# Divorce in cooperatively breeding long-tailed tits: a consequence of inbreeding avoidance?

## B. J. Hatchwell[*], A. F. Russell[†], D. J. Ross and M. K. Fowlie

*Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*

The decision of whether to divorce a breeding partner between reproductive attempts can significantly affect individual fitness. In this paper, we report that 63% of surviving pairs of long-tailed tits *Aegithalos caudatus* divorced between years. We examine three likely explanations for the high divorce rate in this cooperative breeder. The 'better option' hypothesis predicts that divorce and re-pairing increases an individual's reproductive success. However, divorcees did not secure better partners or more helpers and there was no improvement in their reproductive success following divorce. The 'inbreeding avoidance' hypothesis predicts that females should disperse from their family group to avoid breeding with philopatric sons. The observed pattern of divorce was consistent with this hypothesis because, in contrast to the usual avian pattern, divorce was typical for successful pairs (81%) and less frequent in unsuccessful pairs (36–43%). The 'forced divorce' hypothesis predicts that divorce increases as the number of competitors increases. The pattern of divorce among failed breeders was consistent with this hypothesis, but it fails to explain the overall occurrence of divorce because divorcees rarely re-paired with their partners' closest competitors. We discuss long-tailed tits' unique association between divorce and reproductive success in the context of dispersal strategies for inbreeding avoidance.

**Keywords:** cooperative breeding; divorce; inbreeding; incest avoidance; long-tailed tit

## 1. INTRODUCTION

In socially monogamous species, individuals seeking to maximize their fitness in a series of discrete reproductive events may have to decide whether to stay with the same partner or find a new partner for successive breeding attempts (Rowley 1983). Divorce occurs when a pair-bond is broken between breeding attempts despite both members of the pair still being alive, and it can have profound implications for future reproductive success (Black 1996). In birds, the rate of divorce varies widely between and within species (Dhondt & Adriaensen 1994; Ens *et al*. 1996), although the reasons for this variation are not fully understood (Choudhury 1995; Ens *et al*. 1996). Explanations for divorce include the 'better option' and 'incompatibility' hypotheses in which one or both members of a pair improve their reproductive success by obtaining a higher quality or more compatible partner or a better breeding site (e.g. Rowley 1983; Grant & Grant 1987; Ens *et al*. 1993; Orrell *et al*. 1994; Desrochers & Magrath 1996). Alternative hypotheses make no prediction about relative reproductive success of individuals before or after divorce. The 'musical chairs' hypothesis proposes that divorce is a side-effect of between-season variation in the order of territory settlement (Dhondt & Adriaensen 1994; Dhondt *et al*. 1996), while the 'accidental loss' hypothesis proposes that divorce occurs due to accidental disruption of a pair-bond coupled with a need to rapidly re-pair (Owen *et al*. 1988). These explanations are likely to apply to species that leave their breeding areas between seasons, i.e. migratory species. Finally, the

'forced divorce' hypothesis proposes that divorce occurs when a third party displaces one member of a breeding pair (Choudhury 1995).

There is some empirical support for each of these hypotheses and it is clear that the ecology of a species influences the divorce rate (Black 1996). Comparative studies show that mate fidelity is generally high among long-lived, sedentary species (Ens *et al*. 1996). These demographic traits are typical of cooperatively breeding bird species (Brown 1987; Arnold & Owens 1998), where long-term pair-bonds may be an important element in family formation (Emlen 1995). Therefore, it is not surprising that many studies of cooperative breeders have reported very low rates of divorce (e.g. Stacey & Koenig 1990; Walters 1990; Marzluff *et al*. 1996; Russell & Rowley 1996).

In this paper, we report a high frequency of divorce in the cooperatively breeding long-tailed tit *Aegithalos caudatus*. The musical chairs and accidental loss hypotheses are unlikely to apply to this sedentary species, but we consider three other explanations for this species' high divorce rate.

### (a) *The 'better option' hypothesis*

In long-tailed tits, divorcees might achieve higher reproductive success in two ways. First, they may secure a better partner. Second, in cooperative species where helpers have a positive effect on the fitness of breeders, divorce may be a strategy to increase the number of helpers in later breeding attempts if divorcees find new partners with more potential helpers. Long-tailed tit helpers increase nestling provisioning rates (Hatchwell & Russell 1996) and have a positive effect on breeder fitness by increasing offspring recruitment (Glen & Perrins 1988; Russell 1999; B. J. Hatchwell, unpublished data).

