

The effect of helping behaviour on the survival of juvenile and adult long-tailed tits *Aegithalos caudatus*

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Summary

1. In the cooperative breeding system of the long-tailed tit *Aegithalos caudatus* failed breeders may become helpers at the nest of another pair to whom they are usually related. The aim of this study was to determine the effect of helping behaviour on the survival of helpers and the recipients of their help.
2. We used capture–mark–recapture data and the MARK program to analyse survival of 482 birds ringed as fledglings and 155 birds ringed as adults.
3. Juvenile males had a higher survival probability than juvenile females across all years whilst their subsequent adult survival was constant. Within sex, the survival probability of juveniles that fledged from nests with helpers was higher than those that did not receive help as nestlings.
4. Failed breeders that became helpers had a higher survival probability (56%) than those failed breeders that did not become helpers (46%). Successful breeders had a survival probability of 56% regardless of whether they received help or not.
5. Failed breeders that became helpers had a lower probability of successfully breeding in a subsequent year (27%) when compared to those failed breeders that did not become helpers (38%).
6. We conclude that helpers gain kin-selected fitness benefits through the increased survival of related offspring but not through the increased survival of related breeders. Furthermore, helpers gain direct fitness benefits through increased personal survival, but at a cost of reduced probability of successful future personal reproduction.

Key-words: *Aegithalos caudatus*, cooperative breeding, helpers, inclusive fitness, kin selection, long-tailed tit.

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Introduction

In cooperatively breeding species some individuals forgo personal reproduction and instead help to rear offspring which are not their own (Stacey & Koenig 1990; Solomon & French 1997). In most avian cooperative breeders helpers are normally offspring which have remained on their natal breeding territory, so helping is seen as the outcome of a two-step process: the decision to delay dispersal and the decision to help feed young in subsequent broods (Emlen 1982). The reasons for delayed dispersal usually focus on ecological or demographic constraints and have been widely

discussed elsewhere (Emlen 1982; Brown 1987; Stacey & Ligon 1987, 1991; Arnold & Owens 1998; Hatchwell & Komdeur 2000). The reason why helpers care for non-descendant offspring rather than breed independently, or simply do nothing, has also been discussed extensively but remains a contentious issue in evolutionary biology (Cockburn 1998).

In avian cooperative breeding systems, the assistance provided by helpers is usually in the form of provisioning offspring and such behaviour should only be carried out when the fitness gains outweigh the costs of providing care (Clutton-Brock 1991). In many species, helpers assist close relatives and gain indirect (i.e. kin-selected) fitness benefits by increasing the productivity of those relatives (e.g. Emlen & Wrege 1991). Moreover, experimental studies have shown a decrease in reproductive success after helpers were removed (Brown

et al. 1982; Mumme 1992; Komdeur 1994, 1996; but see Leonard, Horn & Eden 1989). Helpers may also gain deferred kin-selected benefits by reducing the costs of reproduction for breeders (Crick 1992), thereby allowing relatives more breeding attempts during the course of a breeding season (Brown & Brown 1981; Russell & Rowley 1988) or increasing their survival to the following season (Koenig & Mumme 1987; Curry 1988). As a result of such strong evidence, kin selection has been widely accepted as the ultimate explanation for cooperative behaviour (Emlen 1991, 1997). However, helpers are not always related to the helped brood (Dunn, Cockburn & Mulder 1995) and they do not always increase productivity (Legge 2000). Therefore, it has recently been argued that the kin-selected benefits of helping behaviour have been over-emphasized as a selective force and that the direct component of inclusive fitness may have a more influential role in the evolution of cooperative behaviour than previously assumed (Cockburn 1998; Clutton-Brock 2002).

Helpers may accrue the direct fitness benefit of direct access to parentage both within and outside the group (Mulder *et al.* 1994; Richardson, Burke & Komdeur 2002) and/or increased access to mates or territories in the future (Woolfenden & Fitzpatrick 1984; Reyer 1990). An additional direct benefit is the experience of parental care so that helpers become better parents (Heinsohn 1991; Komdeur 1996; but see Emlen & Wrege 1989; Khan & Walters 1997). Helping behaviour has also been viewed as 'payment of rent' for access to the benefits of group living (Gaston 1978; Cockburn 1998). For example, the energetic benefits from group huddling have been reported as essential for the survival of acorn woodpeckers *Melanerpes formicivorus* Swainson (Duplessis, Weathers & Koenig 1994) and green woodhoopoes *Phoeniculus purpureus* Miller (Duplessis & Williams 1994).

In this paper, we investigate survival rates of juveniles and adults in the unusual cooperative breeding system of the long-tailed tit *Aegithalos caudatus*, Linnaeus. In this species, some breeders that fail in their own breeding attempt become helpers at the nest of another pair, to whom they are usually closely related (Russell & Hatchwell 2001). It has previously been shown that helpers have no effect on fledging success, a short-term measure of productivity, but that they do have a positive effect on recruitment of juveniles as breeders in the following season (Hatchwell *et al.* in press). Here, we use more robust capture-mark-recapture analyses of observational data to examine: (i) the effect of helpers on the survival of the assisted young through their first year and in subsequent years; (ii) the effect of helpers on the survival of assisted breeders; and (iii) whether failed breeders that become helpers have higher survival than failed breeders that do not help. We also examine whether helping is related to the probability of successful reproduction in the future.

