Breeding ecology of ground tits in northeastern Tibetan plateau, with special reference to cooperative breeding system

Xin LU*, Ran HUO, Yang LI, Wenbo LIAO, Chen WANG

Department of Zoology, College of Life Sciences, Wuhan University, Wuhan 430072, China

Abstract  Data on breeding ecology of a color-band marked population of the ground tit Parus humilis were collected in north Qinghai on the Tibetan plateau, during 2008 and 2009. In spring the birds excavated 0.8–3.2 m long nesting burrows under the ground. First-egg laying occurred between late April and late June during which a pair produced one brood. Incubation was done by female alone for 15–16 days and nestling-feeding by both sexes and helpers in any for 23–25 days. Average brood size at fledging was 5.8 (± 1.4 SD, 3–8) and all the 27 observed nesting attempts fledged at least one young. At the population level, brood sex ratio did not differ from 1:1. The birds are a territory-living resident, with annual resight rates being 48% (22 of 46) in adult breeders and 10% (7 of 67) in yearlings. Pairs were socially monogamous, of which 23% (9 of 40) contained one and sometimes two male helpers, most likely being philopatric sons of the breeders. The formation of cooperative groups is similar to the population in central Tibet but differs from that in south Guansu where breeding ground tits exhibit a high level of annual turnover [Current Zoology 57 (6): 751–757, 2011].

Keywords  Burrow-nesting, Cooperative breeding, Life history, Parus humilis, Tibetan plateau

The ground tit Parus humilis is a passerine inhabiting alpine meadows of 2500–5500 m elevation on the Tibetan plateau (Zheng, 2002). Over the species’ range, climate conditions vary greatly, from lower than −3°C to more than 8°C in annual mean air temperature, and from less than 50 mm to more than 700 mm in annual total precipitation. This must lead to divergence among populations in life-history strategy and social system. Studying the variance across populations may provide insight into the evolution of life history and social behavior of birds.

We have obtained data on demography and social organization of two ground tit populations that occurring in different climate regimes (central Tibet, Peng, 2007; Ke, 2009, Ke and Lu, 2009; Johannessen et al., 2001; south Gansu, Ma, 2007; Du and Lu, 2009, 2010; Wang and Lu, 2011). In particular, although our studies showed that both populations exhibited facultative cooperative breeding behaviors, i.e. more than two adult individuals care for offspring in the same nest (Emlen, 1997), they also had an obvious regional difference in social system. In central Tibet, monogamous pairs have helpers at the nest and almost all helpers are the breeders’ male offspring coming from the last breeding season. In contrast, for the south Gansu population, we revealed that helpers, despite being closely related male relatives of the breeders, were not young from a previous brood and they joined the breeding pair with the failure of their own nesting attempts. The former social system may be associated with typical year-round residence of the population, whereas the latter with a high annual turnover of the breeding population.

The current paper reports a two-year study on breeding ecology of a ground tit population occurring in north Qinghai, far from the central Tibet and the south Gansu sites where previous data were collected. Our objectives were (1) to offer the basic information of natural history of this species to learn how its life history traits vary according to environmental conditions, (2) to investigate whether there is an intraspecific geographical difference in social system, and (3) to compare aspects of breeding adaptation between the primary cavity-nester and sympatric secondary cavity-nesters.

1 Materials and Methods

Ground tits are a burrow-nesting passerine endemic to alpine tundra on the Tibetan plateau. They excavate one burrow in spring for reproduction and roosting, and another in autumn for roosting over winter (Ke and Lu, 2009). Both types of burrows are built underground with a straight tunnel that connects with an ellipsoid-like chamber. The birds rely almost completely on soil
arthropods. As in the case of other insectivorous birds (Emlen and Wrege, 1991; Covas et al., 2008; Cockburn et al., 2008), rainfall during the breeding season is a key factor limiting their food availability. Ground tits live in group during the non-breeding periods. When breeding the groups break up and socially monogamous pairs form. Incubation is undertaken by females alone, and nestlings are fed by both parents and helpers, if any. After fledging, juveniles continue to be reliant on adults for food for up to one month (Peng, 2007). For further details about general natural history knowledge of this species were provided elsewhere (central Tibet, Ke, 2009; Ke and Lu, 2009; Johannessen et al., 2001; south Gansu, Ma, 2007; Du and Lu, 2009, 2010).

