

## REPRODUCTIVE SUCCESS AND NEST-SITE SELECTION IN A COOPERATIVE BREEDER: EFFECT OF EXPERIENCE AND A DIRECT BENEFIT OF HELPING

B. J. HATCHWELL,<sup>1</sup> A. F. RUSSELL, M. K. FOWLIE, AND D. J. ROSS

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

**ABSTRACT.**—We determined whether nest-site characteristics influence reproductive success and whether experience influences nest-site selection in a population of cooperatively breeding Long-tailed Tits (*Aegithalos caudatus*). Nest predation was high; only 17% of breeding attempts resulted in fledged young. The height of nests was an important determinant of success; low nests were significantly more successful than high nests. A breeder's age, natal nest site, and breeding experience had no significant effect on nest-site selection. However, failed breeders who helped at the successful nests of conspecifics built subsequent nests lower than nests built prior to their helping experience. Failed breeders who did not help showed no reduction in the height of subsequent nests. Moreover, the subsequent reproductive success of failed breeders who helped was significantly higher than that of failed breeders who did not help. We conclude that helpers gain information on nest-site quality through their helping experience and thus gain a direct fitness benefit from their cooperative behavior. We suggest that experience as a helper offers a more reliable cue to nest-site quality than breeding experience because helpers are associated with nests only during the nestling phase when few nests are depredated. In contrast, although successful breeders may experience success with a low nest, they are even more likely to have experienced the failure of low nests because of the high rate of nest predation. Received 26 December 1997, accepted 28 July 1998.

A MAJOR DETERMINANT of reproductive success for many organisms is the ability of breeders to protect their offspring from predation. This is particularly true of many open-nesting passerines where the rate of nest predation may be extremely high (Lack 1954, Ricklefs 1969, Martin 1995). A variety of antipredator strategies has evolved among birds to reduce nest predation, including colonial or dispersed breeding, use of cavities, nest concealment or camouflage, elaborate nest design, and protective nesting associations (see Collias and Collias 1984). Numerous studies have shown an intraspecific relationship between nesting success and various characteristics of nests or nest sites, e.g. nest structure (Baeyens 1981), nest density (Andersson and Wiklund 1978, Potts et al. 1980, Hatchwell 1991, Chamberlain et al. 1995, Meilvang et al. 1997), and nest conspicuousness (Picman et al. 1993, Hatchwell et al. 1996), although other studies have shown no such effect (e.g. Holway 1991, Colwell 1992, Filiater et al. 1994, Cresswell 1997a). If predation risk is random with respect to nest-site char-

acteristics, then no consistent selection may exist for choice of particular nest sites. However, if breeding success is consistently related to certain nest traits, then high rates of nest predation will exert strong directional selection against the choice of low-quality sites by breeders, resulting in low variance in the critical characteristics. Alternatively, in the absence of consistent selection for particular nest sites, site choice may be a variable trait, with adaptive nest-site choice occurring either through a learning process of trial and error, or as a conditional behavior depending on predation risk or habitat type.

Individual breeding performance can increase with age and experience in many vertebrates (see Clutton-Brock 1988), and this has often been attributed to increased foraging efficiency (e.g. Desrochers 1992a,b) or increased reproductive effort; i.e. the "constraint" and "restraint" hypotheses of Curio (1983). Individuals may acquire foraging skills at any time, but more specialized parenting skills, such as nest placement or incubation, may only be acquired through breeding. Such experience may be gained through personal reproduction (e.g. Marzluff 1988, Marzluff and Balda 1992) or

<sup>1</sup> E-mail: b.hatchwell@sheffield.ac.uk

through observation of others (e.g. Boulinier et al. 1996), but among cooperative breeders it also may be acquired by helping a breeding pair rear its offspring (Brown 1987). Few studies have shown a direct benefit to helpers of increased experience, although notable exceptions exist. In White-winged Choughs (*Corcorax melanorhamphos*), helpers acquire foraging skills during their long prebreeding association with cooperative groups (Heinsohn et al. 1988), and in Seychelles Warblers (*Acrocephalus sechellensis*), both helpers and breeders gain experience in nest building, nest guarding, and incubation (Komdeur 1996).

