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# Temporal Variation in Fitness Payoffs Promotes Cooperative Breeding in Long-Tailed Tits *Aegithalos caudatus*

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ABSTRACT: Cooperative breeding is paradoxical because some individuals forego independent reproduction and instead help others to reproduce. The ecological constraints model states that such behavior arises because of constraints on independent reproduction. Spatial variation in constraints has been shown to co-vary with the incidence of cooperative breeding in correlational and experimental studies. Here, we examine whether temporally variable ecological constraints can act in a similar way to promote cooperative breeding in the atypical system of long-tailed tits *Aegithalos caudatus*. In this species, individuals may switch reproductive tactics from breeding to helping within the same breeding season. Using 7 yr of field data, we show that reproductive success declined seasonally because of declines in brood size, nestling weight, and juvenile survival. The survival to breeding age of chicks from nests with helpers was higher than for chicks from nests without helpers, and since helpers usually helped at the nest of a close relative, they accrued inclusive fitness benefits. We used these data to model the expected fitness payoffs of breeding and helping at different times during the season. The model shows that late in the breeding season, the fitness payoff from a kin-directed helping tactic becomes greater than that from independent breeding. The behavioral switch predicted by the model is consistent with the observed switch from breeding to helping, which shows that cooperative breeding may evolve as a way of making the best of a bad job at the end of a temporally constrained breeding season.

*Keywords:* ecological constraints, reproductive tactics, inclusive fitness, fledging weight, helpers-at-the-nest, overwinter survival.

The evolution of societies has been described as one of the major evolutionary transitions in the history of life on Earth (Maynard Smith and Szathmary 1995), and the occurrence of apparently altruistic behavior between social animals has provided an invaluable testing ground for evolutionary theory. In cooperatively breeding species, some individuals forego independent reproduction and instead help others to reproduce. The ecological constraints model states that such behavior arises because of constraints on independent reproduction (Emlen 1982, 1991). Spatial variation in constraints, such as a shortage of breeding territories, has been shown to co-vary with the incidence of cooperative breeding in correlational (Maynard Smith and Ridpath 1972; Reyer 1980; Woolfenden and Fitzpatrick 1984; Ligon and Ligon 1990; Russell 1999) and experimental studies (Pruett Jones and Lewis 1990; Komdeur 1992; Walters et al. 1992).

Analogous temporal constraints limit independent reproduction in many bird species. Birds may be precluded from early breeding by weather (McCleery and Perrins 1998; Stevenson and Bryant 2000), while the productivity of nests and subsequent survival of fledglings is often lower toward the end of the season (Perrins 1965; Arcese and Smith 1985; Price et al. 1988; Linden et al. 1992; Norris 1993). This is often linked to a decline in the weight of fledglings (Tinbergen and Boerlijst 1990; Linden et al. 1992; Both et al. 1999) and ultimately is probably caused by a decline in the favorability of ecological circumstances for breeding.

In typical cooperative breeding systems, individuals delay dispersal, help to raise offspring from subsequent broods, and then disperse permanently to breed themselves. However, in several cooperatively breeding species, individuals may switch from breeding to helping within a season; this behavior is termed "redirected helping" (Emlen 1982; Lessells 1990; Dickinson et al. 1996). Emlen (1982) suggested that one of the constraints that may promote cooperative breeding is a low probability of successful reproduction, and this may explain the occurrence of redirected helping. However, no study has yet demonstrated that a switch in reproductive tactics from breeding to helping is caused by a change in fitness payoffs from each tactic through the season.

In this article, we investigate whether temporally vari-

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able constraints on reproductive success promote cooperative breeding of long-tailed tits. Individuals of this species may switch reproductive tactics from breeding to helping within the same breeding season. We analyze seasonal variation in the reproductive success of long-tailed tits using observational data from a 7-yr field study. We use the results of this analysis in a model of different reproductive tactics to calculate within-season temporal variation in expected fitness payoffs from independent breeding and from helping and relate these to the tactics that individuals adopt at different times during the season.

