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Effect of Site Fidelity on Cooperative Breeding in the Long-tailed Tit *Aegithalos caudatus*

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ABSTRACT

We examined whether a low site fidelity has an effect on group territoriality and the occurrence of helpers in the Long-tailed Tit *Aegithalos caudatus*. This species was seen all the year round, except for summer, at the edge of Kasuga-yama Woody Hills in Joetsu City, but none of the banded birds were residents. Winter groups were stable in membership but on one occasion two groups joined together. Group territorialism was loose because winter home ranges overlapped each other and few aggressive interactions were observed. Pairs were formed not only within but also between groups. Helpers were all failed breeders and some were from different winter groups. Typical cooperative breeders are seen among resident birds which live in groups all the year round. Although Long-tailed Tits in our area were not residents, the birds still expressed cooperative breeding. We conclude that a strong site fidelity may be a necessary condition for group territoriality but it is not a prerequisite for helping behaviour in this species.

KEY WORDS

Cooperative breeding, Helper, Long-tailed Tit, Site fidelity, Territoriality

Introduction

The characteristic features of typical cooperative breeding birds include a strong site fidelity, group living and long-term bonds between the members (Brown 1978, 1987, Stacey & Koenig 1990, Emlen 1991). The group usually defends an all-purpose territory against neighbors and the members breed within it. Gaston (1978) considered that cooperative breeding would be facilitated by a strong site fidelity and group territorial behaviour. Matthysen (1990, 1993) emphasized that residency and individual associations maintained across seasons are important for access to mates and/or breeding sites. Then, unless a cooperative breeding species stays in the same area year-round, would group territoriality and helping behaviour occur in the species ? The aim of this paper is to answer this question in the Long-tailed Tit *Aegithalos caudatus*.

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The Long-tailed Tit is a cooperative breeding bird that lives in family groups (Glen & Perrins 1988). Since Skutch (1961) reported "helper" in this species, many studies (Nakamura 1969, 1972, 1976, Gaston 1973, Perrins 1979, Glen & Perrins 1988, Ezaki *et al.* 1991) revealed the following five points: (1) this species is highly sedentary in most years and (2) defends a group territory during winter; (3) the group is stable in composition throughout the winter; (4) in early spring, the group breaks up into monogamous pairs nesting inside the winter territory; and (5) almost all helpers are failed breeders from the same group. Many authors have regarded this species as a resident, but few reports have actually demonstrated the degree of site fidelity by monitoring the banded birds for more than one year. Here, we describe that Long-tailed Tits banded in our study area were not residents and discuss the possible effects of a low site fidelity on group territory and helping behaviour.

Study area and methods

This study was conducted at the edge of Kasuga-yama Woody Hills in Joetsu City, Niigata Prefecture, Japan (37°08' N, 138°14' E, 300 ha, 15-25 alt.) from May 1994 to January 1996. Half of the study area is occupied by mixed forests dominated by oaks *Quercus acutissima* and *Q. serrata,* pine *Pinus densiflora* and cedar *Cryptomeria japonica.* The other half comprises (1) wasteland including *Miscanthus sinensis* and *Pueraria lobata,* (2) farmland, (3) nonvegetated area including the campus of Joetsu University of Education and the residential area, and (4) some ponds and streams. The Joetsu region is famous as an area of heavy snowfall. Snow fell 1.4 m and 1.3 m deep from December 1994 to February 1995 and from December 1995 to January 1996, respectively. Long-tailed Tits in the study area usually make one nesting attempt from March to August, but there are often second nests if initial attempts fail early enough.