In this study, we used the cooperative breeding system of the Long-tailed Tit (*Aegithalus caudatus*) to investigate the effects of nest site on reproductive success and the effects of experience on nest-site selection. Long-tailed Tits build domed nests in very diverse sites and suffer high rates of failure, largely caused by predation (Lack and Lack 1958, Gaston 1973, Glen and Perrins 1988). A new nest is built for every breeding attempt, and a pair builds between one and four nests in a single season. Each nest constitutes a large reproductive investment because they are among the most elaborate structures of any European bird species and require a lengthy but variable building period (the average building period for first nests of the season was 25 days, although later nests were built in just 8 days; B. J. Hatchwell unpubl. data). The nest is made of moss bound with spider's silk, the exterior is covered by several thousand pieces of lichen, and the interior is lined with an average of about 1,500 feathers (Hansell 1993, B. J. Hatchwell unpubl. data). The sex ratio is 1:1 in the cooperative breeding system of Long-tailed Tits, and all birds attempt to reproduce in pairs. If their own breeding attempt fails, however, breeders may become helpers at the nests of their relatives, assisting in the care of nestlings and fledglings (Lack and Lack 1958, Gaston 1973, Glen and Perrins 1988, Hatchwell and Russell 1996). Thus, helpers may gain information about what constitutes a successful nest site through their own breeding experience and/or by helping another pair.

First, we investigate whether the high predation rate of Long-tailed Tit nests is influenced by characteristics of the nest site. We show that nest placement plays an important role in determining breeding success. Second,

we investigate whether and how individuals acquire information about nest-site quality. In particular, we examine the hypothesis that experience gained through helping at the nest of conspecifics influences subsequent selection of nest sites.

#### METHODS

We studied a population of 15 to 35 pairs of Long-tailed Tits from 1994 to 1997 in the Rivelin Valley, Sheffield, United Kingdom. The study site (ca. 3 km<sup>2</sup>) comprised a variety of habitats including hedgerows, scrub, mature deciduous woodland, and small stands of coniferous trees. The breeding attempts of individually marked birds were closely monitored throughout each breeding season (March to June). We found a total of 178 nests belonging to 67 males and 68 females. Each individual was represented by between one and eight nests in our data set. In some analyses, this raises the potential difficulty of pseudoreplication, but we considered each nest to be independent in analyses of reproductive success with respect to site characteristics. This is justified because although some nests belonged to the same birds, each was located in a different site, and it is nest location that is important for this question (Hatchwell et al. 1996, Cresswell 1997b). Furthermore, nests of the same individual often encompassed the whole range of possible nest sites, and the same individuals did not build successive nests at the same height (males,  $F = 1.33$ ,  $df = 38$  and  $97$ ,  $r = 0.086$ ; females,  $F = 2.28$ ,  $df = 36$  and  $81$ ,  $r = 0.294$ ). In analyses concerning experience and nest sites, we used individuals as independent data. Divorce was frequent both within and between seasons (B. J. Hatchwell unpubl. data), so we treated the sexes separately in analyses of nest-site selection.