This study was conducted in Gangcha, north Qinghai during 2008 and 2009. Annual average temperature at this site is $-0.6 \, ^\circ C$, and annual total precipitation 371 mm, which differ from those in the central Tibet site (1.7 $^\circ C$, 441 mm) and from the south Gansu site (1.2 $^\circ C$, 782 mm) where two previous studies were carried out (Fig. 1). Habitats suitable to ground tits are open meadows consisting mainly of Kobresia pygmaea, Ajania tenuifolia, Pleurospermum camtschaticum and Lonicera tibetica. Some shallow slopes, banks, ditches and pits in the area provide abundant microhabitats for the birds to burrow.

Each spring, we searched for ground tit nests over a 200-ha study plot by watching birds for behavioral clues. For each of most nests located, we dug a vertical shaft at the end of its burrow tunnel during the incubation or nestling period to check nest contents. The shaft was filled with soil-filled bags to facilitate subsequent inspection. Adult ground tits were mist-netted at the entrance of their nesting burrows during the incubation period for a few nests and during the nestling period for most nests. Nestling marking was conducted when they were more than 10 days old. Birds of both adults and nestlings were individually marked using colored-leg rings and a numbered metal ring.

We visited the nests at least once per week to obtain information about nesting behavior, social organization, brood size, nestling development and nest fate. We measure burrow tunnel length after nest building was completed. Some old burrows were also measured for their tunnel length. First-egg dates of the nests found after hatching were back-calculated from the established information on egg-laying interval, duration of the incubation period, and age of nestlings. Ground tits are monomorphic in size and plumage. We sexed adults by behaviors or female-only incubation patches. The method proved to be valid by molecular technique in lab using blood samples collected upon capture (for details see Du and Lu, 2010). We also discriminated the sex of nestlings using the molecular techniques. A cooperative group was defined as any breeding unit where more than two individuals attended a nest. Helper relatedness to the breeders they helped were determined based on pedigree data. Parental behaviors were recoded for selected nests during different breeding stages. In total, 40 active ground tit nests were located during this study. However, not all the nests located were regularly investigated for a full series of nesting parameters.

We used Student’s $t$ tests to compare the differences in average burrow length between bi-parental and cooperative nests, brood size between nestling stages, and pairs-sample $t$ tests to compare the differences in nesting body mass between sexes. We used Chi-square tests to assess offspring sex ratio at a population level, and Mann-Whitney $U$ test to see whether brood sex ratio in non-cooperative broods differed from that in cooperative broods, because the data were not distributed normally (judged with the one-sample Kolmogorov-Smirnov test). All probabilities are two-tailed, and the significant level is set at $\alpha = 0.05$. Values are presented with mean $\pm SD$.

2 Results

2.1 Breeding season

The behaviors of burrow-excavating and carrying nest materials were recorded between 10 and 30 April during which ground tits lived in pairs (14 of 21 territo-
ries investigated) or small groups of 3–5 (3.7 ± 0.8) individuals (7 territories). During the observations of 30 field days before mid-May, a total of six copulations were noted, females calling and flapping the wings to entice the male some meters away. Earliest fledging occurred on 8 June and the latest on 10 July, with the most (61% of 28 broods) between 10 and 25 June. A pair produced only a single brood per year (n = 40 marked pairs).

