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Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits

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Helpers at the nest in the cooperative breeding system of long-tailed tits *Aegithalos caudatus* exhibit kin preference in their helping behavior. The aim of this study was to use multivariate analyses to investigate whether helpers accrue indirect fitness benefits through their cooperation by increasing the productivity of relatives. All birds started each season breeding independently in pairs, but birds that failed in their own breeding attempt often redirected their care to help another pair provision their offspring. About half of all broods had one or more helpers, 86% of which were male. Provisioning rates increased and there was a corresponding increase in the mass of nestlings within broods as the number of helpers increased. Helpers had no significant short-term effect on productivity because nest predation, nestling survival, and brood size were unaffected by the presence of helpers. However, in the long term helpers had a highly significant effect on the recruitment of fledglings, the positive effect of helpers being linear within the range of helper numbers that we observed. We found no evidence to suggest that these results were confounded by the effects of individual or habitat quality. We conclude that long-tailed tits accrue indirect fitness benefits by helping kin. Nevertheless, the inclusive fitness benefit from helping is substantially lower than that of independent breeding, showing that helpers are making the best of a bad job. *Key words: Aegithalos caudatus*, cooperative breeding, inclusive fitness, kin selection, long-tailed tit. *[Behav Ecol 15:1–10 (2004)]*

In cooperatively breeding birds, some individuals, called helpers, forgo independent reproduction and instead help others rear offspring (Brown, 1987). Helpers at the nest usually live in nuclear families that arise because constraints on independent reproduction cause offspring to delay dispersal (Emlen, 1982). Cooperative breeding then results when these delayed dispersers assist in raising subsequent broods, thereby accruing kin-selected, indirect fitness benefits (Hamilton, 1964), and/or direct fitness benefits through increased personal reproduction in the future (Brown, 1987).

Helpers may derive indirect fitness benefits in two ways. First, when assisted by helpers, related breeders may invest less in each reproductive attempt so that they may have either more reproductive attempts per season (Russell and Rowley, 1988) or a higher probability of survival to following breeding seasons (Koenig and Mumme, 1987; Woolfenden and Fitzpatrick, 1984). Second, helpers may increase the productivity of relatives in each breeding attempt (e.g., Emlen and Wrege, 1991; Reyer, 1984). Numerous studies have shown a positive correlation between the number of helpers and group productivity (Brown, 1987; Emlen, 1991). However, breeders of high quality, or those living on high-quality territories, are likely to have larger groups because of past success and are also likely to be successful in the current breeding attempt, resulting in a noncausal, positive relationship between group size and productivity (e.g., Eguchi et al., 2002). Therefore, the most convincing evidence comes from experimental or multivariate analytical approaches that show positive effects of helpers on productivity while controlling for individual or territory effects (Boland et al., 1997; Brown et al., 1982; Emlen and Wrege, 1991; Komdeur, 1994; Mumme, 1992).

However, such findings are not universal. A number of studies have found no relationship between group size and productivity (e.g., Legge, 2000; Leonard et al., 1989; Walters, 1990), and Cockburn (1998) suggested that the negative effects of helper removal experiments on productivity may arise through disruption of social groups rather than through the removal of helpers per se. Furthermore, in some cooperative species, helpers may be unrelated to the brood they help (Dunn et al., 1995; Reyer, 1984), so indirect fitness benefits cannot be accrued. As a consequence, the case for kin selection as an explanation for helping behavior appears less strong than it once did (Clutton-Brock 2002; Cockburn, 1998).

Measuring the fitness consequences of helping presents particular problems. Small increases in breeder survival as a result of reduced parental investment may not be detectable in short-term studies. Similarly, a positive effect of helpers on productivity may be apparent only when conditions are unfavorable (Curry and Grant, 1990; Emlen, 1990), only on certain territories (Komdeur, 1994) or only for certain categories of breeder (Magrath, 2001). Furthermore, helpers may have little opportunity to increase brood size if nestling survival is already high (Hatchwell, 1999), but their additional care may increase nestling condition or enhance postfledging survival, with consequences for their subsequent recruitment into the breeding population. Such effects may be measurable only in long-term studies.

The aim of this study was to investigate whether helpers increase productivity in the cooperative breeding system of long-tailed tits *Aegithalos caudatus*. Long-tailed tit helpers can discriminate kin from non-kin (Hatchwell et al., 2001b), and they exhibit kin preference in their helping behavior, with

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helpers typically being a close relative (usually a brother) of one parent of the assisted brood (Russell and Hatchwell, 2001). Therefore, helpers can potentially accrue indirect fitness benefits if they increase the productivity of their kin. Long-tailed tits are particularly well suited to this study because of their social organization. In typical cooperative breeders, offspring delay dispersal and act as helpers on their natal territory before dispersing when a breeding opportunity arises (Brown, 1987), so the link between prior success and the presence of helpers means that a correlation between helper number and productivity may be an artifact of territory quality. In contrast, the social units of long-tailed tits are not nuclear families, and they do not defend territories (Hatchwell et al., 2001a; Russell, 1999). Helpers are breeders that redirect their care to broods belonging to other pairs after their own breeding attempt has failed (Glen and Perrins, 1988).

In this article, we describe the origin and frequency of helpers in our study populations. We used multivariate statistical analyses to investigate the effect of helpers on nestling provisioning and condition and on short-term and long-term measures of productivity. Short-term measures included nest predation, nestling survival, and brood size. The long-term effect of helpers was assessed through an analysis of offspring recruitment in relation to the number of helpers. Finally, we calculated the indirect fitness consequences of cooperation from the perspective of breeders and helpers.

METHODS

Study sites and study species

We studied three populations of long-tailed tits in South Yorkshire, UK. One population (Rivelin Valley, Sheffield, 53° 23′ N, 1° 34′ W, area 300 ha) comprised 18–53 pairs and was studied from 1994–2000, while the other two populations (Ecclesall Wood, Sheffield 53° 20′ N, 1° 30′ W, area 100 ha; and Melton Wood, Doncaster 53° 31′ N, 1° 13′ W, area 100 ha) were studied from 1996–1998 and comprised 30–33 and 30–35 pairs, respectively. All three sites contained woodland (mostly deciduous) and scrub and variable amounts of farmland and gardens (for further details, see Hatchwell et al. 1999b; Russell, 2001). The sites were within 27 km of each other, and the only major difference between them was in their degree of isolation from other long-tailed tit habitat (Russell, 2001). In general, there was little variation among study sites in the occurrence and effect of helpers, but study site was included as a factor in analyses, where appropriate.