The great majority of nests was found during the early stages of building. Although we made particular efforts to find replacement nests following nest failure, a few nests were never found; this was usually attributable to renesting of failed pairs outside the study area and so was unlikely to bias the sampling of nests. Nests were visited every one to three days during building, laying, and incubation and were observed every two days during the nestling period to record the presence and identity of helpers. Frequent nest visits might elevate nest predation rates if potential predators observe such visits or if visits reduce nest concealment (Mayfield 1975, Lenington 1979). We do not consider that an observer effect on nest predation biased our results in any way for three reasons. First, depredated nests were usually torn apart (see below), creating a "drift" of feathers from the lining, so the survival of the great majority of nests could be checked from a distance of several meters. Nest contents of accessible nests were

checked only to confirm the start of laying, clutch size, hatching, and during banding of nestlings. Second, most of the nests placed high in trees were relatively inaccessible and so were visited only if they survived to day 11 of the nestling period, when chicks were banded (laying, incubation, and hatching dates for these nests were recorded by observation of parental behavior). Therefore, if nest visits increased predation rates, low nests would have had a lower success rate than high nests, the opposite of the pattern found (see below). Third, evidence from an extensive experimental study ( $n = 766$  nests) of open-nesting passerines in Britain found no effect of nest visits on predation rates (Mayer-Gross et al. 1997).

We recorded the plant species that provided the main support for the nest. Nests were found in 15 plant species, mainly bramble (*Rubus fruticosus*; 23%), gorse (*Ulex europaeus*; 16%), holly (*Ilex aquifolium*; 15%), or hawthorn (*Crataegus monogyna*; 11%). The remainder were in conifer, birch (*Betula* spp.), or alder (*Alnus glutinosa*) trees. Nest sites were classified as being either in a tree fork or supported by peripheral branches and also by the type of vegetation being either "protected" by thorns on stems or leaves (e.g. holly, bramble, gorse, etc.) or "unprotected" (mostly other tree species, but also honeysuckle [*Lonicera periclymenum*] and bracken [*Pteridium aquilinum*]). Nest height was measured to the nearest 0.5 m; a simple triangulation technique was used to measure the height of nests that could not be reached directly.

Nest predators were identified from nest remains; corvids typically tear off the top of the nest, whereas mammalian predators gain access via the nest hole or enlarge the nest entrance in a less destructive manner than avian predators (Gaston 1973). Fourteen nests that were surrounded with chicken wire for protection against predators were included in analyses of nest-site selection because the nests were initiated before we protected them; these same nests were excluded from analyses of breeding success. Means are given  $\pm 1$  SD unless otherwise indicated.

## RESULTS

**Reproductive success.**—Only 17% ( $n = 158$  total) of the nests produced fledglings. The main cause of breeding failure was predation (79%) and abandonment (15%). The remaining losses were caused by bad weather (2%), death of a parent (1%), or unknown factors (3%). Nest remains suggested that birds were the main predators (85% of 95 nests where the likely predators were identified), the remainder being mammals. Eurasian Jays (*Garrulus glandarius*) and Black-billed Magpies (*Pica pica*) were the

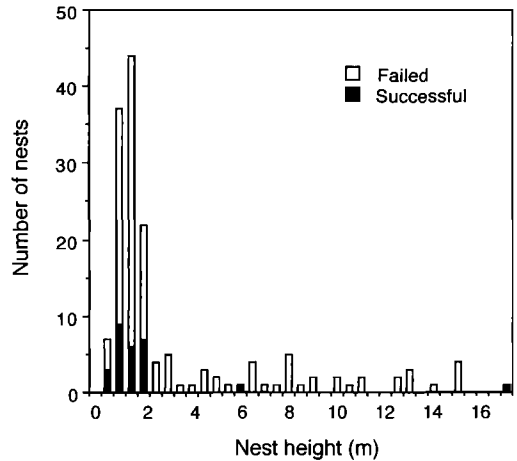


FIG. 1. Frequency distribution of heights at which Long-tailed Tits built their nests ( $n = 158$ ).

most likely avian predators; in three instances predators were seen at nests (two were jays and one a magpie). Other bird species use active Long-tailed Tit nests as a source of nest material and may have been responsible for a small proportion of abandonments; however, they were not implicated as a cause of nesting failure once eggs had been laid. Weasels (*Mustela nivalis*) and gray squirrels (*Sciurus carolinensis*) were abundant in the study area and probably were responsible for all depredations by mammals.

