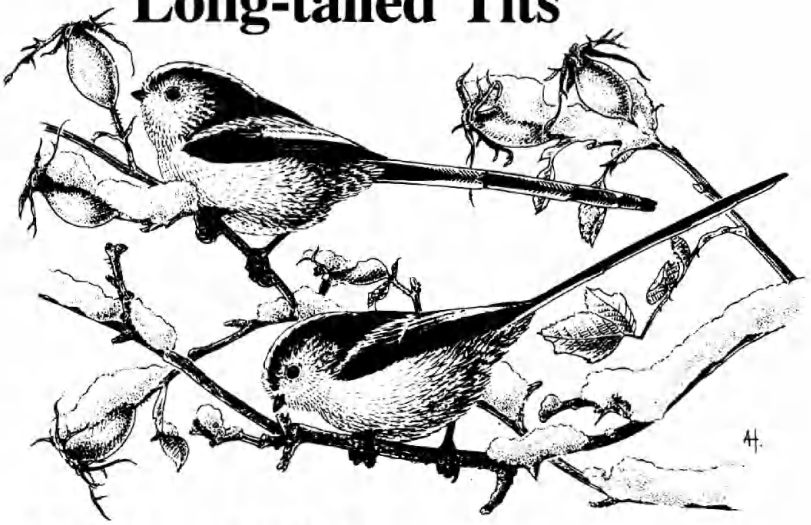
Co-operative breeding by Long-tailed Tits



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For most of this century, ornithologists have tended to believe that the majority of birds breed monogamously, with either the pair or, in some species, the female alone raising the brood; to find more than a single pair at a nest was considered to be atypical. Nevertheless, a few species were known where this occurred, and one of these was the Long-tailed Tit *Aegithalos caudatus*; there are many early references to three or more individuals attending the young at a nest (see Lack & Lack 1958 for some of these).

During the last 15 years or so, the view that co-operative breeding was rare has been shattered by a great many studies which have shown that it is in fact widespread among birds. The 'error' seems to have arisen because the vast majority of early studies of birds took place in the north temperate region (mainly in Europe and North America), whereas the large majority of the birds that breed co-operatively occur in the tropics and in southern latitudes.

The reasons for this geographic variation have been, and still are, extensively debated. An over-simplification, certainly not tenable in all cases, runs as follows. Some bird species that breed in geographical areas where the climate is relatively equable throughout the year may occupy all the habitat available to them; there are no times of year—as there is, for example, in Britain—when life is so difficult for the birds that many die and there are vacant territories. In addition, in these species, the territory owners tend to defend their territories all the year around. When their young reach the age of independence, they face a serious problem: there is no empty area where they can settle.

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As a result, the young tend to stay at home, remaining in the natal territory in some cases for several years; usually, they do not breed during this period, though they do help to defend the territory and may also help to raise their parents' young from later broods (i.e. their own brothers and sisters). Such birds are normally referred to as helpers.

'Everybody' gains from this (otherwise the habit would not have evolved). The parents gain from these activities, since larger groups can more successfully defend a territory than can smaller ones, and they get help with raising the young. The juveniles gain because their survival and chances of eventually gaining a breeding place are enhanced. There are differences between the sexes here. Presumably because of the long-term disadvantages of close inbreeding, both sexes cannot remain in the natal territory for ever; eventually (though in some cases not for a year or more), the young females tend to go into neighbouring groups and be accepted by them. The young males obtain a breeding site either by inheriting the natal one when their father dies or, if the group is sufficiently successful and grows in size, by budding off a territory with a small gang (consisting of brothers and immigrant females) from the parents' territory. If large enough, this group stands a chance of flourishing and establishing itself, especially if neighbouring groups have been less successful and are small.

There is another advantage in helping one's parents raise young. Natural selection favours animals which leave many offspring because offspring share genes with their parents; hence those animals that leave many offspring leave many copies of their own genes. But organisms also share genes with relatives other than their own offspring, and hence, if a young bird cannot itself breed, it can still ensure that some of its genes are passed on to future generations by helping to raise, for example, its brothers and sisters, or even their offspring. This is known as kin selection (Hamilton 1964; Woolfenden & Fitzpatrick 1985).