## Methods

### *Study Site and Population*

The data were collected between 1994 and 2000 on a population of 18–53 pairs of long-tailed tits in the Rivelin Valley, Sheffield (130–280 m; 53°23′N, 1°34′W). The study site includes approximately 3 $km^2$ of mature oak *Quercus robur* and beech *Fagus sylvatica* woodland, birch *Betula* spp. and hawthorn *Crataegus* spp. scrub, farmland, and gardens. For further details of the study population and methods, see Hatchwell and Russell (1996) and Hatchwell et al. (1999).

Long-tailed tits spend the nonbreeding season in flocks comprised of both relatives and nonrelatives (Russell 1999; Hatchwell et al. 2001). Flocks break up in February as birds pair up to breed; males usually adopt part of the flock range as their breeding range and either pair with an unrelated female from the same flock or with an immigrant female. Initially, all birds attempt to breed independently as pairs, but most nests fail because of predation (Hatchwell et al. 1999). Failed breeders either renest or they may become helpers at the nest of another pair, assisting them by feeding nestlings and fledglings (Glen and Perrins 1988).

Adults were color banded before breeding started or, in some cases, during the nestling period. Helpers from outside the study area were color banded on arrival at a nest. Nests were located by observation of pairs and were checked at least every other day. In this way, the date on which the first egg was laid was recorded, and clutch size was recorded after the onset of incubation. In all analyses dates were calculated as the number of days after March 1 each year. "Modal laying date" was the date in each year on which the largest number of first clutches was initiated. If a pair failed in a breeding attempt, we relocated the birds and any subsequent nest by extensive searching of the study area. Nests containing nestlings were watched every other day from hatching (day 0) to fledging (day 16 or 17), usually for a period of 1 h, to determine the identity of all adults provisioning the nest and thus whether helpers were present. The date of breeding failure and the date when failed breeders became helpers were usually known to within 2 d. Chicks were counted (brood size), weighed to 0.1 g (nestling weight), and banded with unique color combinations when they were 10–13 d old. Ninety-one percent were weighed at 11 d ($n = 93$ broods). Chicks were sexed with a molecular technique (Griffiths et al. 1998) using blood that was taken by brachial venipuncture at the time of banding. At the beginning of each breeding season we assessed the survival of chicks that were known to have fledged in the previous year, by resighting them during intensive fieldwork. By measuring survival in this way, we do not take account of disperal, but this should not bias our conclusions unless chicks from nests with helpers have different dispersal patterns from those without helpers. Female long-tailed tits disperse farther than males, which is common among passerines.

As we were examining seasonal variation in reproductive success, we also looked for obvious effects of weather on the timing of breeding. A priori considerations led us to expect that a small insectivorous passerine like the long-tailed tit would be most affected by temperature (Stevenson and Bryant 2000). The earliest that we have recorded nest-building activity by long-tailed tits in our study site was February 9, 2000, and the earliest laying date was March 23, 1998. We therefore selected the period from February 15 to March 15, when most nests are initiated, as the time in which weather was most likely to influence the timing of reproduction. We calculated the mean minimum temperature for this period from weather data recorded at the Sheffield City Museum meteorological recording station at Weston Park, Sheffield, 5 km from the center of the Rivelin study site at an altitude of 140 m.

### *Statistical Methods*

Analyses were done in SAS version 8 (SAS Institute 1999). Laying date, clutch size, and brood size data were analyzed with linear regression. The probability of renesting following failure was analyzed with logistic regression. Other analyses involved measurements on several chicks from the same brood. To control for this, nest of origin was included in analyses as a random factor, and mixed models were used for these analyses. Random effects in mixed models allow for the analysis of stratified data with more than one error term (Milner et al. 1999). The incorporation of a random effect in a model, for example "nest," takes care of dependency among measurements from the same nest. Mixed models with normal errors were performed in PROC MIXED (Littell et al. 1996), and survival analyses with binomial errors were performed with the GLIMMIX macro (Brown and Prescott 1999). The best-fitting model was constructed by sequentially dropping the least significant terms from a maximal model containing all effects and biologically meaningful second-order interactions (Crawley 1993). Significance of terms was assessed using Type I *F*-tests when the term was fitted last in the model. Denominator degrees of freedom used in *F*-tests were calculated in SAS with Satterthwaite's formula (Littell et al. 1996).