Materials and methods

STUDY SPECIES

During the non-breeding season (July–February), long-tailed tits form flocks comprising relatives and non-relatives (Russell 1999; Hatchwell *et al.* 2001a), which roost communally (Riehm 1970; Gaston 1973). At the start of the breeding season, flocks break up and all birds attempt to breed independently in monogamous pairs. However nest failure is high due to predation (Hatchwell *et al.* 1999) and if failure occurs after early May then instead of re-nesting failed breeders may become helpers at a nest belonging to another pair (Glen & Perrins 1988; MacColl & Hatchwell 2002). In our study population approximately 50% of broods have one or more helpers. These failed breeders that redirect their care usually choose to help at the nest of a close relative (Russell & Hatchwell 2001). All helpers are probably failed breeders, but not all failed breeders become helpers; these alternatives of either helping or not helping occur within the same population and even within the same non-breeding flocks (Russell & Hatchwell 2001). Helpers increase nestling mass (Hatchwell *et al.* in press) and they allow assisted breeders to reduce their provisioning rate (Hatchwell & Russell 1996).

STUDY POPULATION AND FIELD OBSERVATIONS

A colour-ringed population of 18–53 pairs of long-tailed tits was studied from 1994 to 2000 in the Rivelin Valley (53°23' N 1°34' W), Sheffield, UK. The study site is approximately 3 km² and is comprised of areas of mature oak *Quercus robur* L. and beech *Fagus sylvatica* L. woodland, birch *Betula* and hawthorn *Crataegus* scrub, farmland and gardens. Each year, fledglings (56 in 1994, 82 in 1995, 79 in 1996, 56 in 1997, 105 in 1998, and 150 in 1999, total = 528) and most immigrant breeders (39 in 1994, 19 in 1995, 26 in 1996, 27 in 1997, 20 in 1998 and 24 in 1999, total = 155) were ringed with a numbered metal ring and a unique combination of colour rings. Survival of ringed birds was determined by observation during thorough searches of the study site in subsequent years. Blood samples were taken from most individuals (under Home Office licence) and birds were sexed using molecular techniques (Griffiths *et al.* 1998). The breeding attempts of all individuals were closely monitored during the breeding season (February–June) in each year. Breeding success was classified as either successful (offspring fledged), or failed (no offspring fledged). In order to determine the identity of carers, the great majority of nests were observed for one hour on alternate days from day 2 of the nestling period until day 16 of the nestling period. Helpers were any individuals, other than the breeding pair, that were observed provisioning nestlings. In this study, birds were considered to be juvenile from the

point of fledging until the start of breeding the following year and thereafter birds were considered to be adults.

SURVIVAL ANALYSES

Survival parameters were estimated via maximum likelihood methods using the program MARK (White & Burnham 1999). This program is based on general capture–mark–recapture (CMR) theories (Cormack 1964; Jolly 1965; Seber 1965; see Lebreton *et al.* 1992 for summary). According to theories of CMR analysis the probability of encountering a previously marked and released individual is a product of the probability of remaining individuals available for recapture (Φ ; survival probability) and the probability of recapture (p ; re-sighting probability). Therefore, birds that emigrate from the study area are treated as having died and so the term ‘survival probability’ should be read to mean the probability of being alive and available for recapture. Birds were considered to have survived if they were observed during the course of the breeding season in year $n + 1$, having been ringed in year n or earlier. The 3-step approach to CMR analysis (see Burnham *et al.* 1987 and Lebreton *et al.* 1992 for detailed descriptions) was employed, which results in the final model selection being based on corrected Akaike Information Criterion (AICc). This considers both the deviance and number of estimated parameters. Ultimately, the model with the lowest AICc value is deemed to be the best fitting model.

Our primary aim was to determine the effect of helping behaviour on the survival of juvenile and adult long-tailed tits. Therefore, we investigated: (i) the effects of sex, year and presence of helpers on the survival of juvenile long-tailed tits and their subsequent survival as adults, and (ii) the effects of sex and breeding/helping status on the survival of adult long-tailed tits. The procedure for each analysis was as follows.

(i) Modelling juvenile survival with the effects of sex, year and presence of helpers

The survival probabilities of all birds ringed as nestlings were modelled for two age classes: (1) juveniles and (2) adults. Data were split by sex (s ; male or female) and also by the presence of helpers (b ; helped or not helped). The sex of 46 fledglings was not known and these were removed from the data set, leaving 482 individuals from 67 broods. The global model $\{\Phi[1(s \times b \times t)1(s \times b \times t)]p(s \times b \times t)\}$ allowed survival probability to vary with year (t) within each of the two age categories and within each combination of sex and presence of helpers. The re-sighting probability was allowed to vary with year within each combination of sex and presence of helpers. There was no age split in the re-sighting probability as all re-sightings were of adult birds. All possible candidate models that could be constructed from the global model were considered but

only the 15 best fitting models are represented in the results.

This type of CMR analysis makes two basic assumptions: first, every marked animal present in the population at time i has the same probability of recapture p ; second, every marked animal in the population immediately after time i has the same probability of surviving to time $(i + 1)$. In order to test these assumptions we performed a goodness-of-fit (GOF) test on our global model using the parametric bootstrapping procedure contained within the program MARK (White & Burnham 1999). Our data did not violate the basic assumptions of the CMR modelling approach (GOF test: $P = 0.30$).