The purpose of this present paper is to describe the behaviour of the Long-tailed Tit in the context of its co-operative behaviour. It is based largely on field studies carried out in Wytham Wood near Oxford during the years 1980-83 by NWG (Glen 1985).

Long-tailed Tits in winter

Winter flocks

As is widely known, Long-tailed Tits live in small parties. By ringing broods together with their parents, we have been able to show that these flocks are essentially family parties, made up of a brood, its parents and any extra adults that helped to raise that brood. These flocks are fairly constant in membership (except for losses due to death) from the end of one breeding season until they start to break up at the beginning of the next one. In Wytham in the winter of 1981/82, the size of 15 flocks varied from six to 17 and averaged 10.6; while, in 1982/83, the size of 21 flocks varied from six to 14, with an average of 8.8.

Each flock maintains a winter territory. In Wytham, 15 territories averaged about 25 ha in 1981/82, and 21 territories averaged 17 ha in 1982/83. Since the territories are quite large, the birds in one flock do not

often come into contact with those in another; when they do, they defend their boundary vigorously. In each of the two years of the study, the larger the flock, the larger the area of the winter territory.

Winter survival

The reasons why Long-tailed Tits live in these communal flocks may be different from those of their tropical counterparts. Long-tailed Tits are unusually small for a bird living at this latitude, and small birds are particularly vulnerable in cold weather. The reason for this is obvious when one realises that such small birds, weighing only 6-8 g, have a body temperature of over 40°C and yet, from time to time, they have to survive night temperatures of −20°C, a feat which is an amazing advertisement for the insulating properties of feathers.

336. At least nine Long-tailed Tits *Aegithalos caudatus* roosting under eaves of house, Dumfriesshire, January 1965 (see *Brit. Birds* 71: 362) (*Robert T. Smith*)

Nonetheless, winter survival is often difficult for small birds, and prolonged periods of hard weather may wreak havoc with populations of Long-tailed Tits, Wrens *Troglodytes troglodytes* and Goldcrests *Regulus regulus*. For example, large declines in numbers were noticed after the hard winter of 1946/47 (Ticehurst & Hartley 1948) and after the long, cold winter of 1962/63 (Dobinson & Richards 1964); indeed, after the latter winter, Long-tailed Tits seemed to be virtually extinct in Wytham.

Some of these small birds have special ways of minimising the effect of extreme cold. Wrens (like many of the tits) roost in holes, which gives them some protection from the most severe weather; in very cold periods, they have often been reported to roost communally, so helping to keep each other warm. Long-tailed Tits do not roost in holes, but they do roost together in groups. On mild nights, they may just sit close to each other,

but not in contact; on cold nights, however, they huddle very close (plate 336). We suggest that this is not only extremely important for birds, but that it may also be the factor which has resulted in them living in parties throughout the winter. Going to roost on its own in a cold period in winter may be tantamount to suicide for a Long-tailed Tit. It may also be important for them to live in groups during the day; they are one of the very few British species that are almost entirely insectivorous even during the winter, and it may be crucial for them to defend a feeding area; certainly, they have serious-looking interactions with adjacent flocks of Long-tailed Tits on their territory boundaries.

Preparing for breeding

In early spring (as early as February in a mild year), Long-tailed Tits start to prepare for breeding. The first signs of this are that they are seen moving about in twos, and not in flocks, during the day. These couples are of interest. It will be remembered that the flocks are composed primarily of family parties. Hence pairs from a winter flock would be made up mainly of brothers and sisters, In fact, at this time, there is considerable shuffling between flocks, with the females moving from the flock they lived in all winter into another. Usually this is an adjacent flock, but, obviously, those that go farther are more likely to be missed, so that it is difficult to give unbiased proportions. Hence, pairs seen in spring are made up of males from the winter flocks and females that have come into that flock area in early spring.