To study the site fidelity of Long-tailed Tits, we visited the study area almost every three days from May 1994 to January 1996 and banded them. We identified 46 birds during the study period and 35 of them were captured with mist net. Each captured bird received a numbered aluminium ring and a unique combination of coloured leg rings. In the Long-tailed Tit, only females engage in incubation (Gaston 1973). Therefore, adults were sexed by incubation behaviour and by the presence of an incubation patch in the breeding season. Each banded bird is referred to by a unique number preceded by a character, "M" or "F", indicating the sex, for example, M1 and F1. UB indicates an unbanded bird. When we observed Long-tailed Tits, we recorded the location on the map with the group size, the identity of individuals and their behaviour. These were recorded until we lost sight of them. Two criteria were used to define grouping: (1) all members had to be within 25 m of an individual of each other; (2) they had to move at least about 30 m in the same general direction. Nakamura (1961) reported that all Long-tailed Tits disappeared from May to September from the marginal area near human habitation, while large sized flocks com-

posed of different families were formed in the central area of the wood. Our study area is backed by Kasuga-yama Woody Hills. Thus, we searched the hills (about 500 ha) for banded birds for a week after they disappeared from the study area.

To study the relationship between wintering ecology and cooperative breeding in detail, we searched the study area for Long-tailed Tits in 134 days from November 1994 to March 1995. In the nonbreeding season, we observed the degree of sociality between members of a winter group and their home range. The degree of sociality between individual birds was calculated using Ekman's (1979) coherence index. This index was defined as:

$$\text{Coherence index} = \frac{Tc}{Ta + Tb + Tc} \times 100$$

Where Ta and Tb are observation minutes of individuals a and b in the absence of the other individuals, and Tc are observation minutes of a and b within 25 m of each other. Coherence was calculated only if observation minutes per individuals were over 10 min. Group's position was plotted by dots on the map card every 5 min. Home range was determined by connecting the outer most dots of observation with straight lines. To examine how many observations were responsible for the overlap of two group home ranges, we calculated home range overlap in a similar way as coherence, giving the proportion of the pooled dots shared by two groups. After the nesting season started, we attempted to locate nest sites by tracking pairs. Once a nest was found, we visited it to record the activity of the pair and to determine the home range.

Results

1. Site fidelity

Seven different groups were confirmed in the study area from May 1994 to January 1996 (Fig. 1). We named the seven groups as Group A (including 3 banded birds and 3 UB), Group B (including 5 banded birds and 1 UB), Group C (including 9 banded birds), Group BC (including 14 banded birds and 1 UB), Group D (including 9 banded birds), Group E (including 6 unbanded birds) and Group F (including 9 banded birds and 1 UB).

Group A bred in spring 1994 but disappeared from the study area after the nesting season ended. Groups B and C entered the study area on 5 October 1994 and 12 December 1994, respectively (Fig. 1). Groups B and C were united into a new group, Group BC, on 20 December 1994. However, Group BC disappeared from the study area on 30 January 1995. Groups D and E settled the study area on 1 November 1994 and 4 March 1995, respectively. They bred in the study area in the 1995 breeding season but had disappeared by August 1995 (Fig. 1). Group F entered on 10 November 1995. Neither three breeding groups (Groups A, D and E) nor one wintering group (Group BC) returned to the study area in the next season (Fig. 1).

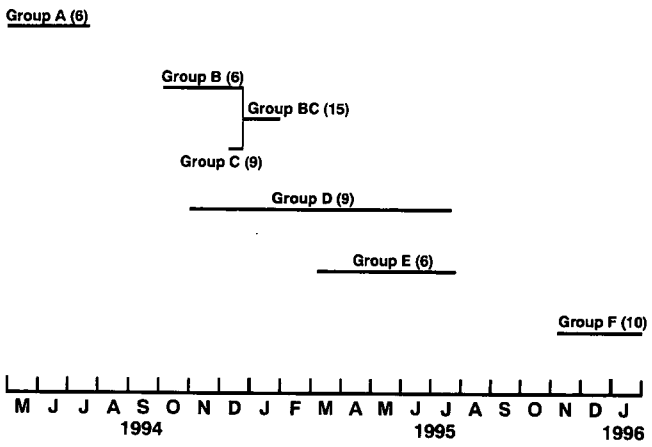

Figure 1. Site fidelity of Long-tailed Tits inhabiting the study area from May 1994 to January 1996. The lines indicate the presence of each group, with the number of group members in parentheses.