2.2 Nest building
Most nest burrows were built on vertical banks (53 of 56), and a few (3 of 56) on slopes or meadows. A few pairs (7 of 40) nested in winter-roosting burrows or reused old burrows. Both sexes and helpers if present excavated the burrow with the bill and pushed the flaked soil with the feet. An excavation bout lasted usually less than five minutes. While excavating, only one bird worked in the burrow in most cases with its mate staying nearby the burrow entrance. In the late nest-building period, however, both pair members often were in the burrow. On average 15.1 cm (± 3.6, 9–21, n = 7) tunnel was finished per day. Burrow tunnel length (including the chamber) ranged between 79-315 cm (167 ± 55, n = 56), with no difference between bi-parental (170 ± 55, 79-315, n = 47) and cooperative nests (175 ± 56, 95–270, n = 9; t54 = 0.45, P = 0.65). Thus it took about two weeks to build a burrow. Then, the birds carried nest materials into the burrow. The nests weighed 217 g (± 13, 200–232, n = 4), consisting of grass stems in the outer wall and yak and sheep fur in the inner wall.

2.3 Incubation and young care
Females incubated only. During observations of 320-min on three nests, females were remaining in the nest for 56%–72% (63% ± 8.1) of daily time, during which the female received food 1 or 2 times from her mate. Upon leaving the nest, the female called, which led to the arrival of her mate. Then both pair members foraged together, and sometimes the female solicited food from the male. Incubation period was estimated to last 15–16 days according to regular observations on parental behaviors of two nests.

Both sexes and helpers if any fed the nestlings with insects for 23–25 days (24.3 ± 1.2, n = 3 nests). Data from two pair-fed and one group-fed broods suggest that nests with helpers are fed more frequently than those without them (Table 1).

Newly-fledged juveniles continued to receive provision at the nest burrow entrance or small holes nearby. Then they followed after their parents and searched for food through digging in the ground over extended activity ranges. About 30 days after fledging, juveniles reached nutrition independence.

Fledged juveniles roosted in the nest burrow together with their parents. In the morning, the first individuals that left the burrow were always juveniles, followed by parents and other juveniles (5 observations on 4 nests). In the evening, parents often guarded at a high position and entered the burrow when all juveniles had been in (8 observations on 7 nests).

2.4 Brood size and breeding success
All the 27 known-fate nests fledged at least one young, with brood size at fledging varying from 3 to 8 (5.8 ± 1.4). Eighteen broods checked before day 15 after hatching had 6.5 (± 0.9, 5–8) nestlings on average, significantly larger than 4.4 (± 1.1, 3–6) of the 9 other nests checked after day 15 (t25 = 5.06, P < 0.001), suggesting the death of partial nestlings (which was confirmed to occur in two of the five nests that were checked regularly). For the data obtained in the early nestling period, pair-fed broods (6.5 ± 1.0, n = 11) did not differ in size from group-fed broods (6.4 ± 0.8, n = 7; t16 = 0.25, P = 0.80).

2.5 Offspring sex ratio
A total of 72 male and 66 female nestlings from 23 broods monitored since the early nestling period yielded a balanced sex ratio (0.52, χ²1 = 0.13, P = 0.72). Offspring sex ratios of eight cooperative broods averaged 0.59 ± 0.16 and 15 bi-parental broods 0.50 ± 0.22, with the former than the latter tending to be, though non-significant, male-biased (Mann-Whitney U test, z = 1.69, P = 0.09). Pairwise comparison of body mass between male and female offspring within a brood showed

Table 1 Feeding visits made by individuals of different identities for three ground tit broods

<table>
<thead>
<tr>
<th>Brood type</th>
<th>Brood size</th>
<th>Observation time (min)</th>
<th>Male parent</th>
<th>Female parent</th>
<th>Helper</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pair-fed</td>
<td>4</td>
<td>82</td>
<td>3.7 (5)</td>
<td>3.7 (5)</td>
<td>–</td>
<td>7.3 (10)</td>
</tr>
<tr>
<td>Pair-fed</td>
<td>6</td>
<td>62</td>
<td>1.9 (2)</td>
<td>2.9 (3)</td>
<td>–</td>
<td>4.8 (5)</td>
</tr>
<tr>
<td>Group-fed</td>
<td>6</td>
<td>143</td>
<td>3.8 (9)</td>
<td>3.8 (9)</td>
<td>3.4 (8)</td>
<td>10.9 (26)</td>
</tr>
</tbody>
</table>

The numbers of observation bouts are given in parentheses.
a nearly significant difference, with the former being slightly heavier than the latter ($t_{20} = 2.03, P = 0.056$).