(ii) Modelling adult survival with the effects of sex and breeding status

This analysis was restricted to adult birds with known breeding status and sex, whether they had been first ringed as immigrant adults or as chicks (136 males and 114 females). Individuals that were ringed as chicks were treated as having been encountered for the first time when they were first seen as adults. Birds were classified as falling into one of four breeding status categories: successful breeder with no helpers (N), successful breeder with helpers (A), failed breeder that helped (H) and failed breeder that did not help (F). A multi-strata modelling approach was adopted with these data. In this type of analysis the probability of encountering a marked individual is the product of three probabilities; the probability of remaining available for recapture (Φ ; survival probability), the probability of recapture (p ; recapture probability), and the added probability of changing status (ψ ; change in breeding status). We considered breeding status in four different ways: (i) full breeding status effect ((g) : N, A, H, F), (ii) successful breeder effect ((o) : $N = A, H = F$), (iii) helper effect ((w) : $N = A = H, F$), and (iv) no breeding status effect ($(.)$: $N = A = H = F$). Our global model $\{\Phi(s \times g)p(s \times g)\psi(s \times g)\}$ allowed survival, re-sighting and change of status probability to vary with sex and breeding status. All possible candidate models that could be constructed from the global model were considered but only the top 15 best fitting models are represented in the results. At present there are no GOF tests available for multi-strata models (G.C. White pers. comm.).

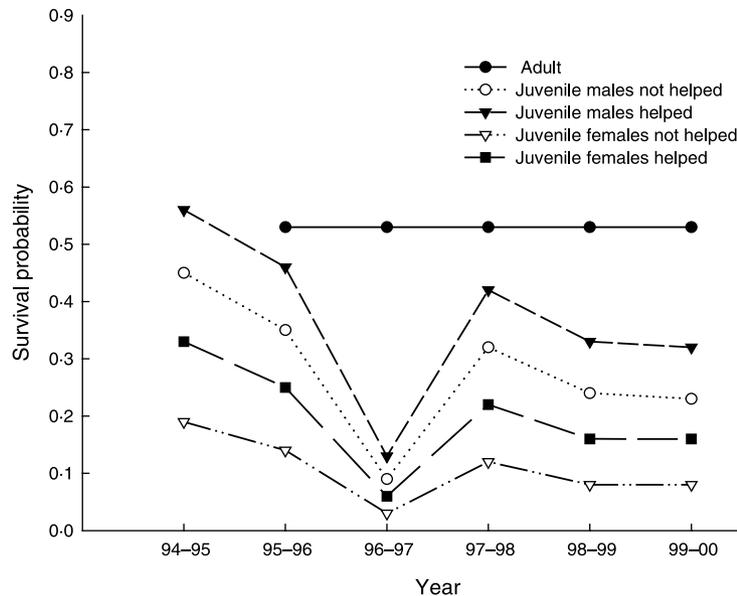
Results

(i) Modelling juvenile survival with the effects of sex, year and presence of helpers

In the final accepted model the survival of juveniles varied with year, with additive effects of sex and brood status and this model was almost twice as good as the next best fitting model in terms of AICc weighting (Model 1 in Table 1). The final accepted model allowed

Table 1. Modelling the survival probability of juvenile long-tailed tits and their subsequent survival as adults in relation to sex, year and presence of helpers. Φ = survival probability, p = re-sighting probability, (s) = sex, (t) = time, (b) = presence of helpers, (.) = constant, and \times = interaction

Model	AICc	Delta AICc	AICc weight	Number of parameters	Deviance
1. $\Phi(1(s + b + t)1(.)p(t))$	677.32	0.00	0.47	16	88.41
2. $\Phi(1(s + b + t)1(b)p(t))$	678.63	1.32	0.24	17	87.62
3. $\Phi(1(s + b + t)1(s)p(t))$	679.26	1.95	0.18	17	88.25
4. $\Phi(1(s + b + t)1(s \times b)p(t))$	682.61	5.30	0.03	19	87.33
5. $\Phi(1(s + b + t)1(t)p(t))$	683.16	5.85	0.02	20	85.74
6. $\Phi(1(s + b + t)1(b + t)p(t))$	683.22	5.91	0.02	21	83.65
7. $\Phi(1(s + b + t)1(s + t)p(t))$	685.28	7.97	0.01	21	85.71
8. $\Phi(1(s + b + t)1(s + b + t)p(t))$	687.08	9.77	0.00	23	83.19
9. $\Phi(1(s + b + t)1(s \times t)p(t))$	687.32	10.01	0.00	25	79.08
10. $\Phi(1(s + b + t)1(b \times t)p(t))$	688.14	10.83	0.00	25	79.89
11. $\Phi(1(s + b + t)1(s \times b \times t)p(t))$	699.96	22.64	0.00	35	69.48
12. $\Phi(1(s + t)1(s \times b \times t)p(t))$	701.83	24.51	0.00	33	75.87
13. $\Phi(1(b \times t)1(s \times b \times t)p(t))$	706.81	29.50	0.00	37	71.80
14. $\Phi(1(s \times b)1(s \times b \times t)p(t))$	708.12	30.81	0.00	30	88.65
15. $\Phi(1(s \times t)1(s \times b \times t)p(t))$	708.40	31.08	0.00	37	73.38

**Fig. 1.** The effects of sex, year and presence of helpers on the survival probability of juvenile long-tailed tits and their subsequent survival as adults (see Table 1 for statistics). All values shown are best fitting model parameter values.

parameter estimates for re-sighting and survival to be calculated. The probability of re-sighting an individual in the first re-sighting year (1995) was 80% and this rose to approximately 100% by 1997 and was maintained at this level for all subsequent years. This indicates that the probability of seeing a bird that was alive and present in the study area was very high.