The cause of nesting failure varied throughout the nesting cycle. Most of the abandonments (95%;  $n = 20$ ) occurred during the building phase, often when bad weather disrupted early nests. Nest predation ( $n = 104$ ) occurred during all phases but was most frequent during incubation (40%, vs. 15% during nest building, 27% during laying, and 17% during the nestling phase;  $\chi^2 = 14.96$ ,  $df = 3$ ,  $P < 0.01$ ). Failure during building occurs because avian predators cannot see a nest's contents without first removing its roof. Avian predators were most likely to destroy nests during the laying and incubation phases (70% of cases;  $n = 81$ ), whereas mammalian predators were more likely to destroy nests during the nestling phase (50% of cases;  $n = 14$ ), when olfactory and auditory cues may facilitate nest location.

**Nest sites and reproductive success.**—Nest height varied from 0.5 to 17 m (Fig. 1) and had a significant effect on reproductive success; 23% of the nests within 2.25 m of the ground ( $n$

TABLE 1. Nest height ( $\bar{x} \pm$  SE, with number of breeders in parentheses) in relation to age of breeders for all nests built by known-age Long-tailed Tits in each year and the first nest built by known-age birds in each year.

Sex	Age of breeder <sup>a</sup>		
	First year	Second year	Third year
<b>All nests</b>			
Female	4.47 $\pm$ 1.72 (5)	3.44 $\pm$ 1.29 (3)	—
Male	3.89 $\pm$ 0.77 (25)	2.97 $\pm$ 0.70 (13)	1.38 $\pm$ 0.37 (2)
Total	3.99 $\pm$ 0.69 (30)	3.06 $\pm$ 0.61 (16)	1.38 $\pm$ 0.37 (2)
<b>First nests only</b>			
Female	4.20 $\pm$ 2.71 (5)	1.30 $\pm$ 0.17 (3)	—
Male	3.74 $\pm$ 0.77 (25)	2.62 $\pm$ 1.08 (13)	1.25 $\pm$ 0.25 (2)
Total	3.82 $\pm$ 0.76 (30)	2.38 $\pm$ 0.88 (16)	1.25 $\pm$ 0.25 (2)

<sup>a</sup> All differences among ages within sexes and for totals were not significant (Kruskal-Wallis or Mann-Whitney tests,  $P > 0.05$ ).

= 110) were successful versus only 4% ( $n = 48$ ) of the nests higher than 2.25 m above ground ( $\chi^2 = 6.87$ ,  $df = 1$ ,  $P < 0.01$ ; Fig. 1). Thus, successful nests were significantly lower than nests that failed (successful nests,  $\bar{x} = 2.09 \pm$  SD of 3.15 m,  $n = 27$ ; failed nests,  $\bar{x} = 3.63 \pm$  3.90 m,  $n = 131$ ; Mann-Whitney  $U$ -test,  $z = 2.44$ ,  $P < 0.02$ ). Indeed, the highest of the two successful nests that was more than 2.25 m above ground (17 m; see Fig. 1) was attacked by a predator two days before normal fledging age of the young, but because three of the brood of approximately nine chicks escaped predation and fledged, this nest was classified as successful.

Nests in forks were less successful than those in peripheral branches (forks, 0% success,  $n = 22$ ; branches, 20% success,  $n = 136$ ;  $\chi^2 = 3.96$ ,  $df = 1$ ,  $P < 0.05$ ). Nests in protective vegetation tended to be more successful than those in unprotected vegetation, although the difference was not significant (protective, 21% success,  $n = 110$ ; unprotected, 8% success,  $n = 48$ ;  $\chi^2 = 2.90$ ,  $df = 1$ ,  $P < 0.09$ ). Nest height and plant species clearly are not independent, but height was probably the more important factor; none of the nests in protective vegetation above 2.25 m was successful ( $n = 10$ ), whereas 23% of those below 2.25 m succeeded ( $n = 100$ ; Fisher's exact test,  $P = 0.08$ ).