### 2.6 Social organization

Over the 200 ha plot, we recorded approximately 30 breeding pairs during each breeding season, indicating a nest density of 0.15 nests per ha and mean territory size of 6.7 ha per pair. Among 25 breeding males and 21 breeding females banded in 2008, 13 (52%) and 9 (43%) were resighted in 2009 within or nearby their previous territories respectively. From the 2008 to 2009 breeding season, four (20%) of the 20 marked pairs remained, two breeding males and three females paired with a new mate, and the remaining 10 (50%) disappeared from the study plot. It was 12% (4 of 33) for juvenile males and 9% (3 of 34) for juvenile females born in 2008 that were recruited to the 2009 population.

All the 40 pairs located during the two years were socially monogamous. Of them, 23% (9) contained helpers, lower in 2008 (14%, 3 of 21 nests) than in 2009 (32%, 6 of 19). Of the nine helped nests, eight (89%) had only one helper, and one two helpers (11%). All the helpers were males. For three 2009 cooperative nests, pedigree data suggested that helpers were the breeders’ philopatric sons. Kinship between group members in other nests was unknown.

### 3 Discussion

Nesting parameters of the three ground tit populations are listed in Table 2. We find that the first-egg laying occurs earlier in south and north Qinghai populations than that in central Tibet one, probably as a result of climate harshness in the former than the latter. South Gansu ground tits have longest nesting burrow. This might be associated with loose soil due to a high precipitation in this region, which would allow the birds to construct long burrows with relatively few efforts. A ground tit pair produces only a brood per year in all the three populations. The south Gansu ground tits lay clutches similar in size to those in the central Tibet ground tits. However, they fledge more offspring compared with their con specifics in two other localities. Differences in annual precipitation and thus food supply can explain the variation in productivity, because poor foraging conditions may cause brood reduction (Lack, 1954). It seems to have no difference in incubation period among populations. However, ground tits in south Gansu spend relatively fewer days feeding young at the nest compared with their counterparts in two other

### Table 2  A comparison of nesting parameters and social systems of three ground tit populations

<table>
<thead>
<tr>
<th>Nesting parameter</th>
<th>Central Tibet</th>
<th>South Gansu</th>
<th>North Qinghai</th>
</tr>
</thead>
<tbody>
<tr>
<td>First egg date</td>
<td>Early May</td>
<td>Late April</td>
<td>Late April</td>
</tr>
<tr>
<td>Burrow length (cm)</td>
<td>$147 \pm 39 (80–290, n = 211)$</td>
<td>$177 \pm 57 (64–313, n = 195)$</td>
<td>$167 \pm 55 (79–315, n = 56)$</td>
</tr>
<tr>
<td>Clutch size</td>
<td>$6.3 \pm 0.8 (4–8, n = 56)$</td>
<td>$6.6 \pm 0.4 (4–9, n = 12)$</td>
<td>–</td>
</tr>
<tr>
<td>Brood size at fledging</td>
<td>$4.7 \pm 1.4 (1–8, n = 50)$</td>
<td>$5.9 \pm 1.4 (1–8, n = 170)$</td>
<td>$4.4 \pm 1.1 (3–6, n = 9)$</td>
</tr>
<tr>
<td>No. of broods per year</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Incubation period (d)</td>
<td>15–16</td>
<td>15</td>
<td>15–16</td>
</tr>
<tr>
<td>Nestling period (d)</td>
<td>24–26</td>
<td>19</td>
<td>24.3 ± 1.2 (23–25, n = 3)</td>
</tr>
<tr>
<td>Social system</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% adults relocated annually</td>
<td>50.4 (n = 391)</td>
<td>3.7 (n = 242)</td>
<td>47.8 (n = 46)</td>
</tr>
<tr>
<td>% juveniles relocated annually</td>
<td>15.6 (n = 739)</td>
<td>0.6 (n = 468)</td>
<td>10.4 (n = 67)</td>
</tr>
<tr>
<td>Territoriality</td>
<td>Present</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td>% nest with helper</td>
<td>28 (n = 127)</td>
<td>12 (n = 117)</td>
<td>23 (n = 40)</td>
</tr>
<tr>
<td>No. of helper per nest</td>
<td>$1.1 \pm 0.4 (1–3, n = 32)$</td>
<td>$1.6 \pm 0.8 (1–4, n = 20)$</td>
<td>$1.1 \pm 0.3 (1–2, n = 9)$</td>
</tr>
<tr>
<td>% young with within-group extra-paternity</td>
<td>0 (n = 101)</td>
<td>23.3 (n = 120)</td>
<td>–</td>
</tr>
<tr>
<td>% young with extra-group extra-paternity</td>
<td>0.3 (n = 352)</td>
<td>8.6 (n = 547)</td>
<td>–</td>
</tr>
<tr>
<td>% young with within-group extra-paternity</td>
<td>0 (n = 101)</td>
<td>4.2 (n = 120)</td>
<td>–</td>
</tr>
<tr>
<td>% young with extra-group extra-paternity</td>
<td>0 (n = 352)</td>
<td>4.2 (n = 547)</td>
<td>–</td>
</tr>
<tr>
<td>Ref.</td>
<td>1, 2, 3, 4, 5</td>
<td>6, 7, 8, 9</td>
<td>10</td>
</tr>
</tbody>
</table>