Long-tailed tits in our study sites spend the nonbreeding season (June–February) in relatively fluid social groups of about 16 individuals that occupy large, nonexclusive ranges (Hatchwell et al., 2001a). These groups comprise overlapping generations of kin augmented by unrelated male and female immigrants, and their average composition at the end of the winter is about 30–40% previous breeders, 25–40% philopatric recruits, and 30–40% unrelated immigrants (Hatchwell et al., 2001a; Russell, 2001). Monogamous pairs form in early spring, each occupying a nonexclusive breeding range within the group range. Long-tailed tits are single brooded, and all birds start the season breeding independently in pairs, but nest failure is frequent (Hatchwell et al., 1999b), and failed breeders may become helpers by feeding the offspring of another pair (Gaston, 1973; Glen and Perrins, 1988).

Field observations

We captured adults using mist-nets and ringed them with unique color-ring combinations. Most were caught at the start of the breeding season during the building phase of the first nesting attempt (mean proportion of adults color-ringed: Rivelin Valley, 91%, $n = 7$ years; Melton Wood, 81%, $n = 3$; Ecclesall Wood, 50%, $n = 3$). Adults were sexed from measurements (males usually have longer wings and tarsi than females), behavior (incubation is by females only), and by molecular genetic means (Griffiths et al., 1998). Nestlings from 129 broods from all three populations were uniquely color-ringed, weighed (to 0.1 g), and their right tarsus was measured (to 0.1 mm) on days 9–13 (mostly on day 11) of the 16- to 17-day nestling period (hatch day = day 0).

We knew the age of breeders that had been ringed as nestlings with certainty, and unringed immigrants were assumed to be 1 year old when captured as breeders. This is a reasonable assumption because most breeders were ringed, and there is no evidence that significant dispersal occurs after a bird's first winter (McGowan et al., 2003). The adult mortality rate of long-tailed tits is 46–56%, depending on helper/breeder status (McGowan et al., 2003), so most individuals attempt to breed in just 1 or 2 years. Therefore, in statistical models incorporating breeder age, we classified adults as first year or older.

We closely monitored the breeding attempts of all members of our populations throughout the breeding season (February–June) in each year of the study. Nests were first located by following pairs during nest building and were then checked at regular intervals until nestlings had fledged or the breeding attempt failed. After the failure of a breeding attempt, we searched for replacement nests belonging to the failed pair. A small number of nests that failed were not found, but during a total of 13 site-years very few broods (about 10 broods) that fledged successfully within the study sites or immediately adjacent to them were not located before fledging.

The timing of laying of first clutches varied significantly among years and among study sites (two-way ANOVA: year $F_{6,360} = 69.5$, $p < .001$; site $F_{2,360} = 13.4$, $p < .001$). However, there was no significant variation among sites or years in the fledging date of successful broods (two-way ANOVA: year $F_{5,85} = 2.00$, $p = .09$; site $F_{2,85} = 0.61$, $p = .55$). Thus, the start of breeding, but not the end of breeding, varied significantly with year and site, so in analyses we controlled for seasonal effects using relative lay date (relative to the median lay date per year per study site) and/or absolute lay date (days after 1 March).

Long-tailed tit nests are domed with a small entrance hole, so the date of egg laying and hatching was determined by feeling inside nests for the presence of eggs or hatchlings. Some nests were inaccessible, so we determined laying and hatching dates by observing the behavior of parents. We determined the clutch size (typically 8–10 eggs) of accessible nests by removing (then replacing) eggs from nests with a plastic teaspoon. Unhatched eggs remain in the nest, so for those nests of known clutch size, initial brood size was found by subtracting any unhatched eggs on day 11. We calculated nestling survival as the proportion of the initial brood still alive on day 11.

During the nestling period, we conducted hide observations of provisioning behavior on alternate days from day 2 (Rivelin Valley population), or every 1–4 days (Ecclesall and Melton woods) until fledging or predation of the brood. Observation periods varied from 0.5 h to 17 h, but most lasted 1 h. During these observations we recorded the identity of each carer and their provisioning frequency (see Hatchwell, 1999, for further details of provisioning observations). Any unringed birds that appeared as helpers were ringed as soon as possible after they first appeared at the nest. A few helpers were observed to initiate helping after a brood had fledged, but we were unable to obtain systematic observations during this phase of the breeding cycle, so we used nestling observations only in analyses of the effects of helpers on productivity. Our analysis is conservative because if a small number of broods acquired helpers postfledging, this would have the effect of weakening any relationship between recruitment and number of helpers.

Some nests in each of the study sites were protected from avian predators by cages of 6 cm wire-netting, which permits access by long-tailed tits, but not corvids (Glen, 1985). Protected nests were excluded from analyses of brood survival during the nestling phase, but were included in analyses of provisioning rates, nestling weight and survival, and the survival of fledglings.

We measured survival of fledglings as local recruitment (i.e., the proportion of fledglings that became breeders within the study populations in the year after fledging). This is not an exact survival estimate because nonrecruits may be dead or they may have dispersed. Long-tailed tits exhibit sex-biased dispersal, and males are the more philopatric sex, so that local recruitment of male fledglings (~30%) is higher than that of female fledglings (~10%), even though the adult sex ratio is 1:1 (McGowan et al., 2003). Therefore, recruitment underestimates the true survival rate, particularly of females.

The absence of stable territories or groups in long-tailed tits means that categorization of individuals to social units is not straightforward. Nevertheless, it is possible that survival rates of nestlings and fledglings might be influenced by spatial factors or by the identity of their social group. To investigate whether these factors influenced measures of productivity, we included a variable, "group," in statistical models. Individuals or nests were categorized according to their location in each of the study sites (six groups in the Rivelin Valley, five in Melton Wood, six in Ecclesall Wood), each being defined using observations of winter flocks and the distribution of relatives' nests (Hatchwell et al., 2001a; Russell, 1999). This variable will not perfectly reflect group identity because of the labile nature of group membership and ranges, but it does provide a close approximation to social grouping.