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## (b) The 'inbreeding avoidance' hypothesis

Inbreeding avoidance is generally regarded as a driving force in the evolution of dispersal strategies (Johnson & Gaines 1990; Weatherhead & Forbes 1994), because of the deleterious effects of inbreeding (Ralls *et al*. 1986; Keller *et al*. 1994; Pusey & Wolf 1996; Keller 1998; Koenig *et al*. 1999). In cooperative species, there is a risk of inbreeding if pairing occurs within an intact family group. This possibility is generally averted because reproduction usually follows dispersal (Brown 1987) and the act of dispersal takes offspring away from opposite-sex relatives. However, an inbreeding risk may arise when one parent dies leaving a parent with opposite-sex offspring as potential breeders on a territory (Emlen 1995). The ensuing conflict over who reproduces may result in a non-breeding stalemate (Koenig *et al*. 1998), in an individual or coalition of one sex evicting the opposite-sex relative(s) (Hannon *et al*. 1985; Zack & Rabenold 1989; Zahavi 1990), or in apparently voluntary dispersal by one sex (Walters 1990). A similar situation arises when philopatric offspring (typically males in birds) are reproductive, as in long-tailed tits, and risk pairing with a relative (e.g. their mother). In such circumstances, inbreeding may be avoided by the eviction or voluntary dispersal of one party. This may result in divorce and subsequent re-pairing outside the family group.

## (c) The 'forced divorce' hypothesis

Increased competition for partners is predicted to increase the frequency of divorce. In long-tailed tits, the most likely source of competition for partners is from non-relatives within the winter flocks which represent the main social structure during the non-breeding season.

## 2. METHODS

The study was conducted at three sites in Yorkshire, UK. One population of 18–35 pairs was studied in the Rivelin Valley (Sheffield) from 1994 to 1998, and two populations of about 35 pairs each were studied in Melton Wood (Doncaster) and Ecclesall Wood (Sheffield) from 1996 to 1998. The study sites comprised mixed woodland, scrub, farmland and gardens.

Long-tailed tits spend the non-breeding season in family groups of 10–15 birds, who occupy a flock range. Flocks break up in early spring; males occupy part of the flock range, and females either disperse to other ranges to find a partner or remain within the flock range and pair with a male from that flock. All birds start the season breeding independently in pairs, but nest failure is frequent (Hatchwell *et al*. 1999), and if a pair fails after early May they may become helpers by moving either individually or together to help another pair care for their offspring by feeding nestlings (Gaston 1973; Glen & Perrins 1988). All pairs breeding in each study site were known, and the majority (80–90%) of birds in each population were colour-ringed before breeding started. Pairs were readily identified during breeding because both sexes build the nest, the male feeds the incubating female on the nest, and both sexes feed the nestlings. Furthermore, paired males and females maintain close contact when foraging (mean distance between partners outside the fertile period = $7.2 \pm 2.8$ m, $n = 24$ pairs), and helpers appear only during the nestling period. Therefore, we are confident that we assigned all pairings correctly. We monitored the breeding success of all pairs in the study populations (see

Hatchwell *et al*. 1999) and observed nests for at least 1 h every 1–3 days throughout the 16-day nestling period to determine the identity of carers. The measure of a breeder's reproductive success used in this paper was simply whether or not a brood was fledged.

Divorce rates were calculated for pairs that bred in one year and from which both adults were known to be alive in the following year. If a bird bred with a new partner this was scored as a divorce. Those pairs from which both adults survived to the following season and bred together are described as 'faithful'. Data for males and females were analysed separately and sample sizes for males and females differ in some analyses because in a few cases we were not certain that both members of a pair had bred following their divorce, even though both were known to be alive. We use the notation year $N$ and year $N + 1$ to describe the breeding seasons before and after divorce, and the first and second seasons for faithful pairs.

Mate fidelity was scored in 49 cases for males and 48 cases for females. These totals include six males who were scored twice and one male who was scored three times. Five females are included twice, and one is included three times. These cases raise the potential difficulty of pseudoreplication, but we have included them for two reasons. First, there was no consistent pattern in the occurrence of divorce for these individuals: six divorced twice, two were faithful twice, and seven divorced in one year and were faithful in another. These are precisely the frequencies expected given a 63% divorce rate (see § 3) and the random occurrence of divorce within individuals, so the multiple inclusion of particular individuals was unlikely to bias the results towards either divorce or mate fidelity. Second, the social and ecological circumstances of an individual vary among seasons and in the following analyses we consider season-specific rather than lifetime factors as predictors of divorce.