Juvenile survival was extremely variable across years. Juvenile males had a higher survival probability than juvenile females, whilst juveniles that were raised by parents and helpers survived better than those that were raised by parents alone (Fig. 1). There were particularly low survival probabilities in 1996–97. In contrast to the results for survival through the first year, there were no effects of sex or helper presence on the subsequent survival of these juveniles once they

became adults (Fig. 1). Furthermore, subsequent adult survival probability was constant across all years (Fig. 1).

(ii) Modelling adult survival with the effects of sex and breeding status

In the final accepted model the survival of adult long-tailed tits varied with breeding status but not with sex (Model 1 in Table 2); this was 1.6 times better than the next most parsimonious model, in terms of AICc weighting. Failed breeders which became helpers had the same survival probability as successful breeders (56%), whilst those birds which failed to breed successfully and did not become helpers had a 46% chance of survival (Fig. 2). However, there was no difference in

Table 2. Modelling the survival probability and change in breeding status probability of adult long-tailed tits in relation to sex and breeding status. Φ = survival probability, p = re-sighting probability, ψ = change in breeding status probability, (s) = sex, (g) = full breeding status effect: successful breeder not helped (N), successful breeder helped (A), Helper (H), Failed breeder (F), (w) = worker effect: N = A = H, F, (o) = breeder effect: F = H, N = A (.) = no breeding status effect: N = A = H = F, and \times = interaction

Model	AICc	Delta AICc	AICc weight	Number of parameters	Deviance
1. $\Phi(w)p(s)\psi(g)$	997.90	0.00	0.32	16	502.53
2. $\Phi(.)p(s)\psi(g)$	998.80	0.90	0.20	15	505.62
3. $\Phi(o)p(s)\psi(g)$	999.47	1.57	0.14	16	504.10
4. $\Phi(s \times w)p(s)\psi(g)$	999.66	1.76	0.13	18	499.86
5. $\Phi(s)p(s)\psi(g)$	1000.82	2.92	0.07	16	505.45
6. $\Phi(g)p(s)\psi(g)$	1002.31	4.41	0.03	18	502.52
7. $\Phi(s \times o)p(s)\psi(g)$	1003.08	5.18	0.02	18	503.29
8. $\Phi(w)p(s)\psi(s \times g)$	1003.52	5.63	0.02	25	487.83
9. $\Phi(.)p(s)\psi(s \times g)$	1004.41	6.51	0.01	24	491.02
10. $\Phi(s \times g)p(s)\psi(g)$	1004.64	6.74	0.01	22	495.84
11. $\Phi(o)p(s)\psi(s \times g)$	1005.18	7.28	0.01	25	489.49
12. $\Phi(s \times w)p(s)\psi(s \times g)$	1005.63	7.74	0.01	27	485.27
13. $\Phi(s)p(s)\psi(s \times g)$	1006.55	8.65	0.00	25	490.85
14. $\Phi(g)p(s)\psi(s \times g)$	1008.18	10.28	0.00	27	487.81
15. $\Phi(s \times o)p(s)\psi(s \times g)$	1009.05	11.15	0.00	27	488.68

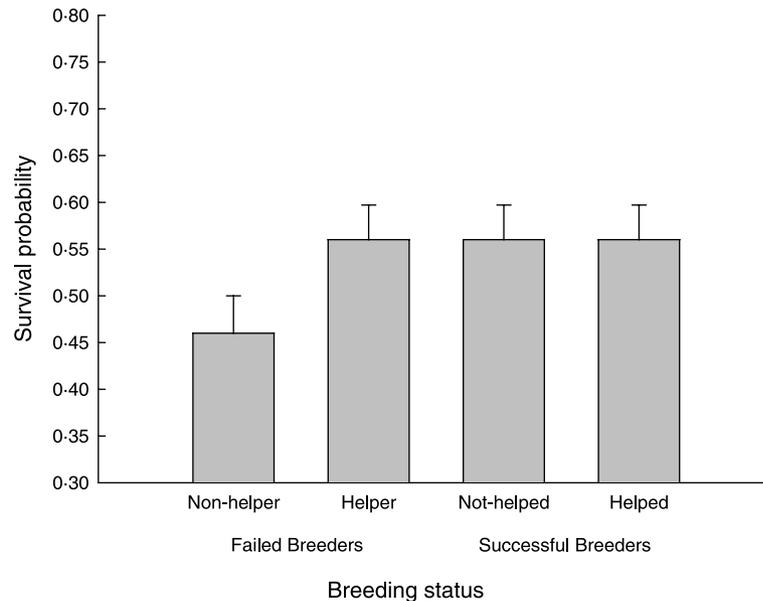


Fig. 2. The effect of breeding and helping status on the survival probability (\pm SE) of adult long-tailed tits (see Table 2 for statistics). All values shown are best fitting model parameter values.

the survival of successful breeders according to whether they had helpers or not (Fig. 2).