Statistical methods

We conducted all analyses investigating helper effects using residual maximum likelihood (REML) or iterated residual maximum likelihood (IRREML) models in Genstat 5, release 4.1. (Genstat, 1993). REML and IRREML analyses are forms of generalized linear models (GLMs) with normal and nonnormal error structures, respectively, in which both fixed and random terms can be fitted; random terms control for the use of repeated measures within individuals and nests (Schall, 1991). We assessed the significance of terms from Wald statistics (distributed as chi square) when the term was fitted last. We excluded random terms from models if they had a negative component of variance, and where this was the case for all random components in a model we used a GLM. The number of helpers at a nest was fitted as a continuous variable in all models, but due to the small sample of nest with four, five, or six helpers, we illustrate results in relation to zero, one, two, or three or more helpers (see figures for sample sizes). In all models, continuous variables were fitted as linear and polynomial functions, but in tables we report all linear functions and only those polynomial functions that were significant.

To investigate whether helpers had a significant effect on the rate at which broods were fed and the weight of nestlings within each brood, we conducted two REML analyses. In the first we used 963 observations of provisioning frequencies for 156 broods obtained between day 1 and day 16 of the nestling period. In the second we used the weights of 1030 nestlings from 129 broods. In each analysis, in addition to the number of helpers, we fitted study site, year, group, date, time of day, female age, male age, brood age, and brood size as fixed effects and nest identity nested within female identity as random terms. Male identity was dropped from the random component of the model because it had a negative component of variance. We also fitted temperature (recorded at 0900 h GMT at Sheffield City Museums meteorological station at Weston Park, Sheffield, 5 km from the study site) in the provisioning analysis, and we fitted nestling tarsus length and sex in the nestling weight analysis.

To investigate whether helpers influence the survival of nestlings within broods, we conducted two IRREML analyses. In the first we modeled brood survival (0 or 1) as a binomial variable with logit link function to analyze the probability that a brood would survive any 2-day period ($n = 774$ periods, $n = 113$ broods from the Rivelin Valley population that were visited at 2-day intervals throughout the nestling period). Here, in addition to the number of helpers and helper arrival (i.e., an incremental change in the number of helpers: yes/no), we fitted year, group, date, female age, male age, and brood size as fixed effects and nest identity nested within female identity as random effects. In the second analysis, to investigate nestling survival, we modeled brood size at weighing with the same error structure and link function and brood size at hatching as the binomial denominator ($n = 132$ broods). We fitted number of helpers (on day 5 and day 10), site, year, group, date, female age, and male age as fixed effects and female identity as a random effect. In both analyses, male identity was dropped from the random component of the model because it had a negative component of variance.

Finally, to investigate the effect of helper number on offspring recruitment, we used an IRREML model in which the number of offspring that recruited was modeled as the response term and the number of offspring that fledged fitted as the binomial denominator ($n = 93$ broods), with a binomial error structure and logit link function. Fixed effects were the number of helpers at fledging, site, year, group, date, female age, male age, and brood size, and female identity was fitted as the random term. Male identity had a negative component of variance and so was dropped from the random component of the model.

Pair identity was not fitted as a random term in any analysis because the relatively high mortality rate of long-tailed tits and the high divorce rate among successful pairs (Hatchwell et al., 2000) resulted in few pairs being represented more than once in productivity data sets. In the analyses of nestling survival and offspring recruitment, the second attempts of pairs represented more than once ($n = 3$ and $n = 1$, respectively) were omitted. In these analyses, repeated measures from the same individuals were retained because individuals always bred with a different partner, and female and male identity could be entered into each model as a random factor.

Means are reported ±1 SD, unless specified otherwise.

RESULTS

Prevalence and origin of helpers

Most helpers were not apparent until the nestling and fledgling periods (Figure 1a). Just seven birds (3.9% of 179 helpers) were observed either assisting a pair in the later stages of nest building or feeding an incubating female, despite extensive observations (Hatchwell et al., 1999a). Of the 145 helpers that were first observed during the nestling phase, their arrival was spread throughout the entire nestling period (Figure 1b).

Helpers were recorded at 41.8% of nests ($n = 194$ nests)

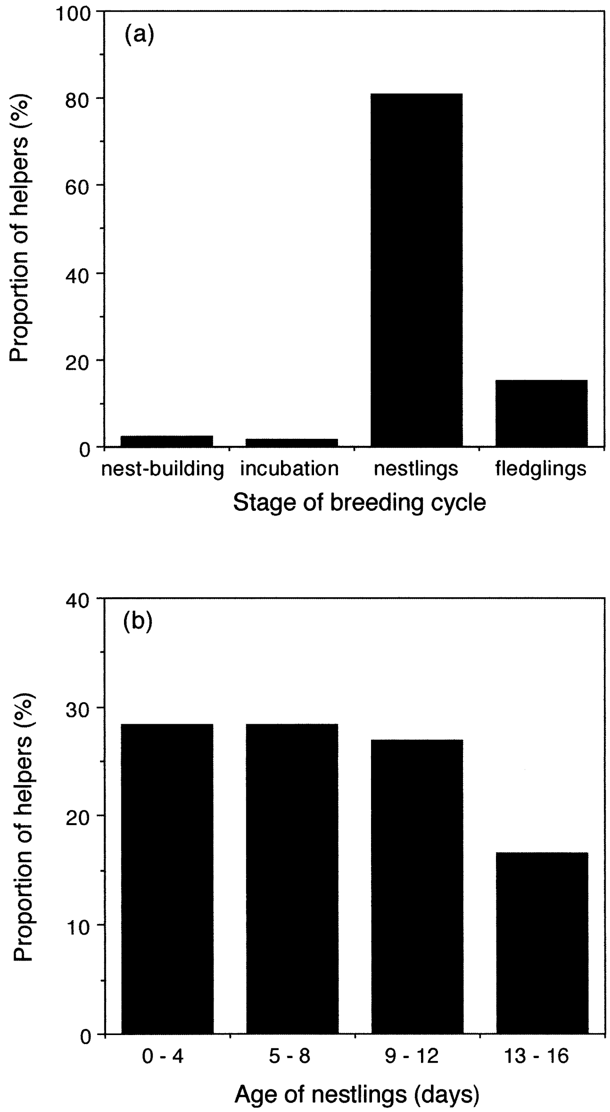

Figure 1
The timing of first appearance of long-tailed tit helpers at nests: (a) timing with respect to stage of the breeding cycle (*n* = 179 helpers); (b) timing with respect to nestling age for those helpers that appeared during the nestling period (*n* = 145 helpers).

