



Cooperative Breeding of Buff-Throated Partridges in Two Natural Populations: Demographic Comparison with a Habituated Population

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ABSTRACT

The buff-throated partridge (*Tetraophasis szechenyii*) is endemic to western China and is known to cooperatively breed in a population habituated to supplemental feeding by humans. The social structure and demography of this species, however, have not been examined in natural populations. To determine if cooperative breeding occurs in populations unassociated with humans, we surveyed two natural populations in the Ganzi Tibetan Autonomous Prefecture in western China. We compared the demography of the natural populations with that of the habituated population. The results showed that facultative cooperative breeding occurred in the two natural populations, but population density, group density, and the frequency of cooperative breeding were lower in the two natural populations than in the habituated population. We conclude that the cooperative breeding system is a facultative breeding strategy in both natural and habituated buff-throated partridge, and suggest that variation in food resources might cause variation in demography and the frequency of cooperative breeding among populations.

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Authors' Contributions

JR conceived and designed the study. BW conducted field survey at Gexigou, analyzed the data and wrote the article. BZ helped in collection of field data from GXG. NY provided data on partridge population at Pamuling. LD conducted field surveys in ZGS and collected data.

Key words

Breeding group, Galliformes, Parental care, Phasianidae, Precocial.

INTRODUCTION

The order Galliformes is characterized by precocial offspring, with breeding systems that reduce parental investment comparing with altricial birds (Royle *et al.*, 2012). The majority of Galliformes have typical maternal care (including biparental and female-only) (Cockburn, 2006; Royle *et al.*, 2012), but uniparental male care (Birks, 1997), double-nesting (Casas *et al.*, 2009) and brood parasitism (Krakauer and Kimball, 2009) are adopted by some species. Some incubator birds (Megapodiidae) have even evolved strategies to escape parental care by using environmental heat sources (Sinclair *et al.*, 2002; Harris *et al.*, 2014).

Cooperative breeding is a social system that typically involves the presence of adult helpers in addition to the breeding pair providing parental care to the young of a single nest or brood (Brown, 1987; Stacey and Koenig, 1990). Auxiliary help is often explained to have adaptive significance in terms of its direct and indirect fitness benefits (Bergmüller *et al.*, 2007; Riehl, 2013). For a long period, this breeding system was not thought to occur in Galliformes, since in general opinion, such parental care is not favored by species with highly precocial hatchlings (Arnold and Owens, 1998; Cockburn, 2006). However, in recent years, there have been four reported cases of cooperative breeding in this order (Lu and Zheng, 2005; Hale, 2006; Xu *et al.*, 2011; Zeng, 2014). These rare cases are important for understanding the pattern of cooperative breeding without constraints of extensive parental care and the

underlying evolutionary mechanisms (Ligon and Burt, 2004).

The buff-throated partridge (*Tetraophasis szechenyii*), an endangered and endemic Galliform in the mountains of southwest China (Madge *et al.*, 2002; Lu, 2006), is a recently reported facultative cooperative breeder (Xu *et al.*, 2011). However, this finding is from a partridge population habituated to humans and fed ad libitum by local people for many years (Xu *et al.*, 2011; Yang *et al.*, 2011), which is special and different from the other reported cases of cooperative Galliforme breeders (Lu and Zheng, 2005; Hale, 2006; Zeng, 2014). One remarkable effect caused by artificial supplemental feeding is facilitating the formation of cooperative societies (Dickinson and McGowan, 2005; Baglione *et al.*, 2006). More recently, Yang *et al.* (2016) conducted a study at the same site where cooperative breeding of buff-throated partridge was found (Xu *et al.*, 2011), and demonstrated that partridges' reproductive success was enhanced by supplemental feeding practice as well as the presence of helpers. Yet, the percentage of cooperatively breeding groups did not differ significantly between feeding and neighboring non-feeding areas (Yang *et al.*, 2016). Their work provides evidence on the benefits gained by the breeders within cooperative groups, but it should be noted that the partridge groups they compared were adjacent to and connected with each other, and were likely to be from one single population sharing the majority of ecological traits. Comparisons between isolated populations of buff-throated partridge are still absent. It is unclear whether cooperative breeding occurs in natural populations. Moreover, it is unknown how demography and the frequency of cooperative breeding vary among populations and between habituated and natural populations. In the present study, we (1) surveyed two natural populations of the buff-throated partridge to determine whether cooperative breeding

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occurred in natural populations; then (2) compared the demographic and breeding characteristics of the natural populations with those of the habituated population studied by Xu *et al.* (2011).