regions, due probably to good food availability resulting from a high level of annual precipitation. Nevertheless, further data are still needed to address how the ecological factors cause differences in demographic parameters among ground tit populations.

Our data show an obvious geographic variation in social system of the ground tits (Table 2). Ground tits in both central Tibet and north Qinghai live within permanent territories year around; 50% of adults and 10%–15% of juveniles survive to the nest breeding season; cooperative breeding occurred regularly in the two populations, with most helpers being philopatric sons of the breeders, typically following most avian cooperative breeders (Brown, 1987; Emlen, 1997; Cockburn, 1998; Koenig and Dickinson, 2004). In contrast, the ground tit population in south Gansu exhibits a very high rate of annual turnover: only 4% of adults and 0.6% of nestlings are rediscovered in the next breeding season. When breeding the birds establish socially monogamous pairs but they do not exhibit territoriality. This population is unusual as a cooperative breeding system in that helpers consisted of males (75% of helped nests) or females (15%) or both sexes (10%). Helpers are likely to come from failed breeders that are related to the breeders (Du and Lu, 2009). The inter-population difference in social structure could also be responsible for the difference in genetic mating system. In Gansu, helpers regularly produced offspring with the females they helped, and both extra-pair and extra-group paternity as well as maternity was common in both bi-parental and cooperative broods, suggesting a cooperatively polygynandrous system. For the central Tibet and north Qinghai populations, however, helpers never obtained any paternity in their own families, and extra-group extra-pair paternity appears to be very low and extra-pair maternity is never observed (Johannessen et al., 2001).

The flexibility of social system among populations of a species in terms of cooperative behaviors has been demonstrated in other species (Emlen, 1982; Curry, 1989; Baglione et al., 2002). Inter-population differences in environmental condition could be the ultimate factors affecting the expression of different social organizations in the ground tit. For some cavity-nesting cooperative birds such as red-cockaded Woodpeckers Picoides borealis (Walters et al., 1992), cavity availability is thought to be responsible for delayed dispersal of young, presumably because the cost to create a cavity is high. In acorn woodpeckers Melanerpes formicivorus, Hooge et al. (1999) revealed that large groups can construct high-quality nests. An earlier study showed that long nest burrows may benefit the nesting ground tits in terms of thermoregulatory protection for eggs or nestlings against harsh climates in the extreme environments (Ke and Lu, 2009). Although 15-25 days were needed for a pair to finish nest building (excavation of the nest burrow and collection of nest materials), we found no difference in the length of nest burrows between bi-parental and cooperative breeders. The same pattern was observed in two other populations (central Tibet: Ke and Lu, 2009; south Gansu: Ma, 2007). This suggests that the hypothesis does not apply to the ground tits. Future efforts should be made to identify the potential factors and underlying mechanisms.