Groups settled and disappeared at once, but not gradually. After groups disappeared, we searched Kasuga-yama Woody Hills for banded birds for a week but could not find them. Although Long-tailed tits in the study area were seen all the year round except for summer (August and September), clearly, banded birds were not year-round residents.

2. Group membership

There was no group in which the coherence indices between members were below 90%, which means that the member of each group acted in a compact unit and was stable in composition. The members of Group BC also indicated high coherence indices between 90% and 100%, until they disappeared on 30 January. They never separated within a day and all the members roosted together. Although temporary mixing between different groups

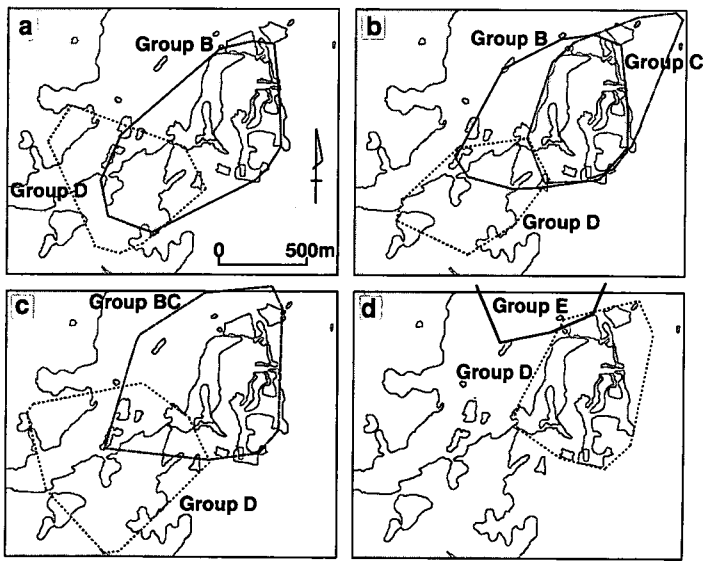

Figure 2. Distribution of group home ranges in November (a) and December (b) 1994, and January (c) and February (d) 1995. Dotted areas indicate mixed forests.

sometimes occurred, no individuals associated with the members of other groups for a longer period, except for the case of Group BC.

3. Home range distribution and territoriality

The home ranges of Groups B and D overlapped each other in November 1994 (Fig. 2a). Group C entered the study area on 12 December 1994 and the home range overlapped that of Group B (Fig. 2b). Even after Groups B and C were united, the home range of Group BC overlapped that of Group D (Fig. 2c). These overlaps were not caused by only one or a few observations because the proportion of the pooled observation dots shared by two groups was over 30% in each case (32% between Groups B and D in November, 46% between Groups B and C in December, 37% between Groups BC and D in January). After the disappearance of Group BC, Group D shifted its range to the vacant area on 12 February 1995 and Group E entered the study area (Fig. 2d).

Although the home ranges of groups overlapped each other, we observed only seven encounters between groups. At that time, birds were highly restless and noisy, but few aggressive interactions were observed. In one notable case, a member of Group B chased a member of Group C aggressively during 40 min on 20 December 1994, and thereafter they joined together to form Group BC.

4. Pair formation and helper

There were two groups (Groups D and E) breeding in the study area in 1995 (Fig. 1). Group D consisted of nine banded birds, including four males (M1, M2, M3 and M4), three females (F1, F2 and F3) and two birds of unknown sex. Group E included six members who were not banded. Five pairs bred in the study area. Two pairs, M1-F1 and UB-F2, bred inside the home range which had been used by Group D in February 1995 (Fig. 3), while the remaining three pairs, M2-UB, M3-F3 and M4-UB, bred in the area where had