*Factors influencing nest-site selection.*—The natal nest may be a reliable cue to first-time breeders as to what constitutes a good nest site. We knew the first nest site of 31 fledglings from the study area that recruited into the breeding population in a subsequent year. The later nests of a further five recruits also were recorded.

The height an individual's first nest as a breeding adult was not significantly correlated with that of its natal nest (Spearman correlation,  $r_s = -0.144$ ,  $n = 31$ ,  $P = 0.77$ ), and a negative correlation existed between an individual's mean nest height and the height of its natal nest ( $r_s = -0.359$ ,  $n = 36$ ,  $P < 0.05$ ). These results are inconsistent with the idea that the natal site provides cues for subsequent nest-site selection. Philopatric recruits were both male ( $n = 30$ ) and female ( $n = 6$ ), but no significant relationship existed between heights of natal and later nests when each sex was analysed separately (Spearman correlations, all  $P > 0.05$ ).

If individuals learn the relative quality of nest sites, a progressive choosing of lower nests might be predicted as birds became older. However, nest height did not decrease significantly as the number of nests built by an individual increased (nest height vs. nest order; males,  $r_s = 0.027$ ,  $n = 64$ ,  $P = 0.83$ ; females,  $r_s = 0.136$ ,  $n = 17$ ,  $P = 0.65$ ). Furthermore, for individuals of known age (i.e. birds banded as nestlings who subsequently bred in the study area) there was no significant effect of age on nest height, using either the mean height of all nests in each year, or just the first nest built in each year (Table 1). The apparent absence of an age effect on nest height should be treated with caution, however, because a nonsignificant tendency existed for nest height to decline with age (Table 1). The sample size for females was very small, and for males and both sexes combined, the power of the tests at detecting a "medium" effect of age on mean nest height between the first and second year was only 0.42 and 0.48, respectively (Cohen 1988).

TABLE 2. Seasonal change in the number of Long-tailed Tit nests built above or below 2.25 m and in the height of nests ( $\bar{x} \pm SE$ ). The frequency distribution of the number of nests built in each height category varied significantly with nest order ( $\chi^2 = 21.6$ ,  $df = 2$ ,  $P < 0.001$ ).

Height category	Nest order		
	First	Second	Third
Below 2.25 m	89	19	11
Above 2.25 m	21	25	7
Mean height (m)	$2.58 \pm 0.30$	$5.03 \pm 0.66$	$3.69 \pm 0.99$

Nest height changed dramatically with season (Table 2) and was not associated with budburst or other seasonal differences in vegetation. Previous studies have suggested that such changes are a response to the experience of failure or success of previous nests (Lack and Lack 1958, Gaston 1973, Glen 1985). A pair whose breeding attempt fails might change nest height and/or move to a new area for a subsequent attempt. For example, Long-tailed Tits may place their first nest of the year in what is perceived to be a "good" location (i.e. a low site) but respond to nest failure by switching to a different location (i.e. a high site) for subsequent nests. In 64 cases, we recorded the height of a failed nest and its replacement within the same season. In 49 of these cases, the pair remained together for the second attempt, but in the remainder the pair divorced and the replacement nest of one or both members of the original pair was recorded. No significant association of height categories was evident, either positive or negative, between successive nests (males,  $\chi^2 = 0.54$ ,  $df = 1$ ,  $P = 0.46$ ; fe-

males,  $\chi^2 = 0.32$ ,  $df = 1$ ,  $P = 0.57$ ; pairs,  $\chi^2 = 0.65$ ,  $df = 1$ ,  $P = 0.42$ ), i.e. failure at one height did not result in a switch to the other height category.