that we observed during the nestling phase. However, helpers may arrive at a nest at any time during the nestling period (Figure 1b), and many nests were depredated well before fledging, so a better indication of the prevalence of helping is that 54.0% of nests (*n* = 124 nests) from which at least one offspring fledged had one or more helpers. Of these successful nests with helpers, the mean number of helpers was 1.97 ± 1.24 (*n* = 67 nests; range = 1–6 helpers). The proportion of nests with helpers did not differ significantly among study sites (χ^2 = 2.80, df = 2, *p* = .25), but Melton Wood had significantly more helpers per helped nest than the other two sites (Rivelin Valley, 1.66 ± 0.78 helpers, *n* = 44 nests; Melton Wood, 3.90 ± 1.66, *n* = 10; Ecclesall Wood, 1.54 ± 0.78, *n* = 13; Kruskal-Wallis test, *H* = 16.8, df = 2, $p <$ .001; see also Russell, 2001).

In all three of our study populations most helpers (121/151, 80.1%) were known to be failed breeders from within our study sites (Rivelin Valley, 81.5%, *n* = 92 helpers; Melton Wood, 76.9%, *n* = 39; Ecclesall Wood, 80.0%, *n* = 20). Of the helpers that were already ringed when first seen at a nest, 96.0% (121/126 helpers) were failed breeders from our study sites, the remaining 4.0% (5/126 helpers) being ringed birds whose breeding history was not known in that year. These failed breeders included a small proportion of birds that had lost their breeding partner, either through divorce (4.1%, *n* = 121) or predation (2.5%, *n* = 121). Of the remaining 30 helpers that were not known with certainty to be failed breeders, 25 were unringed when they first appeared at a nest. These helpers of unknown origin may have been failed breeders from outside our study areas. This is a realistic possibility because failed breeders sometimes traveled a considerable distance from their last breeding attempt to the nest at which they helped. The overall mean distance traveled was 290 ± 198 m (*n* = 121 helpers, range = 25–1100 m), although the distance differed significantly between sites (Rivelin Valley, 340 ± 216 m, *n* = 75; Melton Wood, 210 ± 125 m, *n* = 30; Ecclesall Wood, 212 ± 144 m, *n* = 16; Kruskal-Wallis test, *H* = 12.21, df = 2, *p* = .002). This compares with a mean internest distance of 170 ± 112 m (*n* = 39 pairs) for first nests in the Rivelin Valley in a year of average density (1998).

Most helpers of known sex were males (86.4% male, *n* = 132 helpers), although the sex of 19 helpers was not determined. Female helpers moved significantly farther from their last breeding attempt to the nest at which they helped than males did (female helpers, 416 ± 228 m, *n* = 15; male helpers 273 ± 188 m, *n* = 106; Mann-Whitney *U* test, *z* = 2.48, *p* = .013), so a relatively large proportion of unringed (hence unsexed) helpers that appeared at nests in our study areas may have been females. However, even if all birds of unknown sex were female, helpers were still predominantly male (75.5%, *n* = 151).

Breeders whose nesting attempts failed early in the breeding season renested, but from early May, the renesting probability declined rapidly (Figure 2a). The probability of renesting was also influenced by the stage of breeding at which an attempt failed, independently of date; breeders whose nest failed at the nestling stage were less likely to renest than those birds failing during building, egg laying, or incubation (Figure 2a). Because helpers are recruited from among failed breeders, the cumulative proportion of helpers increased as the number of failed breeders renesting decreased (Figure 2b).

Provisioning rates and nestling condition

There was a highly significant effect of the number of helpers on total provisioning rate (Table 1 and Figure 3a). Provisioning rates also increased with nestling age and brood size and were significantly influenced by time of day, temperature, and year (Table 1). Nestling weight within broods was also significantly affected by the number of helpers (Table 1 and Figure 3b). Several other factors influenced nestling weight. Male nestlings (predicted mean ± SE = 7.59 ± 0.038 g were significantly larger than females (7.41 ± 0.039 g; Table 1), and nestling tarsus length (a skeletal measurement that is highly correlated with age), time of day, date, and brood size were all significant factors (Table 1). Neither breeder age nor group identity were significant factors in either analysis, and maternal and paternal identities were nonsignificant, random terms (Table 1).

Short-term effect of helpers on productivity

On average, 65.5% (*n* = 113 broods) of broods that hatched and that were not protected with wire netting survived to fledging. The main cause of brood failure in our study populations was predation by corvids and mustelids (Hatch-