The estimates generated by the final accepted model also enabled us to examine whether the probability of an individual breeding successfully in a subsequent year (year $n + 1$) depended upon their breeding status in year n . Failed breeders that became helpers had a 27% chance of breeding successfully in the following year, while those failed breeders which did not become helpers had a 38% chance of doing so (Fig. 3). Successful breeders had a 60% chance of breeding successfully again in the following year irrespective of whether they were helped or not (Fig. 3). These estimates of the

probability of successful reproduction are independent of the probability of survival.

Discussion

In the cooperative breeding system of long-tailed tits, capture–mark–recapture analysis showed that juvenile males had higher survival than juvenile females and that helpers appeared to have a positive effect on juvenile survival. Neither of these effects persisted beyond the first year after fledging. Among adults, the survival probability of successful breeders with helpers did not differ from that of successful breeders without helpers,

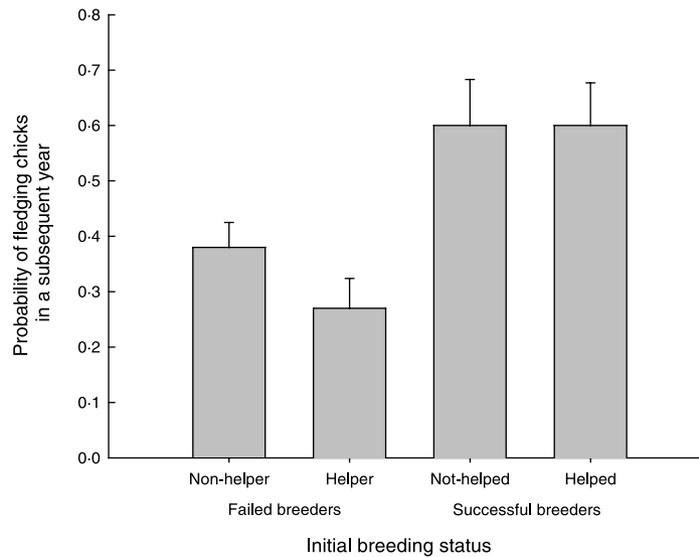


Fig. 3. The effect of current breeding status on the probability of successfully breeding in a subsequent year (\pm SE). All values shown are best fitting model parameter values.

but failed breeders that helped were more likely to survive than failed breeders that did not help. However, failed breeders that did not help were more likely to breed successfully in the subsequent year than failed breeders that did help.

Our analyses were conducted on observational data, so we are unable to demonstrate conclusively the causation of the effects described above. However, various factors suggest that these results are not seriously confounded by the effects of individual or habitat quality. Firstly, long-tailed tits are not territorial and their ranges are large relative to habitat type within our study site (Hatchwell *et al.* 1999, 2001a). In addition, nest location did not significantly affect provisioning rates or reproductive success (Hatchwell *et al.* in press). Secondly, no individuals or pairs were over-represented in our sample because of the high annual mortality of adults (44%) coupled with the high divorce rate of successful pairs between breeding seasons (Hatchwell *et al.* 2000). Finally, the identities of potential helpers and the recipients of help depend on which nests are located and destroyed by predators. There is inevitably a large stochastic element to such events and breeder identity was not retained as a factor in multivariate analyses of productivity (Hatchwell *et al.* in press).

Age was not included in analyses because our data were too sparse when broken down into age categories. Nonetheless, we do not believe that age influenced our results because long-tailed tits are relatively short-lived birds, the average age of our population being around 2 years old. Furthermore, age and breeding status are not correlated because helping behaviour is predominantly expressed within rather than across generations (Russell & Hatchwell 2001), and there was no significant effect of breeder age on productivity (Hatchwell *et al.* in press).

The sex difference in juvenile survival was consistent across years, but should be interpreted with caution because the analytical technique considers individuals that have permanently emigrated as having died. In reality we would expect the survival of males and females to be roughly equal because the adult sex ratio is 1 : 1 (Russell 1999). This is certainly the case for adults because there was no effect of sex on survival of birds from their first year onwards. The observed sex difference in survival must result from first year female long-tailed tits dispersing prior to breeding whilst males are philopatric (Gaston 1973; Glen & Perrins 1988; Hatchwell *et al.* 2002). This difference in dispersal also explains why the majority of helpers are male (Russell & Hatchwell 2001), assuming that kin selection is important in the evolution of the long-tailed tit's cooperative system. It is interesting to note that in an isolated population where female and male juvenile survival was equal, helpers were as likely to be female as they were male (Russell 2001).

When taking sex into account, juveniles from helped broods had higher survival than juveniles fed by parents alone. This result is consistent with previous studies of long-tailed tits (Glen & Perrins 1988; Hatchwell *et al.* in press), but in this paper we have used a more robust technique for the estimation of survival. Furthermore, we show that this increase in survival is effective only through the first winter because in the best fitting model the survival probabilities of all individuals are constant after they have surpassed 1 year of age (Fig. 1). Just as the apparent sex difference in juvenile survival can be attributed to differential dispersal, it is possible that the difference in survival rate between helped and non-helped juveniles is also a consequence of differential dispersal. For example, juvenile Seychelles warblers *Acrocephalus sechellensis* Oustalet on high quality territories with helpers are less

likely to disperse than those birds on low quality territories without helpers (Komdeur 1992), although this is thought to be predominantly a territory effect. We have no evidence to support or reject this possibility, but the labile non-breeding social organization of long-tailed tits with large overlapping ranges and extensive dispersal between flocks (Hatchwell *et al.* 2001a), means that it is difficult to envisage a mechanism that might cause such differential dispersal. Therefore, we conclude that because helpers usually help at the nest of a close relative (Russell & Hatchwell 2001), they gain kin-selected benefits through the increased production of non-descendant kin.