Because Long-tailed Tits are single brooded, we could not compare internest distances following a sequence of successful and unsuccessful attempts in the same year. However, a comparison of the distance moved by failed breeders following nest predation ( $\bar{x} = 175 \pm 132$  m,  $n = 49$ ) or abandonment ( $\bar{x} = 230 \pm 249$  m,  $n = 15$ ) showed that birds did not respond differently to these two causes of failure (Mann-Whitney *U*-test,  $z = 0.357$ ,  $P = 0.72$ ). Glen (1985) suggested that after a nest failure, pairs could either move far away for their next attempt or stay in the same area and switch nest sites, and he predicted a negative relationship between the change in nest height and internest distance. In our study, no such correlation existed for all nest changes ( $r_s = 0.169$ ,  $n = 49$ ,  $P = 0.24$ ) nor for nest changes following predation ( $r_s = 0.282$ ,  $n = 37$ ,  $P = 0.09$ ). Therefore, the variation in nest height within seasons remains unexplained.

Breeding experience had no effect on nest-site selection across seasons. The mean heights of nests built by individuals before and after their first known successful breeding attempt were compared in a population analysis including all successful breeders and in a paired comparison of mean nest heights for the same individuals before and after their first successful breeding attempt (Table 3). In each comparison, experience had no significant effect for either sex. These results suggest that Long-tailed Tits do not respond to the experience of successful reproduction in low nests by building subsequent nests lower down than before that success.

To test for an effect of helping experience on nest-site selection, the mean height of nests built by males before and after their first ex-

TABLE 3. Effect of successful reproduction on nest height in male and female Long-tailed Tits. Values are nest height ( $\bar{x} \pm SE$ , with  $n$  in parentheses) before and after an individual's first successful nest for: (1) all birds that bred successfully at least once, and (2) a paired comparison of birds that bred successfully at least once and for which nest heights were recorded before and after the successful attempt. No differences in before and after nest heights were significant (Mann-Whitney *U*-test and Wilcoxon signed-rank test).

Sex	Before	After
<b>All successful breeders</b>		
Male	$2.34 \pm 0.42$ (24)	$2.31 \pm 0.64$ (13)
Female	$1.91 \pm 0.32$ (27)	$1.65 \pm 0.40$ (12)
<b>Paired comparison</b>		
Male	$2.45 \pm 0.69$ (13)	$2.31 \pm 0.64$ (13)
Female	$2.44 \pm 0.68$ (12)	$1.65 \pm 0.40$ (12)

perience of helping at a successful nest was examined. As before, two analyses were performed, a population analysis including all helpers at successful nests, and a paired comparison of mean nest heights for the same individuals before and after their first experience of helping. The population comparison showed that the mean nest height after helping ( $1.61 \pm 1.05$  m,  $n = 9$ ) was significantly lower than before helping ( $3.82 \pm 3.11$  m,  $n = 18$ ; Mann-Whitney  $U$ -test,  $z = 2.72$ ,  $P < 0.01$ ). Similarly, in the paired comparison of the same individuals, nest height after helping at a successful nest ( $\bar{x} = 1.90 \pm 1.02$  m,  $n = 7$ ) was significantly lower than that before helping ( $\bar{x} = 5.59 \pm 3.75$  m,  $n = 7$ ; Wilcoxon signed-rank test,  $z = 2.37$ ,  $P < 0.02$ ). These results indicate that helpers learn what constitutes a good nest site during their period of helping. Too few female helpers were present to test for an effect of helping experience in females.

Some males whose breeding attempt failed did not help at the nest of another pair, and instead joined a flock of failed breeders. The height of nests of these "nonhelpers" in subsequent seasons ( $\bar{x} = 3.41 \pm 2.19$  m,  $n = 10$ ) did not differ significantly from that prior to their failed breeding attempt ( $\bar{x} = 2.93 \pm 3.96$  m,  $n = 10$ ; Wilcoxon signed-rank test,  $z = 0.95$ ,  $P = 0.34$ ). These results support the previous conclusion that the experience gained by helping during a successful breeding attempt influences subsequent choice of nest sites. Furthermore, the experience of helping had an effect on subsequent reproductive success. Three of seven (43%) failed breeders who helped were successful in the subsequent season, whereas none of the 10 failed breeders who did not help was successful in the following season (Fisher's exact test,  $P = 0.05$ ).