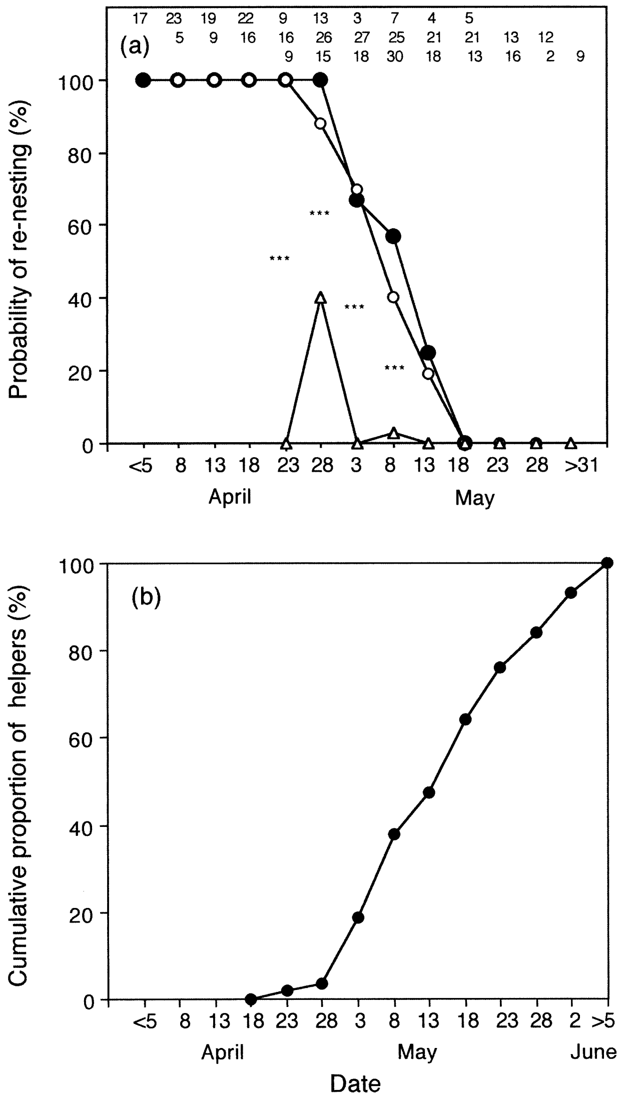

Figure 2
(a) The probability that pairs of long-tailed tits that had failed in a breeding attempt renested in relation to date (5-day periods); renesting probabilities are shown for pairs that failed during nest building or egg laying (filled circles), incubation (open circles), or the nestling phase (open triangles). Pairs that failed during the nestling phase were less likely to renest than those that failed during earlier breeding phases at the same time (χ^2 tests, $p < .001$ for periods centred on 23 April to 8 May). Sample sizes are given above the graph. (b) The cumulative proportion of helpers observed at nests ($n = 145$) in relation to date (5-day periods).

Table 1

The effect of helpers on total brood provisioning rates and mean nestling weights at ringing

Factor	Wald statistic (χ^2)	df	p
Total provisioning rate of broods			
Site	2.89	2	.24
Year	55.82	6	<.001
Group	15.19	16	.51
Date	2.06	1	.15
Time of day	7.13	1	.008
(Time of day)^2	5.82	1	.016
Temperature	8.69	1	.003
Female age	0.91	1	.34
Male age	0.11	1	.74
Brood age	115.91	1	<.0001
(Brood age)^2	19.83	1	<.001
Brood size	59.23	1	<.0001
Number of helpers	76.88	1	<.0001
Nestling weight			
Site	2.30	2	.32
Year	5.71	6	.46
Group	18.64	15	.23
Date	6.53	1	.011
(Date)^2	5.30	1	.021
Time of day	6.61	1	.012
(Time of day)^2	6.26	1	.012
(Time of day)^3	5.53	1	.019
Female age	0.15	1	.70
Male age	0.06	1	.81
Brood size	4.24	1	.04
Tarsus length	788.59	1	<.0001
Nestling sex	58.00	1	<.0001
Number of helpers	13.75	1	<.001

The data comprised repeated measures of individuals' provisioning rates and individual nestling weights within broods and were analysed using REML (see Methods). Provisioning data were natural logarithm transformed. In both analyses, nest identity was a significant random component ($p < .05$), and male identity was dropped because it had a negative component of variance.

well et al., 1999b; Russell, 1999). The presence of helpers and the resulting increase in activity at the nest might increase the probability of detection by predators; alternatively, helpers may increase vigilance and hence reduce predation. Because helpers arrive at nests continuously through the nestling period (Figure 1b), they were inevitably associated with successful nests. Therefore, to investigate whether helpers had a positive or negative effect on nest failure, nest survival probability was examined over a series of 2-day periods from hatching to fledging. We found no evidence that either the number of helpers or an incremental change in helper number influenced the probability of nest survival in the subsequent time interval (Table 2). Of the other factors included in the analysis, only nestling age was significant ($p < .001$; Table 2), nest failure being more likely as nestlings aged (Figure 4). There was no significant effect of the potentially confounding factors of breeder age or group identity, and maternal and paternal identities were also nonsignificant (Table 2).

In those broods that were not depredated, nestling survival was high. Across study sites and years, the mean brood size at hatching (day 0) was 9.07 ± 1.47 nestlings ($n = 133$ broods), and on average 97.7% ± 5.85 of these nestlings survived to ringing on day 11. We investigated whether helpers were associated with high nestling survival by examining survival from day 0 to day 11 in relation to the number of helpers and other factors (Table 3). We used two measures of helping: the number of helpers on day 10 of the nestling period (i.e., close to the time of ringing), and the number of helpers before day 5. The latter was included because any effect of helpers on nestling survival may be apparent only if they were present from early in the nestling period. However, there was no significant effect of the number of helpers on nestling survival, and nor was there any significant effect of group identity, breeder age, or year (Table 3). Absolute lay date was also nonsignificant, but broods that were initiated relatively late (with respect to the median lay date) tended to have lower nestling survival rates ($p = .054$, Table 3). The only significant factor was study site ($p = .003$, Table 3), but the biological significance of the difference among sites is