MATERIALS AND METHODS

Species

The buff-throated partridge is a sexually monomorphic species in the family Phasianidae (Potapov, 2002). The partridge is endemic in China, distributed in southeast Tibet, south Qinghai, west Sichuan and northwest Yunnan. They inhabit in mixed conifer forests, rhododendron shrubs, oak thickets, alpine meadows, and rocky ravines at elevations between 3,350–4,600 m (MacKinnon, 2000; Madge *et al.*, 2002; Lu, 2006). The buff-throated partridge is an endangered species and a first-class national protected wildlife in China, whose population size was evaluated to be continuously declining due to the threats including illegal poaching, habitat loss, fragmentation and degradation (Zheng and Wang, 1998).

Study sites

We conducted surveys at Zagasi Mountain (ZGS) in

2010 and Gexigou Nature Reserve (GXG) between 2012 and 2013. Xu *et al.* (2011) conducted a four-year study (2006–2009) at Pamuling Mountain (PML), where they revealed cooperative breeding in the human-fed partridge population. The three study sites are located in Ganzi Tibetan Autonomous Prefecture, Sichuan Province, China (Fig. 1). GXG is 31 km southwest of PML, separated by the Yalong River. ZGS is located 190 km northwest of PML (Table 1). All the study sites have a similar semi-humid climate, typical of the Qinghai-Tibet plateau, with no obvious variation in monthly mean temperature and precipitation among sites across the study years (climate data were download from “China meteorological data sharing service system” at <http://cdc.nmic.cn/>; *T*-tests, all $P > 0.05$). Altitude, topography and habitat structure is similar among the sites. The habitats of the three study sites are dominated by holly-leaf alpine oak (*Quercus aquifolioides*) forest, flaky fir (*Abies squamata*) coniferous forest and short Rhododendron scrub (*Rhododendron nitidulum*, *Rh. laudandum*, and *Rh. flavidum*). Similar to PML, there is a Tibetan monastery at ZGS, where local people offer similar supplementary food to wildlife. Interestingly, our observations at ZGS suggest that the buff-throated partridge rarely forages at supplementary feeding sites, unlike at PML.