#### DISCUSSION

In the Long-tailed Tits we studied, the main cause of breeding failure was predation, and the probability of predation was higher for nests above 2.25 m than for nests below this height. The choice of nest height by an individual was not influenced by its age at the time of the attempt, by the height of its natal nest, nor by its experience as a successful breeder. However, males who helped at successful nests se-

lected lower sites for their own subsequent nests.

The nesting success rate of 17% was very similar to results of previous studies of Long-tailed Tits conducted in similar habitats (Lack and Lack 1958, Riehm 1970, Gaston 1973, Glen 1985). Small open-nesting passerines often suffer high rates of nest predation in woodlands (Ricklefs 1969, O'Connor and Shrubbs 1986, Møller 1988, Hatchwell et al. 1996), but the proportion of nests lost to predators by Long-tailed Tits was particularly high. Nest-site characteristics had a significant effect on the success of Long-tailed Tit breeding attempts. Nest height was the most important factor measured, and the vegetation providing support for nests had little additional effect on nesting success. The effect of nest height on reproductive success was consistent with previous studies, which have shown similar height profiles and a similar decline in success with increasing nest height (Lack and Lack 1958, Riehm 1970, Gaston 1973). This consistent effect of height on the success of breeding attempts raises an obvious question: why do Long-tailed Tits continue to build nests in predictably unsuccessful sites given the strong selection pressure against high nests? Several explanations are possible for this apparently maladaptive behavior: (1) suitable sites are in short supply; (2) nest building in high sites is maintained by gene flow from areas where high nests are relatively successful; (3) high nest sites may be more successful in some years than in others; and (4) the ability of breeders to choose a successful site may be limited if they have little information as to what constitutes a good site.

*Suitable sites in short supply.*—Long-tailed Tits are relatively unconstrained in their choice of nest site because they occur in low densities and are not territorial during the breeding season, except for a small area immediately surrounding the nest (Cramp and Perrins 1993). Defense of the nesting area by established pairs declines as the season progresses, and in three instances late replacement nests were built within 20 m of active nests. Because a shrub layer of holly and brambles was extensive throughout much of the study site, low nest sites were abundant, and birds did not appear to be forced to attempt breeding in unsuccessful sites (e.g. conifers or tree forks) in any part of the study area. Our contention that suitable

low nest sites were available to all pairs is further supported by the fact that pairs occupied large breeding home ranges ( $\bar{x} = 4.37 \pm 1.91$  ha,  $n = 17$ ) and often moved long distances between successive attempts within a season ( $\bar{x} = 188 \pm 166$  m,  $n = 64$ , range 24 to 1,000 m).

*Gene flow from other habitats and temporal variation in success.*—Although high nests were relatively unsuccessful in this study, it is possible that in adjacent areas or in some years high nests do relatively better. Either possibility could maintain apparently maladaptive selection of nest sites in our study population. Long-tailed Tits are sedentary in nature (Cramp and Perrins 1993), and philopatric recruitment is high within our study area (about 20% of fledglings recruit into the study population). The average distance between an individual's natal nest and its first breeding attempt was 522 m for females and 693 m for males (B. J. Hatchwell unpubl. data). This low dispersal suggests that extensive gene flow into the study population from areas with radically different habitat structure is unlikely. Moreover, previous studies conducted over several seasons have found similar site effects to those reported here (Lack and Lack 1958, Riehm 1970, Gaston 1973), and in this study we found no significant annual variation in success rates of nests with respect to nest height. Therefore, we consider it unlikely that either of the possibilities noted above explains the choice of unsuccessful sites by Long-tailed Tits in our study population.