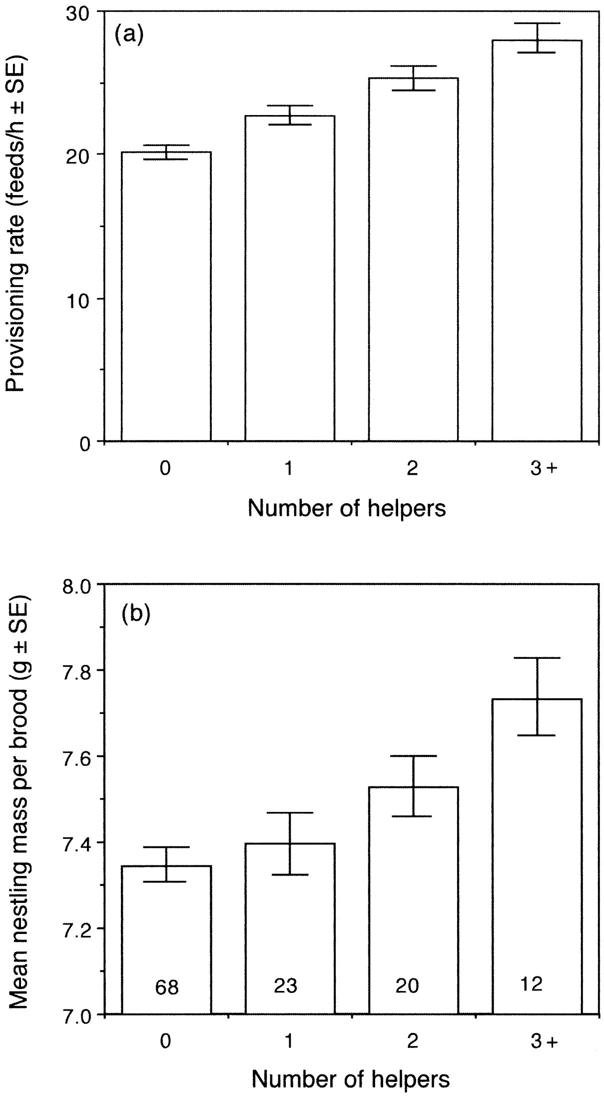

Figure 3
Model estimates of: (a) total provisioning rate (± SE) in relation to the number of helpers attending a nest and (b) mean weight (± SE) of nestlings per brood in relation to the number of helpers present at a nest. For other factors having a significant effect on provisioning rate and nestling weight, see Table 1. Provisioning rates were obtained for 156 broods, but sample sizes are not shown because a single nest could have between zero and six helpers. Sample sizes for nestling mass refer to the number of broods at the last observation before weighing; broods with three helpers ($n = 10$), four helpers ($n = 1$), and five helpers ($n = 1$) are pooled.

probably small because site survival estimates differed only marginally: Rivelin Valley, 96.6%; Ecclesall Wood, 99.1%; Melton Wood, 99.5%. Again, maternal and paternal identities were nonsignificant (Table 3).

Long-term effect of helpers on productivity

The proportion of 93 fledged broods that recruited within our study areas varied between 0% and 80% (mean = 19.5% ± 21.0). Just two factors had a significant effect on recruitment: the number of helpers ($p = .003$) and absolute lay date ($p = .004$; Table 4). The probability of recruitment increased with the number of helpers: fledglings that had been fed by a pair plus three or more helpers had a 41% chance of recruiting compared to just 12% for pair-fed fledglings (Figure 5). Second, recruitment decreased seasonally, a pattern that was common to all three study sites (Figure 6). These results were not significantly influenced by the age or identity of either parent, nor by group identity (Table 4).

Table 2
Factors affecting the probability of long-tailed tit brood survival in a series of 2-day periods from hatching to fledging

Factor	Wald statistic (χ^2)	df	p
Year	0.88	6	.56
Group	2.93	5	.71
Relative lay date	1.52	1	.22
Absolute lay date	0.60	1	.61
Female age	1.91	1	.17
Male age	0.06	1	.80
Nestling age	8.01	1	.005
(Nestling age)^2	4.82	1	.028
Number of helpers	0.33	1	.56
Arrival of helper	0.13	1	.72

The analysis used IRREML with binomial error structure and logit link function, with survival (0 or 1) in a series of 2-day intervals (0–2, 2–4 . . . 14–16) from hatching to fledging as the response and 1 as the binomial denominator. Nest identity was retained as a random factor ($p < .05$), but both maternal and paternal identity were dropped because both had a negative component of variance.

Indirect fitness benefits of helping

The marginal effect of helpers on reproductive success described above can be used to estimate the magnitude of the indirect fitness benefit derived by helpers through increased productivity. The effect of helpers on productivity of the current brood was calculated from the perspective of breeders and from the perspective of helpers using the average brood size of 8.9 fledglings, recruitment rates from Figure 5, and the following coefficients of relatedness. For parents, long-tailed tits have a low rate of extrapair paternity (2.4–6.9%) and negligible intraspecific brood parasitism (Hatchwell et al., 2002), so the coefficient of relatedness for breeders to their brood was estimated to be 0.48. For helpers, using relatedness values from Russell and Hatchwell (2001), we calculated the average coefficient of relatedness between a helper and a nestling in the brood it helps to be 0.22 (helpers typically feed at a nest belonging to an unrelated female and a first-order male relative, usually a sibling). Table 5 shows that from a breeder's perspective, each helper has a positive effect on productivity of the current brood. From a helper's perspective, the marginal effect per helper on productivity is virtually the same regardless of whether they are caring as the sole helper at a nest or caring in a larger workforce of two, three, or more helpers. It is interesting to note that, on average, helpers achieve just 25–30% of the productivity that would be achieved from breeding independently without helpers (0.13–0.15 genetic equivalents versus 0.51 genetic equivalents; Table 5).

DISCUSSION

In the cooperative breeding system of long-tailed tits, the great majority of helpers were birds that failed in their own breeding attempt and then redirected their care to another pair's brood. Helpers had a significant long-term, but not short-term, effect on productivity. Helpers significantly in-

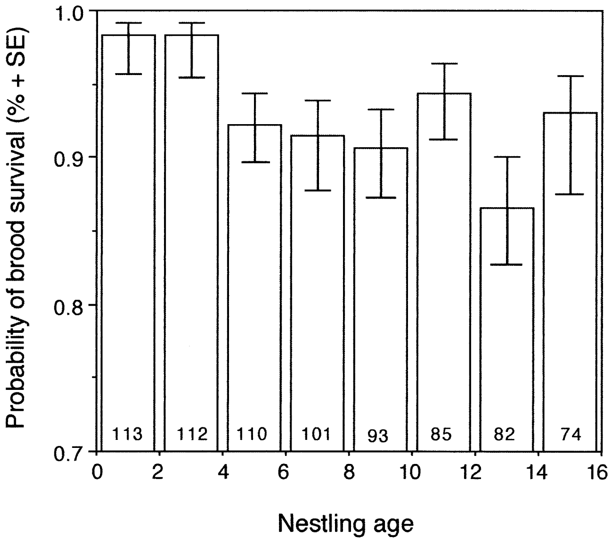

Figure 4
Model estimates of survival (% ±SE) for long-tailed tit broods in the Rivelin Valley population in relation to nestling age (2-day blocks of the nestling period). Sample sizes are shown for the number of nests entering each 2-day age period. See Table 2 for statistics.

Table 3
Factors affecting long-tailed tit nestling survival from hatching (day 0) to day 11 of the nestling period

Factor	*F*	df	*p*
Site	5.84	2,129	.003
Year	1.63	6,123	.13
Group	1.15	14,115	.31
Relative lay date	3.71	1,128	.054
Absolute lay date	1.40	1,128	.24
Female age	0.09	1,86	.76
Male age	0.18	1,86	.67
Number of helpers (day 5)	0.29	1,128	.59
Number of helpers (day 10)	0.88	1,128	.35

Initial analysis used IRREML with binomial error structure and logit link function in which the number of survivors was the response term and number of hatched nestlings was the binomial denominator. However, maternal and paternal identities, fitted as random terms, had a negative component of variance, so a GLM with the same error structure and link function was used. Significant terms explain 10% of total model variance.

creased the rate of nestling provisioning, resulting in heavier broods, but there was no association between helper number and either brood or nestling survival. In contrast, the probability of fledglings recruiting as breeders in the following year increased significantly and progressively as the number of helpers increased.