Another potentially confounding factor is the use of data from three populations. However, the study sites are within 30 km of each other, are ecologically similar (Russell 1999) and there was no difference between populations in the proportion of birds that divorced between seasons (males: Rivelin 58%, $n = 31$, Melton 64%, $n = 11$, Ecclesall 71%, $n = 7$; *G*-test, $G = 1.59$, d.f. = 2, $p = 0.47$; females: Rivelin 63%, $n = 30$, Melton, 64%, $n = 11$, Ecclesall 71%, $n = 7$; *G*-test, $G = 0.92$, d.f. = 2, $p = 0.65$). Therefore, we have no reason to suspect that selection pressures relating to mate fidelity differed between sites. Means are given ± one standard deviation, except where stated otherwise.

## 3. RESULTS

Divorce occurred frequently between seasons: 61% ($n = 49$) of males and 65% ($n = 48$) of females bred with another partner even though their previous partner was known to be alive.

## (a) The 'better option' hypothesis

There was no evidence that the new partners of divorcees were better than their old partners in terms of their previous reproductive success. Divorcees often paired with first-year birds or with immigrants, assumed to be first-year birds (table 1). Those divorcees that did pair with a bird who had bred in the study sites in year $N$ did not gain a relatively successful partner (table 1), indeed the second partner tended to have been less successful than the first partner in year $N$. It should be noted that

Table 1. *The breeding history in year $N$ of the first and second partners of divorced long-tailed tits*

(Comparing first and second partners who had bred previously, there was no significant difference in the proportions of first and second partners that were successful (males: $\chi^2 = 0.564$, d.f. = 1, $p = 0.45$; females: $\chi^2 = 3.03$, d.f. = 1, $p = 0.082$).)

| | breeding history in year $N$ of partners of | | | |
| | male divorcees | | female divorcees | |
| | partner 1 | partner 2 | partner 1 | partner 2 |
|---|---|---|---|---|
| successful breeder | 22 (73%) | 8 (27%) | 22 (71%) | 6 (19%) |
| unsuccessful breeder | 8 (27%) | 6 (20%) | 9 (29%) | 9 (29%) |
| non-breeder (first year or immigrant) | — | 16 (53%) | — | 16 (52%) |

Table 2. *The number of* (a) *potential helpers available to faithful pairs and divorcees, and* (b) *observed helpers at the nests of faithful and divorced long-tailed tits (see § 3(a))*

| (a) | male | | | | female | | | |
| | faithful | ($n = 18$) | divorcees | ($n = 30$) | faithful | ($n = 16$) | divorcees | ($n = 31$) |
| | | | if not divorced | after divorce | | | if not divorced | after divorce |
|---|---|---|---|---|---|---|---|---|
| number of potential helpers ($\pm$ s.d.) | 1.06 ± 2.04 | | 0.93 ± 1.11 | 1.77 ± 2.39 | 1.00 ± 2.07 | | 0.84 ± 1.10 | 1.07 ± 1.50 |
| | | $z = 0.77$ | $z = 2.23$ | | | $z = 0.45$ | $z = 1.84$ | |
| | | $p = 0.44$[a] | $p = 0.026$[b] | | | $p = 0.65$[a] | $p = 0.066$[b] | |

| (b) | male | | | | female | | | |
| | faithful | | divorced | | faithful | | divorced | |
| | $N$ | $N + 1$ | $N$ | $N + 1$ | $N$ | $N + 1$ | $N$ | $N + 1$ |
|---|---|---|---|---|---|---|---|---|
| percentage of nests with helpers ($n$) | 40% (5) | 55% (11) | 68% (22) | 35% (17) | 40% (5) | 56% (9) | 68% (22) | 47% (15) |
| | — | | $\chi^2 = 2.96$, d.f. = 1 | | — | | $\chi^2 = 0.94$, d.f. = 1 | |
| | — | | $p = 0.09$[c] | | — | | $p = 0.33$[c] | |

[a] Mann–Whitney $U$-tests.
[b] Wilcoxon tests.
[c] $\chi^2$-tests.

this test assumes that partner quality in year $N + 1$ is measurable from their reproductive success in year $N$.