The survival probabilities generated by the most parsimonious model in our analysis of adult survival indicated that there was no significant association between the helpers and the survival of the assisted breeders. This result was unexpected because observations and experiments show that long-tailed tit breeders reduce their provisioning effort when helped (Hatchwell & Russell 1996; Hatchwell 1999), and reduced reproductive costs would be expected to result in increased survival (Crick 1992). Among cooperative breeders, parental investment strategies vary in relation to workforce. At one extreme parents may allow the care of helpers to be purely additive (i.e. maintaining a high rate of personal care), the additional care by helpers benefiting their offspring. On the other hand, they may reduce their own effort as the care by helpers increases so that the brood receives the same amount of food, while parents reduce their reproductive costs (Hatchwell 1999). In long-tailed tits, the care of helpers increases the total provisioning rate as well as allowing parents to provision less frequently (Hatchwell & Russell 1996; Hatchwell 1999; MacColl & Hatchwell *in press*). Given the apparent effect of increased food provision on juvenile survival, it is counter-intuitive that helped parents should reduce their own effort, without any apparent fitness consequence. It could be that any survival benefit from a reduced provisioning effort is so small that we were unable to detect it; a similar argument was proposed for stripe-backed wrens *Campylorhynchus nuchalis* Cabanis (Rabenold 1990) and white-browed scrub wrens *Sericornis frontalis* Vigors & Horsfield (Magrath & Yezerinac 1997). Alternatively, breeders that are helped may be of poorer quality and the effect of helpers simply brings their survival up to that of unhelped birds. However, this seems unlikely because failed breeders choose to redirect their care towards close relatives (Russell & Hatchwell 2001) and there is no obvious reason why these should be poorer quality individuals. Furthermore, in this species the identity of potential helpers and potential recipients of help is determined primarily by predators and thus it is unlikely that all helped breeders would be of poor quality.

Our analysis of adult survival rates showed that failed breeders that became helpers were more likely to survive than failed breeders that did not help, indicating

that helpers gain the direct fitness benefit of increased personal survival. We can be confident that this difference in survival is not an artefact of further dispersal by adult birds, as re-sighting probabilities are virtually 100%. The underlying mechanism for this difference in survival is currently under investigation. Survival differences may arise if helpers join relatively large non-breeding flocks over the winter, with helping being viewed as a 'payment of rent' for the benefits of group-living (Gaston 1978; Mulder & Langmore 1993; Kokko, Johnstone & Wright 2002). One benefit that may increase survival is decreased energy expenditure due to communal roosting, as suggested by Glen & Perrins (1988). This has been shown to be important for acorn woodpeckers (Duplessis *et al.* 1994) and green woodhoopoes (Duplessis & Williams 1994). For this to be the case, failed breeders that help must gain access to better roosting positions than failed breeders that do not help. Preliminary data suggests that certain individuals within long-tailed flocks do have access to preferred, central roosting position (A. McGowan unpublished data), but it is not known whether this is influenced by helping decisions.

If helpers have higher survival than non-helpers, then why doesn't every individual help when the opportunity arises? There are several possible explanations. First, our results suggest that there may be a cost of helping because helpers were less likely to breed successfully in a subsequent year (27%) than non-helpers (38%). The process through which this cost manifests itself is unknown. Long-tailed tit helpers may be in relatively poorer body condition at the end of the breeding season, as in pied kingfishers *Ceryle rudis* L. (Reyer 1984) and white-winged choughs *Corcorax melanorhamphos* Vieillot (Heinsohn 1991; Heinsohn & Cockburn 1994). However, if helpers were in poorer body condition at the end of the breeding season why should they subsequently have higher survival? A second possibility is that only high quality individuals help so that differences in survival are attributable to individual quality rather than helping *per se*. But, as explained above, we do not think that body condition or individual quality are the main determinants of whether a failed breeder becomes a helper, indeed current evidence suggests that the main determinant is the availability of close kin with an active nest (Russell & Hatchwell 2001).

Finally, it is possible that all failed breeders would help if they could, but that breeders also play some role in deciding whether a failed breeder becomes a helper at their nest. In a few cases, breeders have been observed preventing other long-tailed tits from feeding their offspring (B.J. Hatchwell unpublished data) and breeders react aggressively to the calls of non-kin close to their nest during the nestling period (Hatchwell *et al.* 2001b). Therefore, breeders may exercise some control over which individuals become helpers. This argument presupposes a cost to breeders of having unrelated helpers that outweighs the benefit of

increased productivity; at present there is no evidence for such a cost.

In conclusion, long-tailed tit helpers appear to gain kin-selected benefits by increasing the survival of related offspring whilst simultaneously gaining the direct benefits of increased survival (56%) relative to non-helpers (46%). However, a helper's prospect of successful reproduction in the future (26%) is lower than that of a non-helper (38%). The net effect of these probabilities is that failed breeders that become helpers have a 15% chance ($56\% \times 27\%$) of surviving and successfully rearing chicks the following year, whilst failed breeders which do not help have a 17% chance ($46\% \times 38\%$) of doing so. Therefore, the direct fitness pay-offs from adopting either strategy are fairly equal in terms of successful future personal reproduction, so it appears that the primary reason why some long-tailed tits adopt a helping strategy is the indirect kin-selected benefit derived from increasing the production of relatives.