The switch in reproductive strategy from independent breeding to helping, a switch that may be repeated in successive seasons, is uncommon among cooperative breeders, although some other species do show similar behavior: white-fronted bee-eater *Merops bullockoides* (Emlen, 1990), European bee-eater *Merops apiaster* (Lessells, 1990), rifleman *Acanthisitta chloris* (Sherley, 1990), Galapagos mockingbird *Nesomimus parvulus* (Curry and Grant, 1990), western bluebird *Sialia mexicana* (Dickinson et al., 1996), and the confamilial bushtit *Psaltriparus minimus* (Sloane, 1996). It is particularly rare for redirected care to be apparently the sole source of helpers. The ultimate basis for this switch in reproductive strategy from breeding to helping is that late in the breeding season the average fitness pay-off from kin-directed helping exceeds that of independent breeding. Helpers appear to switch behavior accordingly as a way of making the best of a bad job at the end of a temporally constrained breeding season (MacColl and Hatchwell, 2002).

The proximate basis for the seasonal decline in breeding success is currently unknown, but one proximate influence on the decison of whether to renest is the stage of breeding at the time of nest failure: birds that failed during the nestling phase were significantly less likely to renest than those pairs failing on the same day but at an earlier stage of breeding. Physiological changes that breeders of both sexes experience at the time of hatching may be responsible for this effect (Ketterson and Nolan, 1994). Alternatively, breeders may incur relatively large costs during the nestling period and so have a lower probability of renesting than birds failing at an earlier stage.

The social organization of long-tailed tits contrasts strongly with typical cooperative species (Brown, 1987). In most cooperative breeders, individuals or pairs occupy the same territory for successive breeding attempts, living with retained offspring that act as helpers. In such systems, differences in habitat or pair quality may produce a potentially spurious correlation between productivity and helper number because successful pairs will tend to have helpers whether helpers actually enhance productivity or not (Emlen, 1991). Our analyses are unlikely to be confounded by such effects for several reasons. First, nonbreeding groups are fluid, so there is extensive mixing of families and dispersal of unrelated individuals among groups (Hatchwell et al., 2001a; Russell, 1999). Second, there is a high divorce rate between breeding seasons, particularly for pairs that have bred successfully (Hatchwell et al., 2000). Third, neither nonbreeding flocks nor breeding pairs defend exclusive territories; instead, they occupy large, nonexclusive ranges with considerable overlap between adjacent ranges (Hatchwell et al., 2001a). Furthermore, in long-tailed tits, the identity of potential helpers and the potential recipients of their care is determined primarily by predators, rather than by prior success. Consistent with this contention that results were unlikely to be confounded by habitat or individual quality, there was no indication that individual identity or group area had any influence on brood survival, nestling survival, or recruitment, and there was no evidence that breeder age was a significant factor affecting productivity. Again, this is not surprising because individuals are able to switch back and forth between breeding and helping throughout their lives. Therefore, although our study was observational, our results indicate that the relationship between helpers and recruitment is a causal one.

Long-tailed tit helpers have a positive effect on provisioning rates, although previous studies have shown that parents reduce their own provisioning rate when assisted by a single helper, so the care of helpers is not simply additive (Hatchwell, 1999; Hatchwell and Russell, 1996). Nevertheless, in this analysis helpers appeared to cause an almost linear increase in total provisioning effort. There was little opportunity for this increase in provisioning to reduce offspring mortality prefledging because nestling survival is high even among pair-fed broods. However, helped nestlings were heavier, and recruitment is positively related to nestling mass in several bird species (e.g., Garnett, 1981; Magrath, 1991), including long-tailed tits (MacColl and Hatchwell 2002), the latter result being independent of helper number. Therefore, it is likely that the effect of helpers on productivity operates through the improved condition of the helped brood.

Alternatively, the positive relationship between helpers and

Table 4

Factors affecting long-tailed tit recruitment (local survival from fledging to the start of the following breeding season)

Factor	*F*	df	*p*
Site	1.54	2,84	.22
Year	1.05	5,81	.40
Group	0.80	16,70	.68
Absolute lay date	9.00	1,86	.004
Female age	0.00	1,66	.99
Male age	0.00	1,61	.95
Brood size	0.42	1,83	.52
Number of helpers	9.56	1,86	.003

Initial analysis used IRREML with binomial error structure and logit link function in which the number of recruits was the response term and number of fledglings was the binomial denominator. However, both maternal and paternal identity, fitted as random terms, had a negative component of variance, so a GLM with the same error structure and link function was used. Absolute and relative lay date were not used together; absolute lay date was preferred because it was much more significant (relative lay date: $p = .07$). Significant terms explain 7% of total model variance.

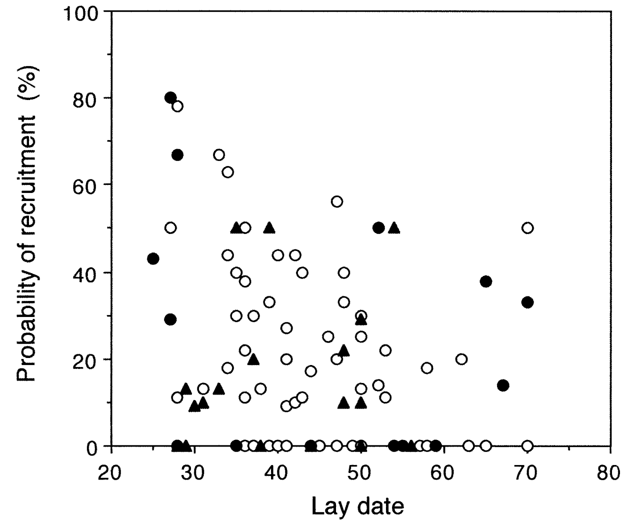

Figure 6
Relationship between the probability of recruitment ($n = 93$ broods) and laying date (days after March 1) for long-tailed tits at Rivelin Valley (open circles, $n = 62$), Melton Wood (closed circles, $n = 14$), and Ecclesall Wood (closed triangles, $n = 19$) study sites. See Table 4 for statistics.