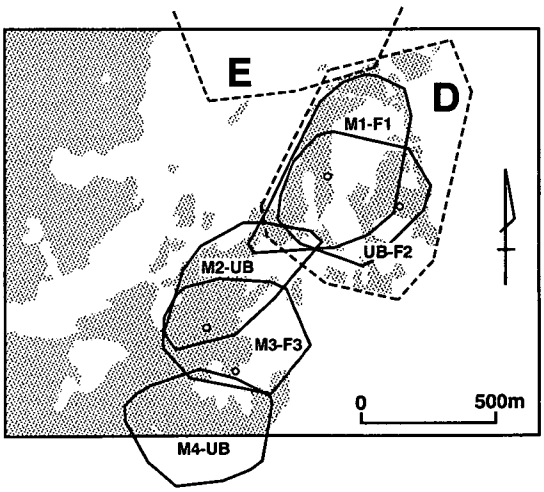

Figure 3. Distribution of group home ranges in February 1995 (dashed lines) and breeding pair home ranges in the subsequent breeding season (solid lines). Positions of nests containing eggs or young are shown by open circles. The nest of pair M4-UB was not found.

been used by Group D from November 1994 to January 1995 (Fig. 2). The two banded birds of unknown sex in Group D disappeared from the study area in March. The unbanded birds that paired with a member of Group D seemed likely to be members of Group E because we could find no other groups near the study area. This means that pair formation did not necessarily take place between the members of a group and that the members of Group D bred outside the winter home range.

We observed three helpers and they were all failed breeders. After the pair UB-F2 failed, an unbanded bird helped pair M1-F1 with feeding young. At that time, F2 followed the unbanded bird (presumably the same UB) but did not help the pair. After another pair M2-UB had lost its own nest, the pair M3-F3 was assisted in feeding young by M2 and an unbanded bird, again the same individual paired to M2.

Discussion

The present study showed that none of the Long-tailed Tits banded in our area were residents. The Long-tailed Tit is highly sedentary in woodland populations (Nakamura 1976, Gaston 1973, Glen & Perrins 1988) and the same members of the previous winter group are reorganized after breeding into a group even in an urban district (Ezaki *et al.* 1991). By contrast, some groups shift their main foraging area to human habitation in a heavy snow region (Nakamura 1976) and to the central area of the wood in a marginal area (Nakamura 1961). Moreover, there are migratory populations at high latitudes (*e.g.*, Scandinavia, Cramp & Perrins 1993). Migratory birds are not sedentary across seasons, although they may show site fidelity within seasons and between years. However, breeding and wintering groups in our population never returned to the study area in the next season (Fig. 1). We did not find disappearing groups in the surrounding area. It is unlikely that all members of a group died at the same time. Thus, we considered Long-tailed Tits in our area as wanderers who roamed a larger area than studied. However, there still remain questions whether habitat characteristics or snowfall in our area brings about the low site fidelity.

Cooperatively breeding birds generally breed within permanent territories (Gaston 1978, Stacey & Koenig 1990, Emlen 1991). The presence of any individuals together for a long period of time in the same territory, whether they are kin or not, facilitates cooperative or mutualistic behaviour (Brown 1987). The existence of group territoriality closely associates with degree of residence (Matthysen 1993). In our area, Long-tailed Tits were not residents and group territorialism was loose. However, the birds still expressed cooperative breeding. This suggests that year-round site fidelity is not a prerequisite for cooperative behaviour in this species.

Then, what brings about the cooperative breeding in Long-tailed Tits? One possible explanation is that the action of helpers increases their inclusive fitness (Emlen 1991). The arrangement of territories of winter groups was stable year after year in the other

study area, Nagano Prefecture (Nakamura 1969). This led Nakamura (1976) to speculate that group members are succeeded by themselves and their descendants year after year. Winter groups in our area were stable in membership at least during a single winter, but we did not know whether the groups were family parties. Recent DNA fingerprinting showed that there would be no kin relationship among winter group members in Hiroshima Prefecture (Satou per. comm.). As well as in the previous studies (Nakamura 1972, Gaston 1973, Glen & Perrins 1988, Ezaki *et al.* 1991), helpers were all failed breeders in our study and that some helpers assisted individuals from a different winter group. Thus, helping behaviours of Long-tailed Tits seem to be best viewed as accidents rather than altruistic adaptations.

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