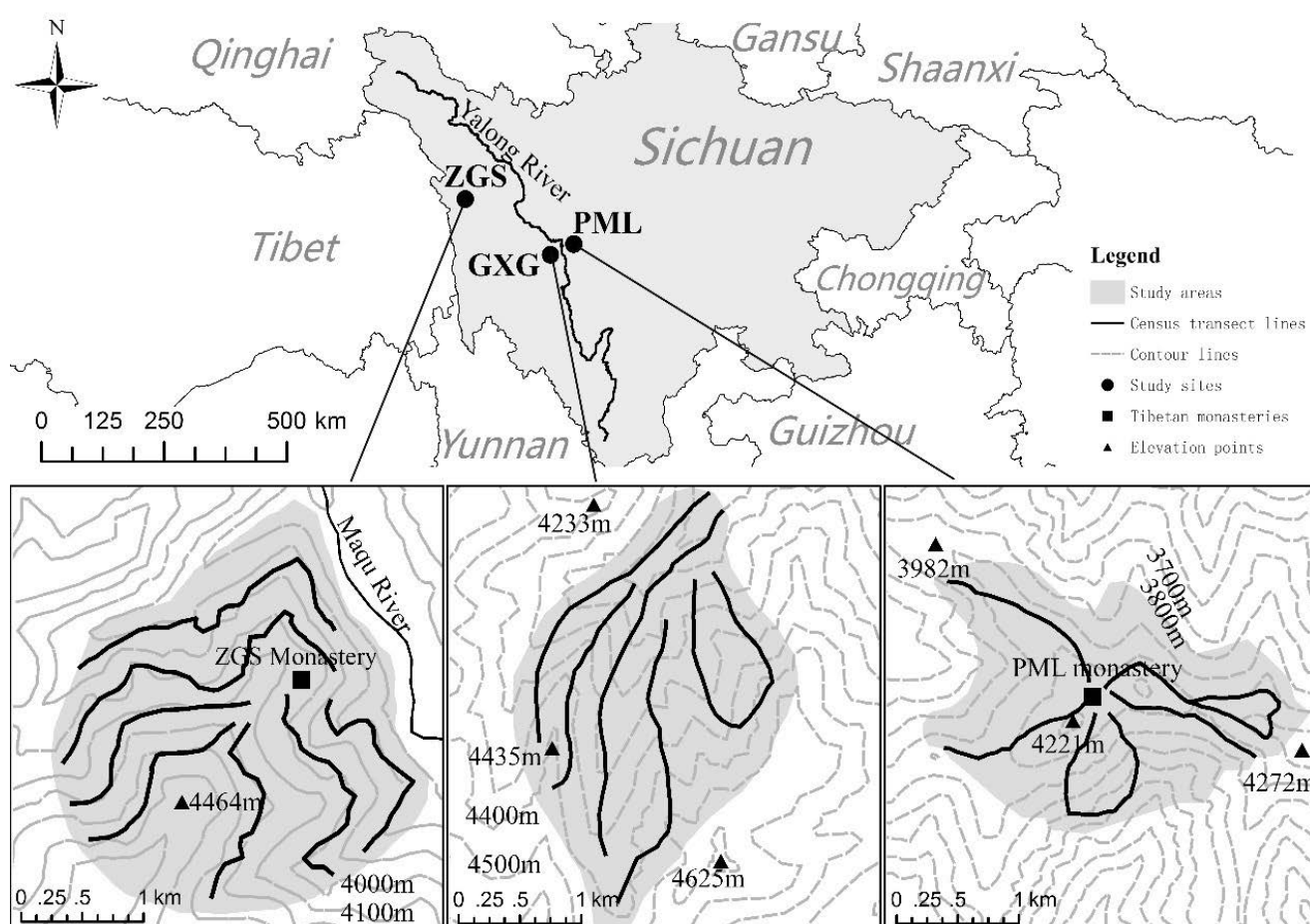


Fig. 1. Map of our two study sites (ZGS and GXG) as well of PML, showing topography, areas and census transect lines.

Table I.- Characteristics comparison of our two study sites (ZGS and GXG) as well as PML.

	Location (N, E)	Altitude (m)	Area (km ²)	Study year(s)
ZGS	30°55'N-30°57'N, 99°13'E-99°15'E	3,700–4,464	5.88	2010
GXG	29°56'N-29°59'N, 100°53'E-100°56'E	3,753–4,435	4.25	2012-2013
PML	30°05'N-30°06'N, 101°10'E-101°11'E	3,800–4,221	3.40	2006-2009

Population survey

We surveyed ZGS and GXG during the breeding season of the partridge, from April to August each year. We used the methods described by Xu *et al.* (2011) to survey partridges. We established seven and five 1.5-3 km transects in ZGS and GXG, respectively, traversing the entire study areas to census the partridges (Wu *et al.*, 2013) (Fig. 1). We walked along the transects, searching for partridges using three methods: (1) direct encounters, (2) tracking their calls, and (3) tracking their calls in response to playback. A 60 second recording of a territorial chorus, recorded at PML in March, 2006, was used in our surveys. The recording was played at 250 m intervals along transects (Bibby *et al.*, 1998), using a 48 watt Jin Ying Q8 loud-speaker placed on the ground. We stopped playback as soon as a partridge responded and then subsequently tracked them. If we had no response, then we repeated playback once every two min for a maximum of three times. Once detected, we recorded the group structures, and observed their behaviors using binoculars from a distance about 20 m (only if they had not been frightened by observers). Specifically, we focused on recording behaviors that reflect cooperative breeding efforts, such as provisioning to young, brooding, vigilance and territory defense (Sherman, 1977; Stacey and Koenig, 1990; Weathers *et al.*, 1990; Theuerkauf *et al.*, 2009).