## Model of Fitness Payoffs

A bird that fails in a nesting attempt can adopt either of two tactics that might produce a fitness payoff: attempt to nest again or help at an established nest. In addition, about 40% of birds that initially attempt to breed fail to raise their own brood and do not become helpers either (Russell and Hatchwell 2001); we assume that their fitness payoff in that season is zero, and we do not consider them further here.

First, if a bird attempts to breed again at time $t$, its expected reproductive success measured as recruits in the following season is

$$E_{\mathrm{B}} = n_{t+x} \times s_{t+x} \times r,$$

where $n$ is the size of brood, $s$ is the survival of the chicks, $r$ is the relatedness to the brood, and $x$ is the delay between deciding to breed again and fledging a new brood of chicks. For the purposes of the model, "fledging" is considered to occur at day 11 since this is when chicks were weighed and all analyses are based on nestlings of this age.

Second, if a bird goes to help an existing brood, its expected increase in inclusive fitness (Hamilton 1964) is

$$E_{\mathrm{H}} = n_{t+y} \times (s_{\mathrm{h}} - s_{\mathrm{u}})_{t+y} \times r,$$

where $s_{\mathrm{u}}$ is the survival of chicks from an unhelped brood, $s_{\mathrm{h}}$ is the survival of chicks from a helped brood, and $y$ is the delay between deciding to help and the fledging of the brood it helps.

These equations represent only a basic model of the principal quantifiable payoffs of the different reproductive tactics. As such, they cannot fully describe the complexities of the cooperative breeding system of long-tailed tits. Instead, we have developed the model as a heuristic tool for attempting to understand the reproductive decisions that individuals make and, hence, for understanding the evolution of cooperative breeding in long-tailed tits and other species with redirected helping. Nevertheless, we believe that all of the key parameters affecting fitness payoffs from the alternative reproductive tactics are included. In particular, we have assumed that the costs of helping and breeding are the same and that there is no direct fitness benefit from helping. These assumptions are reasonable because the survival rate of helpers and breeders is the same, and a helper's probability of successful future reproduction does not differ from that of a failed breeder that did not help (A. McGowan and B. J. Hatchwell, unpublished data).

By substituting estimates of the seasonal variation in reproductive parameters from the statistical models into the equations for expected reproductive success, we made expected reproductive success ($E$) a function only of date. We were then able to calculate the expected payoffs for an individual making the decision to follow the different tactics (breed or help) at different times during the season. Expected reproductive success was calculated as the number of sons alive at the beginning of the next breeding season, assuming a 1 : 1 sex ratio. We used sons because males are the philopatric sex for which measured survival rates were likely to be more accurate. Only chicks from nests with two or more helpers have a significant increase in recruitment when compared to unhelped nests (B. J. Hatchwell, A. F. Russell, A. D. C. MacColl, D. J. Ross, and M. K. Fowlie, unpublished manuscript). However, to retain simplicity in the model, we consider the effect of an average helper on productivity.

We calculated the payoffs of the two tactics for two scenarios. In the first scenario, we calculated the payoffs ignoring the risk of nest failure before fledging. This gives the maximum payoff that an individual could expect to get at any point in the season and on average will overestimate true expected success. In the second scenario, we took account of the probability that a nest fails before fledging but assumed that individuals so affected made no subsequent attempts to breed or help. This gives the minimum payoffs that the bird would expect to gain if it was unable to breed again or help after failing a second time; on average, this will underestimate true expected success. In reality, the payoff an individual gets is likely to fall between the payoffs given by the two scenarios.