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References

- Arnold, K.E. & Owens, I.P.F. (1998) Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society of London Series B*, **265**, 739–745.
- Brown, J.L. (1987) *Helping and Communal Breeding in Birds*. Princeton University Press, Princeton, New Jersey.
- Brown, J.L. & Brown, E.R. (1981) Extended family system in a communal bird. *Science*, **211**, 959–960.
- Brown, J.L., Brown, E.R., Brown, S.D. & Dow, D.D. (1982) Helpers – effects of experimental removal on reproductive success. *Science*, **215**, 421–422.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987) *Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture*. American Fisheries Society Monograph 5, pp. 1–473.
- Clutton-Brock, T.H. (1991) *The Evolution of Parental Care*. Princeton University Press, Princeton, New Jersey.
- Clutton-Brock, T.H. (2002) Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, **296**, 69–72.
- Cockburn, A. (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, **29**, 141–177.
- Cormack, R.A. (1964) Estimates of survival from the sighting of marked individuals. *Biometrika*, **51**, 429–438.
- Crick, H.Q.P. (1992) Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis*, **134**, 56–61.
- Curry, R.L. (1988) Influence of kinship on helping-behavior in Galapagos mockingbirds. *Behavioral Ecology and Sociobiology*, **22**, 141–152.
- Dunn, P.O., Cockburn, A. & Mulder, R.A. (1995) Fairy-wren helpers often care for young to which they are unrelated. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **259**, 339–343.
- Duplessis, M.A., Weathers, W.W. & Koenig, W.D. (1994) Energetic benefits of communal roosting by acorn woodpeckers during the non-breeding season. *Condor*, **96**, 631–637.
- Duplessis, M.A. & Williams, J.B. (1994) Communal cavity roosting in green woodhoopoes – consequences for energy-expenditure and the seasonal pattern of mortality. *Auk*, **111**, 292–299.
- Emlen, S.T. (1982) The evolution of helping. II. The role of behavioral conflict. *American Naturalist*, **119**, 40–53.
- Emlen, S.T. (1991) Evolution of cooperative breeding in birds and mammals. *Behavioural Ecology* (eds J.R. Krebs & N.B. Davies), pp. 301–337. Blackwell Scientific, Oxford.
- Emlen, S.T. (1997) Predicting family dynamics in social vertebrates. *Behavioural Ecology* (eds J.R. Krebs & N.B. Davies), pp. 228–253. Blackwell Scientific, Oxford.
- Emlen, S.T. & Wrege, P.H. (1989) A test of alternate hypothesis for helping in white-fronted bee-eaters of Kenya. *Behavioral Ecology and Sociobiology*, **25**, 303–319.
- Emlen, S.T. & Wrege, P.H. (1991) Breeding biology of white-fronted bee-eaters at Nakuru – the influence of helpers on breeder fitness. *Journal of Animal Ecology*, **60**, 309–326.
- Gaston, A.J. (1973) The ecology and behaviour of the long-tailed tit. *Ibis*, **115**, 330–351.
- Gaston, A.J. (1978) The evolution of group territorial behaviour and cooperative breeding. *American Naturalist*, **112**, 1091–1100.
- Glen, N.W. & Perrins, C.M. (1988) Co-operative breeding by long-tailed tits. *British Birds*, **81**, 630–641.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998) A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.
- Hatchwell, B.J. (1999) Investment strategies of breeders in avian cooperative breeding systems. *American Naturalist*, **154**, 205–219.
- Hatchwell, B.J., Anderson, C., Ross, D.J., Fowlie, M.K. & Blackwell, P.G. (2001a) Social organization of cooperatively breeding long-tailed tits: kinship and spatial dynamics. *Journal of Animal Ecology*, **70**, 820–830.
- Hatchwell, B.J. & Komdeur, J. (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, **59**, 1079–1086.
- Hatchwell, B.J., Ross, D.J., Chaline, N., Fowlie, M.K. & Burke, T. (2002) Parentage in the cooperative breeding system of long-tailed tits *Aegithalos caudatus*. *Animal Behaviour*, **64**, 55–63.
- Hatchwell, B.J., Ross, D.J., Fowlie, M.K. & McGowan, A. (2001b) Kin discrimination in cooperatively breeding long-tailed tits. *Proceedings of the Royal Society of London Series B*, **268**, 885–890.
- Hatchwell, B.J. & Russell, A.F. (1996) Provisioning rules in cooperatively breeding long-tailed tits *Aegithalos caudatus*: an experimental study. *Proceedings of the Royal Society of London Series 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 of helping. *Auk*, **116**, 355–363.
- Hatchwell, B.J., Russell, A.F., Fowlie, M.K. & Ross, D.J. (2000) Divorce in cooperatively breeding long-tailed tits: a consequence of inbreeding avoidance. *Proceedings of the Royal Society of London Series B*, **267**, 813–819.
- Hatchwell, B.J., Russell, A.F., MacColl, A.D.C., Ross, D.J., Fowlie, M.K. & McGowan, A. (in press) Helpers increase