These pairs set up individual territories within the area occupied by the male's flock in winter. The boundaries of these do not seem to be very vigorously defended, so they are difficult to delineate. One might expect them to be more strongly defended on those sides where they coincide with the edge of the winter flock's territory, but we do not know whether this is so or not.

The pairs continue to rejoin the flock (including, now, the new females) each night and to roost communally. This goes on throughout the nest-building stage until the roof of the nest is completed, when the pair starts to roost in it. What happens to the last pair to complete a nest, or when a pair loses its nest to a predator, does not seem to be known, but there are some records of three or more Long-tailed Tits roosting in nests quite early in the season (e.g. Casement 1951); possibly these extra birds are ones which have suddenly found themselves homeless.

Nesting, loss of nests and helpers

The nesting of the Long-tailed Tit has been described in some detail on a number of occasions (e.g. Lack & Lack 1958; Gaston 1973), and this aspect will not be covered in detail here, except to say that, as in previous studies, there was a high loss of nests to predators. Only some 16% of nests yielded fledged young (this does not mean that only 16% of pairs raised young: a pair might have two or more further nesting attempts if it failed the first time).

In most species of birds, if a pair loses its nest, it can either nest again or

give up breeding for that year. The Long-tailed Tit has a further choice: the failed breeders can go and help at another nest. The later in the season that they lose their nest, the more likely they are to do this.

Observations of colour-ringed individuals which had been known to be breeding produced another rather surprising fact. Virtually all those that arrived and helped at nests were known to have lost a nest of their own (and one male whose own brood had fledged three days previously helped briefly at an adjacent nest). In this study, Long-tailed Tits were found to help only at a nest that contained chicks and not at ones in an earlier stage. Failed *pairs* did not, however, go together and help at adjacent nests.

337. Long-tailed Tit *Aegithalos caudatus* collecting nest material, Sussex, April 1988 (*Maurice K. Walker*)

338. Long-tailed Tit *Aegithalos caudatus* with food for young, at nest, France, June 1975 (*G. Olioso*)

Although only 12 colour-ringed helpers, whose relationship with the nesting pair was known, were seen helping at nests, in all 12 cases the helper was related to the male parent (seven helpers were male, one female, and four unsexed). In other words, in all cases, helpers were assisting their brothers to breed. The suspicion has to be, therefore, that the failed breeders go to help relatives raise their young, not just any neighbour. The fact that more males than females were identified amongst the helpers would be expected if this were the case, since the males in adjacent nests within the same winter territory are related, whereas the females are not. In order to find a pair which included a relative, a female would have to go back to her own winter territory, as the single female identified above did. That this was not just a fluke is supported by observations of two other known females which lost nests within the area of one winter territory and were found helping at nests in different ones, although in neither of these cases were the relationships between the female helper and the pair known. In contrast, of the nine males (including the seven noted above) which, having lost nests, went to help at another, none crossed a winter territory boundary to do so.

Effect of helpers on breeding success

The presence of helpers at nests has a number of noticeable effects on the breeding effort. If a helper joins a nest early on, the female spends a greater proportion of the day brooding the chicks than she does in the absence of a helper; as a result, her feeding rate to the chicks is markedly lower than that of a female at a comparable nest without a helper. Consequently, in the early stages, the young in nests with helpers may not benefit by receiving a greater number of feeds, though they do benefit by

[The inclusion of plates 338 & 339 in colour has been subsidised by *ZEISS West Germany*]

339. Long-tailed Tit *Aegithalos caudatus* with feather for nest-lining, at nest, Grampian, April 1981 (*Don Smith*)

being kept warmer by the female (which results in them needing less food to maintain their body temperature). As the young become larger, however, the effects of the helper become more obvious. The number of feeding visits made per day is some 16% higher in the presence of a helper than it is at nests without helpers. The fact that the feeding rate does not increase by 50% is not merely due to the helper not doing his full 'share', but is also due to the fact that both parents decrease their work-load (females reduce their feeding rate from about 9.9 to 7.8 visits per hour, males from about 11.2 to 8.8 visits per hour).