To calculate the expected reproductive payoffs of the different tactics, we made a number of assumptions. We assumed that breeders raise their own offspring; this is reasonable because rates of extrapair paternity and intraspecific brood parasitism are very low in long-tailed tits (Hatchwell et al. 2002). We also assumed that helpers go to a nest where they are the first-order relative of one parent, and therefore their relatedness to the chicks they help is 0.25. This was true for the majority of helpers (69%), although we know that in some instances helpers were closely related to both parents (10%) and were either more distantly related or unrelated to both parents in the remaining cases (21%; Russell and Hatchwell 2001). To calculate the expected payoffs, we also needed to know the delay between failing and raising another set of fledglings

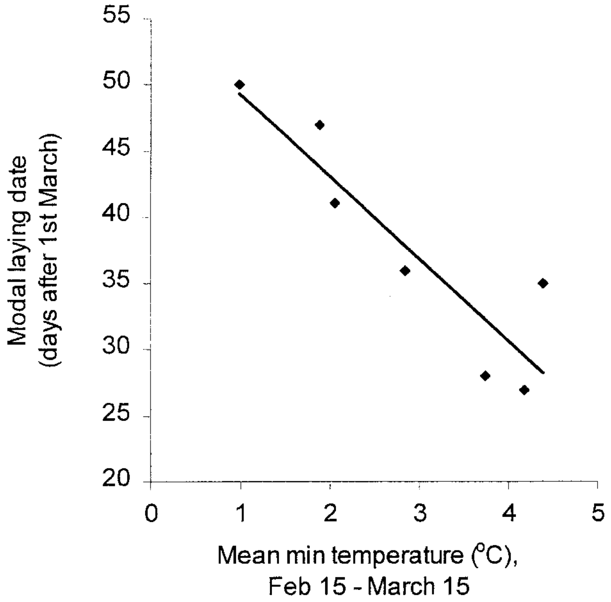

**Figure 1:** Relationship between modal laying date and mean minimum temperature in the period February 15 to March 15, 1994–2000. Modal laying date = 55.44 − 6.19 × mean minimum temperature ($R^2 = 0.81$, $F = 21.8$, df = 1, 5, $P = .006$).

(11-d-old nestlings for the purposes of the model). Using data from our study population, we estimated that the time from failing to beginning to lay was 7 d, that the incubation period was 15 d, and that the average age of chicks when helpers start helping was 6 d. We therefore assumed that if a bird decided to help, the chicks it helps would be 11 d old in 5 d. The time spent laying a clutch depended on the size of the clutch laid since eggs were laid daily. The chicks produced by a bird that decided to breed would be 11 d old in 7 + (clutch size) + 15 + 11 d time. The probability that a second nesting attempt failed was 0.91 ($n = 88$ second nesting attempts). For birds that went to help, we used the Mayfield estimate of daily survival (Mayfield 1961) to calculate the probability that a nest survived from when the helper started helping until fledging (0.748; $n = 1{,}456$ nest days; 39 losses).

In calculating the expected payoffs of the different tactics, we chose to ignore variability among years in seasonal change in reproductive parameters since, for the sake of keeping the model simple, we assume that long-tailed tits will be adapted to average conditions. In fact, year was only significant as a factor in the relationships between nestling weight and date (see "Results"), where the variation between years was largely due to the data from different years occupying different, overlapping parts of the same humped relationship. Thus, to obtain parameter values for the relationship between weight and date across all years, we have dropped year from the model.

## Results

First clutches were laid later in years when the period during which nest building started was colder (fig. 1). The size of second clutches declined through the season (table 1; fig. 2*A*), but the size of first clutches did not (change in fit of model when slope for first clutches constrained to 0: $F = 0.49$, df = 1, 73, NS; Crawley 1993). The size of second broods also declined through the season (table 1; fig. 2*B*), but the size of first broods did not (change in fit of model when slope for first broods constrained to zero: $F = 0.26$, df = 1, 81, NS).