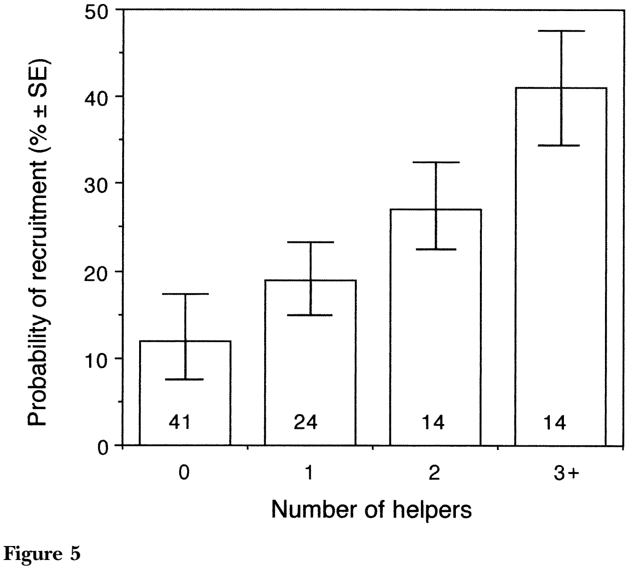

Figure 5
Model estimates of recruitment probability for fledged broods of long-tailed tits in relation to the number of helpers at the nest. Sample sizes show the number of broods; broods with three helpers ($n = 8$), four helpers ($n = 2$), five helpers ($n = 2$), and six helpers ($n = 2$) are pooled. See Table 4 for statistics.

recruitment may be explained by group augmentation (Kokko et al., 2001). If every additional helper increases the size of the family by one, individual survival could increase through dilution (Hamilton, 1971), enhanced vigilance or food-finding ability (e.g., Kenward, 1978; Ward and Zahavi 1973), or thermoregulatory benefits in communal roosts (DuPlessis and Williams, 1994). However, the labile composition of nonbreeding flocks means that there is no simple relationship between the number of helpers and the size of the nonbreeding flock (Hatchwell et al., 2001a). Therefore, the effect of helpers is most likely to operate through the improved condition of nestlings at fledging (MacColl and Hatchwell, 2002). We have no quantitative data on postfledging care by helpers, but they continue to feed the brood after fledging, so there may be some additional postfledging effect of helpers on condition.

Another possible consequence of a higher provisioning rate is that the additional activity of helpers may attract predators and result in lower brood survival. We found no evidence for this, but older broods were more likely to be predated. The absence of a helper effect on brood survival suggests that this age effect was not a consequence of the higher provisioning rate of older nestlings, but it may be due to the increasing volume of begging calls alerting predators to the presence of a nest (Harper, 1986). There was no evidence that helpers have any antipredator function, as has been noted in some cooperative species (e.g., Austad and Rabenold, 1985; Mumme, 1992).

The positive effect of helpers on productivity was apparent only in offspring recruitment rate and not in brood size or nestling starvation. Such long-term, but not short-term, effects of helpers appear to be rare among cooperative breeders (Stacey and Koenig, 1990). In practice, it may be very difficult to separate long-term effects of additional investment by helpers from the effects of group augmentation (Kokko et al., 2001), but it is clear that a positive effect of helpers on productivity cannot be ruled out unless the possibility of long-term effects has been considered.

Finally, we consider the indirect fitness benefit of helping. Long-tailed tit helpers exhibit kin preference when they become helpers (Russell and Hatchwell, 2001). Therefore, their positive effect on productivity means that, on average, they gain indirect fitness benefits through their cooperation (Table 5). From a breeder's perspective, there is a roughly linear increase in recruitment as the number of helpers increases (Figure 5), suggesting that breeders should recruit as many helpers as possible. From a helper's perspective, the marginal effect per helper is similar regardless of the number of helpers already at a nest, suggesting that potential helpers should decide where to help on the basis of their relatedness to available broods rather than on the basis of the number of providers already at those nests. The apparently linear effect of helpers must level off at some point, but it is unusual to have more than three or four helpers at a single nest in our populations, so in practice this situation may be encountered

Table 5

Productivity of long-tailed tit breeders and helpers in relation to the number of helpers-at-the-nest

	Number of helpers at the nest			
	0	1	2	>2[a]
Probability of recruitment/ brood (%)[b]	12	19	27	41
Number of recruits/brood[c]	1.07	1.69	2.40	3.65
Productivity (genetic equivalents)[d]				
Breeders	0.51	0.81	1.15	1.75
Helpers	0.24	0.37	0.53	0.80
Marginal effect of helpers (genetic equivalents)				
Breeders[e]	—	+0.30	+0.64	+1.24
Per helper[f]	—	+0.13	+0.15	+0.15

[a] Mean number of helpers (*n*) at the 14 nests with more than 2 helpers was 3.86 ± 1.17.

[b] Recruitment rates are taken from Figure 5.

[c] Brood size at fledging is assumed to be 8.9.

[d] Coefficients of relatedness are breeders to fledglings, 0.48; helper to fledglings, 0.22.

[e] Calculated as (productivity with *n* helpers) − (productivity with no helpers).

[f] Calculated as [(productivity with *n* helpers) − (productivity with no helpers)]/*n*.

rarely. It is interesting to note that helpers achieve, at best, only 30% of the productivity achieved from breeding independently without helpers, a result consistent with the view that helping is a best-of-a-bad-job strategy. MacColl and Hatchwell (2002) have shown that this reproductive tactic is adopted only when the expected fitness pay-off from independent reproduction drops even lower than that from helping at the end of a temporally constrained season.

Hatchwell and Russell (1996) showed experimentally that breeders provision chicks less frequently when helped, so helpers may also gain indirect fitness benefits by reducing the reproductive costs of breeders (Crick, 1992). However, we have found no evidence that helped breeders have a higher survival rate than breeders without helpers, nor have we found that long-tailed tit helpers accrue any net direct fitness benefit from helping (McGowan et al., 2003). Therefore, we conclude that the increase in helpers' indirect component of inclusive fitness described here is the primary reason for the evolution and/or maintenance of helping in this species.

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