A further prediction of this hypothesis is that long-tailed tits may divorce to obtain more helpers; these are usually first-order relatives of one parent, most often a brother of the breeding male (Glen & Perrins 1988; Russell 1999; B. J. Hatchwell, unpublished data). In the following analyses, we first consider the number of potential helpers available to divorced and faithful birds, and then the number of nests at which helpers were observed (the latter depends on a nest surviving to the nestling phase). In each study population, we counted the number of known first-order relatives of faithful birds, divorced birds and their new partners. If divorcees had remained faithful to their original partner in year $N + 1$ instead of divorcing, they would have had a similar number of potential helpers as those individuals who were faithful (males $p = 0.44$, females $p = 0.65$; table 2a), i.e. the absence of potential helpers did not explain divorce. Nevertheless, those birds who did divorce and re-pair tended to increase the number of potential helpers (males $p = 0.026$, females $p = 0.066$; table 2a) because their new partner often had first-order relatives nearby. However, divorcees may still not obtain more helpers because following a divorce potential helpers might help at a nest belonging to either divorcee. This is demonstrated by our second analysis using the observed number of nests with helpers. Divorcees were no more likely to have helpers in year $N + 1$ than in year $N$ (males $p = 0.09$, females $p = 0.33$; table 2b), in fact, divorced males tended to be less likely to have helpers following divorce. Furthermore, despite the greater number of potential helpers, divorcees were no more likely to have helpers than were faithful birds in year

Table 3. *Reproductive success of divorced long-tailed tits in years N and N + 1. Sample sizes are lower in year N + 1 because some birds moved out of the study site for late nests*

|  | divorced males | | divorced females | |
|---|---|---|---|---|
|  | year $N$ | year $N+1$ | year $N$ | year $N+1$ |
| percentage successful | 73% ($n = 30$) | 41% ($n = 27$) | 71% ($n = 31$) | 25% ($n = 24$) |
| $\chi^2$-tests | $\chi^2 = 6.19$, d.f. = 1, $p = 0.012$ | | $\chi^2 = 11.44$, d.f. = 1, $p < 0.001$ | |

Table 4. *Association between reproductive success in year N and mate fidelity of male and female long-tailed tits in year N + 1*

| success in year $N$ | male mate fidelity year $N+1$ | | | female mate fidelity year $N+1$ | | |
|---|---|---|---|---|---|---|
|  | divorced | faithful | divorce rate | divorced | faithful | divorce rate |
| successful | 22 | 5 | 81% | 22 | 5 | 81% |
| unsuccessful | 8 | 14 | 36% | 9 | 12 | 43% |
| success rate | 73% | 26% | — | 71% | 29% | — |
|  | $\chi^2 = 8.58$, d.f. = 1, $p = 0.003$ | | | $\chi^2 = 6.11$, d.f. = 1, $p = 0.014$ | | |

$N + 1$ (males 35% versus 55%, respectively, *G*-test, $G = 1.01$, d.f. = 1, $p = 0.3l$; females 47% versus 56%, *G*-test, $G = 0.18$, d.f. = 1, $p = 0.67$; table 2*b*). Thus, divorce did not increase the number of helpers at the nest.

The key prediction of this hypothesis is that divorcees should have higher reproductive success in year $N + 1$ than in year $N$. However, the breeding success of divorcees was significantly lower in year $N + 1$ than in year $N$ (table 3), opposite to the predicted pattern. Furthermore, in year $N + 1$ divorcees were no more successful than faithful birds were (faithful males 37%, $n = 19$, $\chi^2 = 0.00$, d.f. = 1, $p = 0.97$; faithful females 35%, $n = 17$, $\chi^2 = 0.13$, d.f. = 1, $p = 0.71$). Therefore, we conclude that divorce did not increase productivity for either sex.

**(b)  *The 'inbreeding avoidance' hypothesis***

The annual mortality rate of adult male long-tailed tits is 44% ($n = 121$), so the probability of a male partner dying between breeding seasons is high. Philopatric recruitment of male offspring is frequent, while that of females is rare; a total of 250 fledglings have been ringed at our most intensively observed study site (Rivelin Valley), and assuming an equal sex ratio at fledging, male recruitment within the study site was 30% (38 out of 125), while that of females was just 9% (11 out of 125). Male recruits usually breed close to their natal site, so inbreeding is a significant risk if females that were successful in year $N$ remain within their family flock and pair with a male member of that flock in year $N + 1$. This hypothesis proposes that divorce is a consequence of avoidance of inbreeding between females and their philopatric sons.