- long-term but not short-term productivity in cooperatively breeding long-tailed tits. *Behavioral Ecology*.
- Heinsohn, R.G. (1991) Evolution of obligate cooperative breeding in white-winged choughs: a statistical approach. In: *Acta XX Congressus International Ornithologica*, **3**, 1309–1316.
- Heinsohn, R. & Cockburn, A. (1994) Helping is costly to young birds in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society of London Series B*, **256**, 293–298.
- Jolly, G.M. (1965) Explicit estimates from capture–recapture data with both death and immigration–stochastic model. *Biometrika*, **52**, 225–247.
- Khan, M.Z. & Walters, J.R. (1997) Is helping a beneficial learning experience for red-cockaded woodpecker (*Picooides borealis*) helpers? *Behavioral Ecology and Sociobiology*, **41**, 69–73.
- Koenig, W.D. & Mumme, R.L. (1987) *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton University Press, Princeton, New Jersey.
- Kokko, H., Johnstone, R.A. & Wright, J. (2002) The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behavioral Ecology*, **13**, 291–300.
- Komdeur, J. (1992) Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature*, **358**, 493–495.
- Komdeur, J. (1994) Experimental-evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behavioral Ecology and Sociobiology*, **34**, 175–186.
- Komdeur, J. (1996) Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behavioral Ecology*, **7**, 326–333.
- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals – a unified approach with case-studies. *Ecological Monographs*, **62**, 67–118.
- Legge, S. (2000) The effect of helpers on reproductive success in the laughing kookaburra. *Journal of Animal Ecology*, **69**, 714–724.
- Leonard, M.L., Horn, A.G. & Eden, S.F. (1989) Does juvenile helping enhance breeder reproductive success – a removal experiment on moorhens. *Behavioral Ecology and Sociobiology*, **25**, 357–361.
- MacColl, A.D.C. & Hatchwell, B.J. (2002) Seasonal variation in fitness pay-offs promotes cooperative breeding in long-tailed tits (*Aegithalos caudatus*). *American Naturalist*, **160**, 186–194.
- MacColl, A.D.C. & Hatchwell, B.J. (in press) Sharing of caring: nestling provisioning behaviour of long-tailed tit (*Aegithalos caudatus*) parents and helpers. *Animal Behaviour*.
- Magrath, D. & Yezerinac, S.M. (1997) Facultative helping does not influence reproductive success or survival in cooperatively breeding white-browed scrubwrens. *Journal of Animal Ecology*, **66**, 658–670.
- Mulder, R.A., Dunn, P.O., Cockburn, A., Lazenby-cohen, K.A. & Howell, M.J. (1994) Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proceedings of the Royal Society of London Series B*, **255**, 223–229.
- Mulder, R.A. & Langmore, N.E. (1993) Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour*, **45**, 830–833.
- Mumme, R.L. (1992) Do helpers increase reproductive success – an experimental-analysis in the Florida scrub jay. *Behavioral Ecology and Sociobiology*, **31**, 319–328.
- Rabenold, K.N. (1990) *Campylorhynchus* wrens: The ecology of delayed dispersal and cooperation in the Venezuelan savanna. *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Evolution* (eds P.B. Stacey & W.D. Koenig), pp. 157–196. Cambridge University Press, Cambridge.
- Reyer, H.U. (1984) Investment and relatedness – a cost–benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Animal Behaviour*, **32**, 1163–1178.
- Reyer, H.U. (1990) Pied kingfishers: ecological causes and reproductive consequences of cooperative breeding. *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Evolution* (eds P.B. Stacey & W.D. Koenig), pp. 527–558. Cambridge University Press, Cambridge.
- Richardson, D.S., Burke, T. & Komdeur, J. (2002) Direct benefits and the evolution of female-biased cooperative breeding in Seychelles warblers. *Evolution*, **56**, 2313–2321.
- Riehm, V.H. (1970) Ökologie und verhalten der schwanzmeise (*Aegithalos caudatus* L.). *Zoologische Jahrbuecher Systematik*, **97**, 338–400.
- Russell, A.F. (1999) *Ecological constraints and the cooperative breeding system of the long-tailed tit Aegithalos caudatus*. PhD Thesis, University of Sheffield, Sheffield.
- Russell, A.F. (2001) Dispersal costs set the scene for helping in an atypical avian cooperative breeder. *Proceedings of the Royal Society of London Series B*, **268**, 95–99.
- Russell, A.F. & Hatchwell, B.J. (2001) Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. *Proceedings of the Royal Society of London Series B*, **268**, 2169–2174.
- Russell, E.M. & Rowley, I. (1988) Helper contributions to reproductive success in the splendid fairy-wren (*Malurus splendens*). *Behavioral Ecology and Sociobiology*, **22**, 131–140.
- Seber, G.A.F. (1965) A note on the multiple recapture census. *Biometrika*, **52**, 249–259.
- Solomon, N.G. & French, J.A., eds. (1997) *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge.
- Stacey, P.B. & Koenig, W.D., eds. (1990) *Cooperative Breeding in Birds. Long-Term Studies of Ecology and Evolution*. Cambridge University Press, Cambridge.
- Stacey, P.B. & Ligon, J.D. (1987) Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *American Naturalist*, **130**, 654–676.
- Stacey, P.B. & Ligon, J.D. (1991) The benefits-of-philopatry hypothesis for the evolution of cooperative breeding – variation in territory quality and group-size effects. *American Naturalist*, **137**, 831–846.
- White, G.C. & Burnham, K.P. (1999) Program mark: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–139.
- Woolfenden, G.E. & Fitzpatrick, J.W. (1984) *The Florida Scrub Jay: Demography of a Cooperative-Breeding Bird*. Princeton University Press, Princeton, New Jersey.

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