The work done by helpers may have a direct effect on the chances of survival of the breeding pair: by not having to work so hard to bring so much food to the nest, they may be able to be more on their guard against predators. Also, they may be able to keep themselves in better condition. By accustoming the birds to land on electronic weighing perches positioned just in front of their nests, it was possible to obtain a large sample of weights of parents feeding nestlings. Those doing so in the presence of a helper weighed, on average, 7.91 g, while those without a helper were significantly lighter, at 7.59 g.

The presence of helpers had a marked effect on the survival of the chicks. Of 68 chicks in nests with helpers, 26 (38.2%) are known to have survived to the following breeding season, as opposed to only 25 out of 114 (21.9%) in nests without helpers, a significant difference. We do not know exactly how the presence of helpers effects the survival of the young, but it is likely that it is associated with the young being better nourished. As a result of the higher feeding rates at nests with helpers, the young were significantly heavier than those in nests where no helpers were present. Since those chicks which survived to breed were significantly heavier than those which are not known to have survived, it seems that the helpers have a direct effect on the chances of their foster-chicks' survival by providing them with more food. (Statistical analysis confirmed that the higher feeding rates at nests with helpers was due to the efforts of the helpers themselves; it was not because helpers were attracted to nests where there were already high feeding rates.)

Discussion

The Long-tailed Tit's habit of having helpers at the nest plainly does make it atypical for a temperate species. Can we explain why it behaves in this way? We outlined earlier some of the reasons why certain species were thought to have evolved the habit of co-operative breeding. Although by no means all researchers would agree that the 'habitat-full' hypothesis was the only explanation for the behaviour, it does seem a possible explanation in many situations, especially those in warmer climates. This explanation does not, however, seem very good for the Long-tailed Tit. Apart from anything else, the occasional years of extreme cold which lead to such great reductions in numbers of Long-tailed Tits do not appear to alter their behaviour. One might expect that, if the 'habitat-full' hypothesis explained their behaviour, the flocks would break up into more 'normal' pairs at times when numbers were greatly reduced; yet, under such conditions, they remain in flocks.

Further, in typical co-operative breeders, only one pair (or only a very small proportion of the birds) actually participates in the breeding; the others merely help. In the case of the Long-tailed Tit, however, it seems likely that virtually every individual at least attempts to breed.

To some extent, this argument still begs the question. Why should these birds go and help others rather than starting another nest of their own? If it were successful, they would confer more of their genes to the following generation than they would by helping their relatives. There may be a simple explanation for this. It is known that several other species of small insectivorous bird are single-brooded (e.g. Willow Warbler *Phylloscopus trochilus* and Blue Tit *Parus caeruleus*), suggesting perhaps that these species cannot easily find the abundant food they need for raising young over a long period of the summer. Further, for the Great Tit *Parus major*, the chances of raising young successfully fall off very rapidly as the season progresses (Perrins 1979). If this is true for the Long-tailed Tit also, it may explain why they go to help their relatives. A bird which loses its nest will not be able to have young of its own in the nest for at least

340. Long-tailed Tit *Aegithalos caudatus* feeding young in nest, Suffolk, May 1949 (*Eric Hosking*)

another 25 days (four or five days to build a nest, seven days to lay a clutch of eight eggs, and 13 days to incubate them). Hence, any replacement nest will be very late, and may stand much less chance of being successful.

Let us speculate as to the likely productivity of a bird starting to raise its own replacement brood as opposed to going to help a brother. In order to do so, we need to have some figures. Let us assume that:

(1) each pair lays 8 eggs;

(2) a nest in the main part of the breeding season has only a 20% chance of being successful (see above). For simplicity, let us also assume that half the losses (40%) occur prior to and half after the end of incubation; this is the same as saying that 45% survive each period;

(3) that nests with helpers raise 1.7 times as many young as those without (38.2% versus 21.9%, see above);

(4) that late (replacement) nests are only half as successful as early ones.