*Learning and a direct fitness benefit from helping.*—Finally, we consider the question of how individuals may gain information about the relative quality of different types of nest site. In the apparent absence of an innate preference for the most successful sites, what cues are available to birds when deciding where to build their nests?

One possibility is that the natal nest is used as a template for subsequent choices as a breeder. However, no correlation existed between heights of natal nests and first nests, nor between natal nests and the mean height of all subsequent nests. Second, an age-related change may occur in nest-site selection if, for example, individuals acquire information about predator behavior or about what constitutes a good or bad nest site through experience or observation of neighboring nests. No support was apparent for this hypothesis, although a tendency existed for nest height to de-

crease as birds grew older. Thus, some effect of experience may be weakly correlated with age.

Third, an individual's experience of successful reproduction might influence nest-site selection through a mechanism of trial and error, as shown in the Pinyon Jay (*Gymnorhinus cyanocephalus*; Marzluff 1988). No support existed for the hypothesis that an individual's personal reproductive experience influenced its nest-site selection (Table 3). However, the cooperative behavior of Long-tailed Tits offers a further source of experience; viz. the "skills" hypothesis of Brown (1987). In typical cooperative breeders, helping precedes dispersal and independent breeding (Emlen 1991), so helpers may gain direct fitness by improving their parenting skills, e.g. in nest building, incubation, or the provisioning of nestlings. In one of the few studies to demonstrate skill acquisition through helping, Komdeur (1996) showed that female Seychelles Warblers with helping experience constructed better nests than females of the same cohort but with no prior experience. Nests built by birds with helping experience were less likely to fall out of trees, and their reproductive success was consequently higher. Our results support the hypothesis that the experience gained from helping has a positive influence on nest-site selection. Long-tailed Tits are atypical cooperative breeders because they may have repeated opportunities for helping in successive years. Therefore, any tendency for nest height to decrease with age (Table 1) would be consistent with experience in nest placement gained through helping. This benefit of helping behavior was reflected in a higher probability of successful reproduction in subsequent seasons, although the sample size was small, and it is possible that individual quality is a confounding factor that influences success. Long-tailed Tit helpers are known to accrue indirect fitness benefits through their cooperative behavior (Hatchwell and Russell 1996), but the effect of helping experience on nest-site selection may represent a significant source of direct fitness benefits for helpers in this species.

Why should the experience of success through helping at the nest of a conspecific, but not the personal experience of an individual's own success, influence nest-site selection? The most likely explanation is that although low nests are more successful than high nests, they still have a very high failure rate (Fig. 1). Thus,

successful breeders may have experienced success with a low nest, but a high probability exists that they also will have experienced the failure of low nests. In fact the ratio of failures: successes was 3:1 even for low nests, so this criterion would provide a rather poor cue to the attributes of a good nest site.

Experience through helping provides a less ambiguous cue. Helpers arrive at nests to help only during the nestling period. Nesting failure at this stage is much lower (44%), and an even smaller proportion of nests fail after helpers have arrived (18%). Therefore, learning based on helping experience offers a more reliable cue about what constitutes a good nest site. This cue is available mainly to males because females rarely help (Glen 1985, B. J. Hatchwell unpubl. data). In this regard, it is interesting that Riehm (1970) noted from behavioral observations that males assume the primary role in nest-site selection.

In conclusion, our results indicate that Long-tailed Tits learn about nest-site quality through the experience of helping at successful nests and not through a process of trial and error using their own nests. Nevertheless, no reason is obvious why the choice of nest sites with very low probability of success persists despite the strong selection against such apparently maladaptive behavior. Perhaps the most likely explanation is that although low nests are more successful than high nests, the majority of low nests still fail. Therefore, experience of frequent reproductive failure in low nests may result in selection of alternative nest sites, even though their success rate is even lower.

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