survival between the two sites. In addition, the significant difference in the proportion of offspring that was recruited into the two sites was caused, in part, by the more philopatric tendencies of females in the IS. Females are the dispersive sex in long-tailed tits, as they are in most passerines (Greenwood 1980). Therefore, the observed differences in philopatry and immigration between the two sites are likely to have arisen as dispersal costs were greater to and from the IS because of its boundary of unsuitable habitat (Opdam 1990). This conclusion is supported by the facts that dispersal has been shown to be lower to and from ISs than within CSs in ecologically comparable non-cooperatively breeding species (e.g. Matthysen & Currie 1996; Newton 1998; Russell 1999) and that long-tailed tits show a negative association between recolonization of habitats following extinction and the degree of habitat isolation (Hinsley *et al*. 1995).

The differences in recruitment patterns, observed in the two sites, ultimately had a significant impact on the kin structure of the two populations in this study, with clans comprising chiefly surviving adults and philopatric offspring in the IS, but surviving adults and immigrants in the CS. As a consequence, twice as many relatives were present in clans in the IS than in the CS. These findings are consistent with those of another study where, using a large data set of ringing recoveries at 85 sites, breeders were found more often to be previous year's offspring in ISs compared with CSs (Russell 1999). Therefore, because long-tailed tits virtually always redirect their care towards kin following breeding failure (Glen & Perrins 1988; Hatchwell & Russell 1996; Russell 1999), it is likely that the positive association found here between habitat isolation (and dispersal costs) and the number of relatives in clans would lead to differences in the potential for failed breeders to adopt a cooperative breeding strategy.

Although no difference was found between the two sites in the proportion of pairs with helpers, more failed breeders became helpers in the IS than in the CS. The most plausible explanation for these results is that the degree of philopatry and the proportion of individuals that cooperate following breeding failure are causally linked in long-tailed tits. This is supported by the fact that individuals from the same number of broods were recruited in the two sites, but a greater proportion was recruited per brood in the IS. Accordingly, there was no difference in the incidence of cooperative breeding between the two sites and yet there was a greater number of helpers per helped nest in the IS. Additionally, no females were recruited into clans with relatives in the CS whereas several were in the IS, and, correspondingly, no females cooperated following breeding failure in the CS but five did in the IS. These results support the general observation in typical cooperative systems that the degree of philopatry and the abundance of helpers are causally linked (Brown 1987).

In conclusion, this study shows that dispersal costs are likely to be critical to the incidence of helping behaviour in the atypical cooperative breeding system of the long-tailed tit. As a consequence, this study lends weight to the idea that the ecological constraints hypothesis may universally explain kin-based cooperative breeding in birds.

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