Nestling weight peaked in midseason (fig. 2*C*; date, $F = 0.04$, df = 1, 86, NS; date$^2$, $F = 11.5$, df = 1, 86, $P = .001$ in a model containing explanatory variables: time [of day]; time$^2$; time$^3$; age of chicks and brood size; all significant at $P \leq .05$). Nestling weight was also greater in broods with helpers-at-the-nest (table 1; $F = 6.28$, df = 1, 86, $P = .014$ in the same model as above).

Male nestlings and heavier nestlings were more likely to be resighted in the following spring (fig. 2*D*; weight, $F = 4.01$, df = 1, 61, $P = .05$; sex, $F = 20.0$, df = 1, 61, $P < .0001$; other explanatory variables [all NS] were year, helped? [yes or no], brood size, tarsus, and their first-order interactions). Chicks that fledged earlier were also more likely to be resighted in the following spring, even after controlling for weight (fig. 2*E*; date, $F = 5.25$, df = 1, 61, $P = .026$ in the same model as above).

When estimates of the variation in reproductive parameters from statistical models were used to calculate the expected reproductive success of the different tactics, the resultant model showed that the fitness payoff from breeding declined rapidly through the season (fig. 3*A*; table 2). The fitness payoff from helping was initially lower but declined less rapidly and became greater than the payoff from breeding after day 57 (April 27) if the probability of nest failure was taken into account or after day 73 (May

**Table 1:** Results of general linear models of first and second clutch sizes and brood sizes

| | Clutch size | | | Brood size | | |
|---|---|---|---|---|---|---|
| Effect | df | *F* | *P* | df | *F* | *P* |
| Date | 1, 73 | 28.8 | <.0001 | 1, 81 | 16.1 | .0001 |
| Attempt | 1, 73 | 9.2 | .003 | 1, 81 | 5.12 | .026 |
| Date × attempt | 1, 73 | 14.5 | .0003 | 1, 81 | 7.26 | .009 |
| Year | 1, 55 | .81 | .57 | 6, 63 | .97 | .45 |
| Year × date | 1, 55 | 1.23 | .31 | 6, 63 | 2.02 | .08 |
| Year × date × attempt | 1, 55 | .74 | .57 | 6, 63 | .14 | .97 |