The key predictions of this hypothesis are that females that bred successfully in year $N$ should divorce, and that they should pair with a male from a different flock in year $N + 1$. There was a close association between reproductive success and mate fidelity for both sexes. Birds who were successful in year $N$ had a high probability of divorce, whereas those who were unsuccessful had a low

probability of divorce (males $p = 0.003$, females $p = 0.014$; table 4). Furthermore, in no cases did divorcing females pair with a long-term male member of their family flock. These results are consistent with the inbreeding avoidance hypothesis.

**(c)  *The 'forced divorce' hypothesis***

For both sexes, divorce was typical when they had helpers in year $N$ (84% divorce, $n = 19$ for both sexes), and significantly less frequent when a pair had no helpers (males 47%, $n = 30$, $\chi^2 = 6.91$, d.f. = 1, $p = 0.009$; females 52%, $n = 29$, $\chi^2 = 5.30$, d.f. = 1, $p = 0.02$). This association between the presence of helpers in year $N$ and subsequent divorce might have resulted from helpers forcing the divorce of helped pairs. However, it is unlikely that helpers *per se* were responsible for divorces because in just two out of five cases where a male breeder and an unrelated female helper survived to year $N + 1$ did the male divorce and re-pair with the female helper, and in not one out of the nine cases where a female breeder and an unrelated male helper survived to year $N + 1$ did they pair up. Therefore, the observed association of divorce with helpers in year $N$ is probably a consequence of the close association between divorce and reproductive success reported in the previous section.

Nevertheless, this hypothesis may explain some instances of divorce. Thirty-six per cent of males and 43% of females (table 4) who were unsuccessful in year $N$ divorced even though there was no obvious risk of inbreeding. The likely explanation for these divorces concerns a failed breeder's decision of whether to become a helper. Helping is male biased, but the female partners of helpers usually continue to associate with their partner and join the resulting family flock. By contrast, failed pairs of which neither member becomes a helper form adult flocks with other failed breeders who have not helped (Russell 1999; B. J. Hatchwell, unpublished data). We hypothesized that competition for partners (and hence divorce) would be more severe in these adult flocks

than in family flocks, where most members are juveniles. As expected, most failed pairs from which one or both sexes became helpers were faithful in year $N+1$ (92%, $n=12$), and a relatively small proportion of failed pairs in which neither sex helped were faithful in year $N+1$ (30%, $n=10$; Fisher's exact test, $p<0.005$). Furthermore, the new partners of failed, non-helping divorcees had themselves come from failed, non-helping pairs in most cases (67%, $n=9$ cases where status of new partner in year $N$ was known). This difference in divorce rate of failed breeders in adult and family flocks is consistent with the forced divorce hypothesis.

## 4. DISCUSSION

To our knowledge, this is the first documented case of successful breeders being more likely to divorce than unsuccessful breeders. This pattern of divorce does not support the better option hypothesis, but it is consistent with the hypothesis that divorce is a consequence of inbreeding avoidance. There was also some limited support for the forced divorce hypothesis among unsuccessful breeders. Our tests of the competing hypotheses are not strictly independent in the sense that the presence of philopatric sons is closely linked to reproductive success. There may also have been confounding effects of group size on divorce rate. This possibility is difficult to test directly because flock size changes through the non-breeding season due to mortality and female dispersal. However, the fact that failed pairs that joined family flocks were generally faithful (92% partner fidelity) while breeding pairs in family flocks usually divorced (table 4) indicates that flock size *per se* did not affect divorce rate. An alternative explanation for a higher divorce rate among successful pairs than among unsuccessful pairs is that divorcees are seeking to increase the genetic diversity of their offspring, but theory suggests that any advantage accruing from such a strategy is likely to be small (Williams 1975; Brown 1997).

In most monogamous birds, divorce occurs among relatively unsuccessful pairs, or is unrelated to previous breeding success (Ens *et al.* 1996), and the long-tailed tit appears to be unique in showing a higher rate of divorce for relatively successful pairs. Limited evidence for the forced divorce hypothesis was obtained for failed breeders in adult flocks of non-helpers, but there was no evidence that helpers were responsible for the divorce of successful pairs. This differs from Reyer's (1986) study of cooperatively breeding pied kingfishers *Ceryle rudis* in which helpers often evicted breeding males to pair with the female breeder. However, in contrast to long-tailed tits, the usurping helpers in pied kingfishers are unrelated to either breeder and so are likely to be in more direct conflict over reproductive status. It should also be noted that although our observation of frequent divorce and re-pairing within adult flocks of long-tailed tits is consistent with the forced divorce hypothesis, we have no direct evidence of contests over partners in these flocks, and a similar pattern might emerge from random re-pairing within flocks of adults.