Ground tits are the only primary cavity-nesters in the alpine meadow habitats. They are earliest breeders among local passerines nesting in open meadow habitats (mostly between late May and early July; Zhang, 1982). The earlier reproduction of ground tits may be associated with their burrow-nesting habit – which is expected to reduce the demands for shelters against predation and bad weathers, and their nestling diet consisting mainly of insect larvae in soil, the food resources that are available in an earlier time than adult insects consumed by other bird species (Lu et al., 2009).

Relative to several sympatric secondary cavity-nesters, ground tits fledge more nestlings per brood and have a much high proportion of successful nesting attempts (Table 3). It has been shown that secondary cavity-nesters produce larger clutches than primary cavity-nesters, presumably because nest site limitations for the former may promote them to invest more in each breeding attempt to cope with unpredictable breeding opportunities (Martin, 1993). Our results were different from the hypothesis. It is probably because the breeding cavities used by these secondary cavity-nesting birds, mainly pika holes, are abundant and readily available.

Several factors may contribute to the high productivity achieved by ground tits: (1) long, well-structured nest burrows and heavy, well-insulated nests, which, as a form of increased investment in reproduction (Lombardo, 1994), may provide better thermal protection for parents and offspring (Ke and Lu, 2009); (2) only single brood per year, which may receive more resources; (3) male courtship feeding, allowing the females to allocate more energy into egg production and young care (Lifjeld and Slagsvold, 1986); (4) prolonged care for young at the nest, which can improve nestling quality (Stodola et al., 2010); (5) cooperative breeding, which may reduce the probability of nestling starvation (Hatchwell, 1999).
Table 3  A comparison of nesting parameters of the ground tit with those of several sympatric secondary cavity-nesters

<table>
<thead>
<tr>
<th>Species</th>
<th>Nest cavity length (m)</th>
<th>Nest mass /female body mass</th>
<th>No. of broods Produced per year</th>
<th>Courtship feeding</th>
<th>Brood size</th>
<th>Incubation period (d)</th>
<th>Nestling period (d)</th>
<th>Nesting success</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground tit <em>Parus humilis</em></td>
<td>1.7</td>
<td>5.8</td>
<td>1</td>
<td>Yes</td>
<td>5.8</td>
<td>15</td>
<td>19-25</td>
<td>100</td>
<td>1</td>
</tr>
<tr>
<td>Northern wheatear <em>Oenanthe oenanthe</em></td>
<td>0.5</td>
<td>1.8</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>4.0</td>
<td>14</td>
<td>14-15</td>
<td>2</td>
</tr>
<tr>
<td>Black redstart <em>Phoenicurus ochruros</em></td>
<td>0.3</td>
<td>2.7</td>
<td>1-2</td>
<td>No</td>
<td>3.0</td>
<td>14</td>
<td>18</td>
<td>81</td>
<td>3</td>
</tr>
<tr>
<td>White-rumped snowfinch <em>Montifringilla taczanowskii</em></td>
<td>1.3–1.6</td>
<td>1.5</td>
<td>1-2</td>
<td>No</td>
<td>3.2</td>
<td>13</td>
<td>21</td>
<td>66</td>
<td>4, 5, 6</td>
</tr>
<tr>
<td>Rufous-necked snowfinch <em>M. ruficollis</em></td>
<td>1.1</td>
<td>1.4</td>
<td>1-2</td>
<td>No</td>
<td>3.0</td>
<td>13</td>
<td>22</td>
<td>46</td>
<td>4, 5, 6</td>
</tr>
</tbody>
</table>


Acknowledgements We thank D.H. Ke for assistance during the field work and B. Du during the laboratory work. This work was conducted at the Field Research Station for Tibetan Wildlife, which is jointly administered by Wuhan University and Tibet University. Financial support was offered by the National Sciences Foundation of China (Grant 30830019).

References


Martin TE, 1993 Evolutionary determinants of clutch size in cav-
ity-nesting birds: Nest predation or limited breeding opportunities? American Naturalist 142: 937–946.