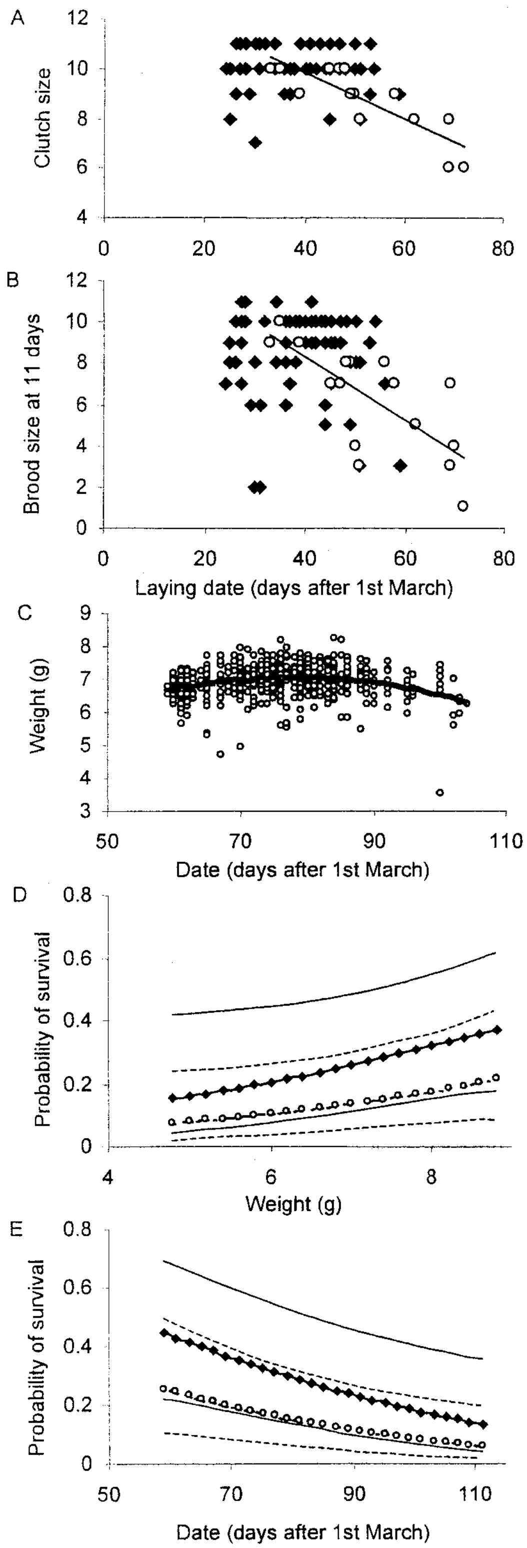

**Figure 2:** Relationships between reproductive success parameters and date. *A*, Clutch size of first (*filled diamonds*; $N = 63$) and second (*open circles*, *solid line*; $N = 14$) nest attempts and date, for all years 1994–2000. *B*, Brood size of first (*filled diamonds*; $N = 69$) and second (*open circles*, *solid line*; $N = 16$) nest attempts and date, for all years 1994–2000. *C*, Nestling weight and date for all years 1994–2000 ($N = 931$ nestlings from 93 broods). Data are partial residuals adjusted to the means of other explanatory variables included in the analysis. *D*, Survival of fledglings ($N = 490$ fledglings from 64 broods) to the following spring and weight at 11 d for male (*filled diamonds*, *solid lines*) and female chicks (*open circles*, *dashed lines*; ±95% confidence intervals of the slopes). *E*, Survival of fledglings to the following spring and date of weighing for male and female chicks (±95% confidence intervals of slopes).

13) if the probability of nest failure was not taken into account. Therefore, the model predicted a switch in reproductive tactics from breeding to helping during this part of the breeding season.

To test this prediction of the model, we quantified two measures of tactic switching by birds following the failure of a first nesting attempt. First, we looked at the propensity of failed birds to renest through the season. We also looked at the pattern of arrival of helpers at nests with respect to date. For both measures, the switch in tactics of failed breeders from breeding to helping corresponded remarkably closely with the predicted switch (fig. 3*B*). Before day 54, all birds attempted to renest, and after day 73, no birds attempted to renest (in a logistic regression of probability of renesting, for date of failure $\chi^2 = 224$, $\mathrm{df} = 1$, $P \ll .0001$). There was no significant variation among years in the timing of the switch (for year $\chi^2 = 3.3$, $\mathrm{df} = 6$, $P > .5$). The cumulative proportion of helpers arriving at nests rose rapidly as the probability of renesting declined (fig. 3*B*), although the slope of this line indicates that there was sometimes a lag between breeding failure and beginning to help.

## Discussion

Our analysis shows that a seasonal decline in reproductive success acts as a constraint on independent reproduction late in the season (figs. 2, 3*A*). Failed breeders switched tactics from breeding to helping when the expected inclusive fitness gain from helping at the nest of a relative exceeded the likely payoff from breeding (fig. 3*B*). Helpers accrued a small inclusive fitness benefit because they increased the fledging weight and hence, presumably, the survival of the chicks that they helped. The payoff from breeding declined sooner than that from helping because the lag inherent in building a new nest and laying and incubating a new clutch meant that the chicks from an independent breeding attempt fledged much later in the season than those from a nest at which a bird went to help, and the probability of survival of later-fledged chicks was much lower. Thus, temporally variable ecological con-