Our favoured explanation for the frequent divorce of successful pairs is founded on the well-established idea that dispersal strategies are driven, in part, by inbreeding

avoidance (Johnson & Gaines 1990; Weatherhead & Forbes 1994). In mongamous species, dispersal by one or both sexes usually occurs prior to reproduction, so there is no need for subsequent dispersal (hence divorce) to avoid incest. Among cooperative breeders, reproduction by subordinates within intact families appears to be rare (Reeve *et al.* 1990; Keane *et al.* 1996). Nevertheless, incestuous pairing may become a possibility when one breeder dies. In such circumstances, contests over reproductive status among opposite-sex relatives have been frequently reported (e.g. Hannon *et al.* 1985; Zack & Rabenold 1989; Zahavi 1990; Koenig *et al.* 1998). These power struggles are usually resolved by the dispersal of one sex, for example, in red-cockaded woodpeckers *Picoides borealis* females leave a territory when their partner dies, leaving philopatric sons to attain reproductive status with immigrant females (Walters 1990). Therefore, a strategy of dispersal to avoid inbreeding is not an unusual feature in cooperative breeding systems. What is remarkable is that in the unusual cooperative breeding system of long-tailed tits, where all philopatric sons are reproductive from their first year, avoidance of inbreeding may result in a counter-intuitive prevalence of divorce among successful breeders. Moreover, in most cooperative breeding systems, selection for mate fidelity may be strong because breeding vacancies are limiting (Emlen 1982) and divorce may result in forfeiture of breeding status. By contrast, constraints on independent reproduction by long-tailed tits are weak (Hatchwell *et al.* 1999), so there may be little cost of divorce in terms of future breeding opportunities. In addition, the adult mortality rate of long-tailed tits is relatively high (Arnold & Owens 1998; Hatchwell 1999), so the opportunity for long-term pair-bonds to develop is limited.

Close inbreeding appears to be rare in long-tailed tits. We have observed just one instance where a female bred with a male from her own nest. In this exceptional case, the juvenile male switched flock shortly after independence and was probably perceived as a member of a different flock by the female, rather than as a member of her own family. Nevertheless, a low level of inbreeding might be expected in any sedentary species with moderate or high survival and frequent re-pairing. Indeed, inbreeding avoidance may not evolve at all if the costs of avoidance exceed the costs of inbreeding (Waser *et al.* 1986), as appears to be the case in song sparrows *Melospiza melodia* (Keller 1998; Keller & Arcese 1998). The absence of a significant level of inbreeding in our populations means that we are unable to evaluate its cost, even using the indirect method of Koenig *et al.* (1999).

If we assume that there is a net cost of inbreeding in long-tailed tits and hence selection for inbreeding avoidance, there are three reasons why females might divorce and leave the family flock. One possibility is that females are evicted by their philopatric sons (Emlen 1995), but at present we have no behavioural observations to indicate whether females are evicted or disperse voluntarily. Second, females may move to pre-empt the death of their partner. In a family flock with no helpers a female has only one unrelated potential partner for year $N+1$ (her partner in year $N$), in a family flock with one helper there are two potential partners (partner and helper), and so on. Each potential partner has only a 56% chance of

survival to the following season. In an unrelated family flock, there may be a similar number of unrelated adults, but also some unrelated juvenile males who are potential partners in year $N+1$. Therefore, the best strategy for a successful female to adopt may be to leave her family and join another flock. The fact that the male partner in year $N$ is often alive in year $N+1$ (hence divorce) suggests that females move away from the family before pair formation in early spring. A third possibility is that recognition errors increase the chance of inbreeding. A successful female has related and unrelated males in her family flock. The kin-recognition mechanism of long-tailed tits is not yet fully understood (Komdeur & Hatchwell 1999), and it is not known whether recognition cues are specific to individuals or families. In the latter case a female may be unable to discriminate reliably between her philopatric sons and her partner. Therefore, it might pay to adopt a cautious strategy of dispersing to pair with a male from another flock to reduce the risk of accidental pairing with kin. Long-tailed tits can discriminate between the calls of familiar and unfamiliar individuals (B. J. Hatchwell, unpublished data), but an understanding of whether recognition cues enable discrimination at the level of the individual or the family is critical for our understanding of the options available to individuals wishing to avoid pairing with their relatives.

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