If we use these figures, it follows that the two choices facing a bird that has just lost a nest are:

(a) to help at another nest which is just hatching. Without helpers this nest would produce
$(8 \times 0.45) = 3.6$ *survivors*
With helpers it will produce 1.7 times as many
$= 6.12$ *survivors*
The net gain in surviving relatives of the helper as a result of helping is therefore $(6.12-3.6)$
$= 2.52$ *survivors*

(b) to attempt another brood of its own. This will produce on average
$(8 \times 0.45 \times 0.45 \times 0.5) = 0.81$ *survivors*

The net gain of offspring related to the helper is therefore greater by helping than by attempting another brood of its own. Remember, however, that nephews and nieces carry only half as many genes of their uncles and aunts as do sons and daughters of their mothers and fathers.

For a helper to leave more genes by helping than by raising its own young, it must, therefore, raise twice as many (or more) nephews and nieces than it would have sons and daughters: in our example this is the case. Further, it should be remembered that a small proportion of the late nesters will, themselves, attract helpers; in doing so, these pairs raise their number of surviving young to 0.48 (i.e. 0.28 × 1.7).

We are not, of course, suggesting that these figures are precisely accurate, but they are likely to be of the right order. They demonstrate that it is possible for helping to be more productive than raising a brood of one's own. Notice that two factors contribute to the differences: one is that the late birds have a reduced breeding success by being late; and the other is that, by going to help at a brood which has already hatched, the helpers are selecting broods which have already survived roughly half of the nesting dangers, and hence have a higher chance of survival than a nest which is just starting.

The theory of kin selection may be adequate to explain why most helpers help. In the case of the Long-tailed Tit, however, there may be another reason for doing so. If, as we suggest, membership of a winter flock is a prerequisite for winter survival, helping a relative may be the way in which childless birds 'buy' their way into a winter flock, so giving themselves a chance of surviving until the next season. Even if the actual helping had only a small effect on the success of the brood, it might still pay the helpers to do so in order to be able to over-winter in a flock.

341. Long-tailed Tit *Aegithalos caudatus* feeding young in nest, Shropshire, May 1980 (*N. A. J. Wilde*)

If this system pays off for Long-tailed Tits, why do we not find it more commonly amongst our other birds? The answer to this may be quite simple. By living in family parties all winter and setting up breeding territories within the winter territory, the Long-tailed Tit is, uniquely, in a position to recognise relatives in a way that almost no other British species can do. Hence, once again, the winter flocking explains why we see this behaviour in Long-tailed Tits and not in other species.

There is a weakness in our argument. We have suggested that membership of a winter flock is essential to the individual, either because the defended winter feeding territory provides secure food supplies or because the birds need to huddle in cold weather (or both). Nevertheless, these requirements do not seem to dictate that the flocks should necessarily be composed of relatives. What makes such a membership essential? Why do flocks not allow any spare birds to join them? Is it because there are disadvantages to increasing the numbers in a flock beyond a certain number?

Future studies

The Long-tailed Tit is a difficult species to study. In the first year of the present study, nesting losses were so high that it was difficult to get enough colour-ringed families for observation in the winter. An attempt to remedy this by surrounding the nests with wire netting, to prevent Jays *Garrulus glandarius* (the most likely major predator) from destroying the nests, proved to be highly successful. Indeed, perhaps too successful, for there were then very few failed breeders available to become helpers.

Apart from the fact that, in view of the small samples of identified helpers, it would be valuable to have further evidence, the study raises a number of other questions. For example:

(1) What happens to the female of the family and any of her mate's sisters who may have helped raise the brood and over-wintered in the flock? Do they stay within the winter flock territory or do they, like the young females, move out? If they remain, they stand a good chance of mating with a relative (i.e. a son or a nephew).

(2) When a failed breeder goes to help another pair in its own winter flock area, does it do so only with a brother, as the data here suggest? The winter flock area also contains (at least at times) the mother and father and aunts and uncles of the helping bird. Out of the 12 observed cases, all were of birds helping brothers. Yet it seems unlikely that the helpers would be able to distinguish these from others in the flock area (genetically, there would be no point in avoiding helping one's parents, though helping an aunt or uncle is only half as good).

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