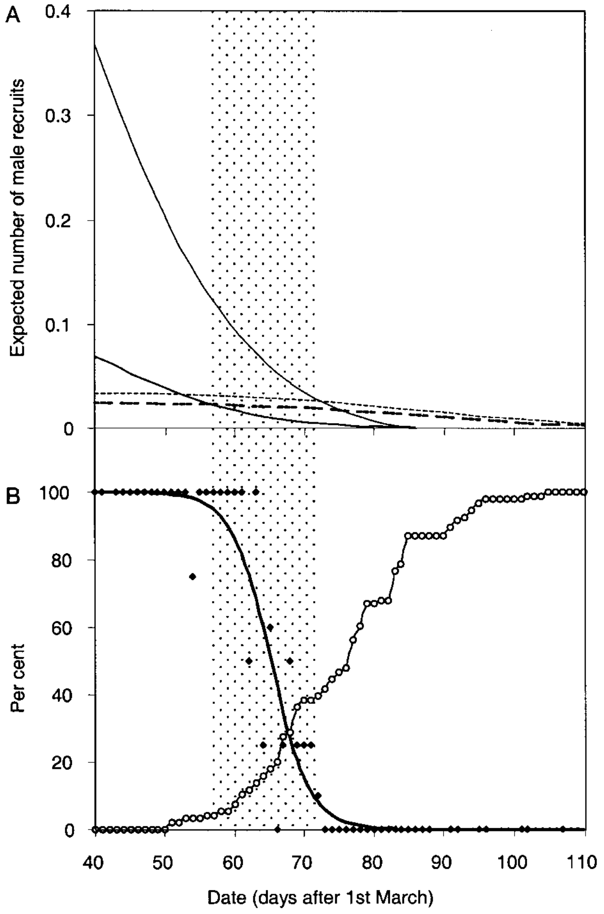

**Figure 3:** Seasonal change in payoffs of independent breeding and helping tactics and change in observed adoption of different tactics. *A*, Model predictions of seasonal change in fitness payoffs of breeding (*solid lines*) and helping (*dashed lines*) for birds that account for the probability of nest failure (gray) and for those that do not (black). The stippled area indicates the window of time during which a switch from breeding to helping behavior is expected. *B*, Observed seasonal change in the probability of birds renesting following failure (*filled diamonds*; $N = 209$ pairs). The dark line is the fitted relationship from a logistic regression. The thin line (*open circles*) is the cumulative percent of helpers arriving at nests ($N = 94$ helpers).

straints can promote the evolution of cooperative breeding in the same way as spatial constraints.

We would expect the decline in reproductive success late in the season to exert selection on long-tailed tits to breed earlier. However, long-tailed tits already breed unusually early for a temperate passerine, and figure 1 shows that they are probably prevented from breeding any earlier by weather conditions. Long-tailed tits thus may be boxed in by environmental conditions at both ends of the season. The constraint of weather on the initiation of breeding is consistent with results for other temperate passerine species (Perrins 1965; Crick and Sparks 1999). The constraint may be nutritional (Perrins 1970), energetic (Stevenson and Bryant 2000), or an interaction between the two (Magrath 1992). As one of the smallest, exclusively insectivorous, nonmigratory passerines in the United Kingdom (Cramp et al. 1993), long-tailed tits are likely to be particularly sensitive to conditions in the prelaying period (Stevenson and Bryant 2000). In particular, the construction of their elaborate nest is unusually time consuming and probably energetically demanding (Glen and Perrins 1988). For example, in our study population, first nests took 25 d to build on average (B. J. Hatchwell, unpublished data).

Our model of seasonal variation in reproductive payoffs may explain the helping behavior of a number of other cooperative species in which some individuals switch from breeding to helping within a season, such as European bee eaters *Merops apiaster* (Lessells 1990), white-fronted bee eaters *Merops bullockoides* (Emlen 1982), bushtits *Psaltriparus minimus* (Sloane 1996), riflemen *Acanthisitta chloris* (Sherley 1990), and western bluebirds *Sialia mexicana* (Dickinson et al. 1996). However, it also raises the intriguing question of why many other bird species that experience seasonal declines in productivity do not adopt similar tactics and make the best of a bad job by becoming helpers at the nest of relatives, thereby increasing their inclusive fitness.

Declines in several reproductive parameters through the season are well documented for temperate passerines. Reductions in brood and clutch sizes as the season progresses are common (Perrins 1965; Crick et al. 1993), and declines in the weight of fledglings are also well known. For example, in great tits *Parus major* and blue tits *Parus caeruleus*, the seasonal decline in fledging weights is attributable to declines in the availability of caterpillars, which form the largest proportion of the diet fed to nestlings (van Noordwijk et al. 1995; Woodburn 1997). We do not know the cause of the change in weight of long-tailed tit chicks through the season (fig. 2*C*), but it may also be the result of changes in food supply. Long-tailed tits are more cath-

**Table 2:** Relationship between reproductive parameters and date ($T$) estimated using the partial regression coefficients from statistical models of the respective parameters

| Parameter | Intercept | $T$ | $T^2$ |
|---|---|---|---|
| Size of second clutch | 13.54 | −.093 | |
| Size of second brood | 14.29 | −.151 | |
| Nestling weight (unhelped) | .277 | .173 | −.0011 |
| Nestling weight (helped) | .539 | .173 | −.0011 |
| Survival (unhelped)[a] | −1.01 | .035 | −.00047 |
| Survival (helped)[a] | −.90 | .035 | −.00047 |

[a] Logit scale.

olic in the diet they feed to nestlings than *Parus* species (Cramp et al. 1993), but they may still be limited by a decline in food availability across the spectrum of prey or of some key species. We intend to examine the variation in food availability in the future by direct assessment of prey abundance.

The relationship between fledging weight, date, and survival again reflects the situation in several other well-studied temperate passerines (Magrath 1991; Linden et al. 1992; Both et al. 1999). Studies of great tits have found that winter survival is related to fledging weight (Tinbergen and Boerlijst 1990), fledging date (Verhulst and Tinbergen 1991; Verboven and Visser 1998), or both (Linden et al. 1992). Blue tits and collared flycatchers *Ficedula albicollis* also suffer declines in weight and survival toward the end of the season (Nur 1984; Linden et al. 1992; Norris 1993). In long-tailed tits, the relationship between fledging date and survival, independent of weight, may be because earlier-fledged chicks have more time to improve their condition before they molt in July (Hussell 1972). In common with these other studies, we measured survival as local recruitment and so could not differentiate between death and dispersal. Given that nonbreeding flocks of long-tailed tits usually remain close to their natal area and do not defend exclusive territories (Hatchwell et al. 2001), there is no obvious reason why natal dispersal should vary consistently with date and bias our measure of survival.

Declines in reproductive success are thus common among temperate passerines, and yet helping as a tactic is rare. A key point here is that for there to be a fitness payoff from the alternative tactic of helping, helpers must assist relatives. Russell and Hatchwell (2001) showed that in long-tailed tits, helpers selectively help at the nests of relatives, and in an experiment, failed breeders without nearby relatives did not become helpers. This choosiness explains why a substantial proportion of failed breeders do not help and also why the magnitude of the slopes for the proportion of pairs renesting and cumulative proportion of helpers arriving at nests differ (fig. 3*B*). For some helpers, there is a delay between the failure of their breeding attempts and the start of helping because, in general, helpers assist breeders only during the nestling and fledgling phases of reproduction. We know that when some birds fail, the nest at which they eventually help does not yet have nestlings in it, but they begin to help soon after the eggs hatch. Therefore, one possible explanation for the scarcity of helping behavior in circumstances where reproductive success declines seasonally is that the demography of long-tailed tits results in populations with greater genetic structure than otherwise ecologically similar species. This provides failed breeders with the opportunity to assist at the nests of relatives, an opportunity that may be lacking in other species (Russell 1999). Cooperative breeding is known to be associated with particular life-history traits such as high longevity (Brown 1987; Arnold and Owens 1998) that are likely to result in genetically structured populations. Under certain conditions, the genetic structuring that results from limited dispersal in viscous populations may be favorable to the evolution of altruism (Hamilton 1964; Queller 1992). This study suggests that demographic patterns coupled with a temporally constrained breeding season may also play a key role in creating the conditions under which cooperation may evolve.

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