During the breeding season, buff-throated partridge territories minimally overlap and remain relatively stable (Yang *et al.*, 2011), and the disappearance of individuals and turnover is rare (Xu *et al.*, 2011). Each group can thus be identified by the territory location and the number of group members. Double counts were thus avoided. We surveyed each transect at least twice each month during the breeding season, resulting in each study site being surveyed over ten times. Given our extensive searching, we are confident that we detected and recorded almost all partridge groups inhabiting in the study sites.

Statistical analysis

The occurrence of cooperative breeding was determined based on population surveys and behavioral observations. Followed the broad definition about cooperation proposed by Cockburn (2006), we considered a group to be cooperative if the group consisted of more than two adults, kept stable during the breeding season, and had cooperative behaviors mentioned above. Newly hatched chicks and juveniles were

not treated as “helpers” and were excluded when calculating group size and population density. We used *U*-tests to determine if group size and helper number of per cooperative group were significantly different between populations. We averaged annually the frequency of cooperative breeding (*i.e.*, the percentage of cooperatively breeding groups) for each population, and used Fisher’s exact tests to compare frequencies between populations. All statistical tests were conducted in SPSS version 21.0 (IBM 2012), and interpreted $P < 0.05$ as being statistically significant.

RESULTS

Cooperative breeding in natural populations

At ZGS, we identified 17 groups in 2010, in which we were able to explicitly observe and record group structure in eight of these groups, and the structures of the rest nine groups were undetermined. The descriptions and calculations presented below are based on these eight known groups. In GXG, we identified 28 groups (14 in 2012 and 14 in 2013) and recorded group structure in all of the 28 groups. We were not able to completely determine whether a group was the same one in different years without the help of banding bird, thus we pooled the data from different years in analysis.

Over a third of the groups at ZGS and GXG were comprised by more than two adults. We observed several cases that all adult members exhibited behaviors associated with cooperative breeding within some of these groups. Most of the time, group members predominantly moved and foraged together. Sometimes a group was frightened and separated, then the members called repeatedly to advertise their positions, moving toward each other until the group was re-established ($n = 7$ at ZGS and $n = 12$ at GXG). The largest female, which was presumably the breeding female in the group, always stayed close to chicks, frequently brooding the chicks (covered chicks under her wings and abdomen to warm and protect them) (2 at ZGS and 3 at GXG). All adults provided parental care toward chicks, including vigilance (2 at ZGS and 5 at GXG) and showing food to chicks by removing mud and leaf litter while foraging (3 at ZGS and 3 at GXG). Cooperative territory-defense was found in these groups as well. In the five territory disputes that we observed (1 at ZGS and 4 at GXG), all adults within the incumbent group participated in territory-defense, repeatedly calling and displaying (bending and straightening their necks) when intruders appeared. These results suggested that cooperative breeding occurs in natural buff-throated partridge populations.

Demographic comparison between populations

The overall mean group sizes of ZGS population and GXG population were similar (range = 2-4 at ZGS and 2-5 at GXG), without significant difference (Table II; *U*-tests, $P = 0.99$). The two natural populations had similar group density and population density (Table II). There were no significant difference in both frequencies of cooperative breeding (Table II, Fisher’s exact test, $P = 1.00$) and helper numbers of per

cooperative group (*U*-tests, $P = 1.00$) between two natural populations.

Table II.- Comparison of density, group size and the frequency of cooperative breeding in three buff-throated partridge populations.

Item	ZGS	GXG	PML
Population type	Natural	Natural	Fed
Mean annual number of groups observed	17	14	17
Mean group size (mean adults/group $\pm$ SD)	2.6 $\pm$ 0.3 ⁺	2.6 $\pm$ 0.2	2.8 $\pm$ 0.1
Mean number of helpers (mean helpers/coop. group $\pm$ SD)	1.7 $\pm$ 0.3 ⁺	1.6 $\pm$ 0.2	1.3 $\pm$ 0.1
Group density (groups/km ²)	2.9	3.3	5.0
Population density (adults/km ²)	7.6	8.7	14.1
Percent of cooperative breeding	37.5% ⁺	39.3%	64.7%

⁺Mean group size, mean number of helpers and the frequency of cooperative breeding at ZGS were calculated based on eight known groups, since structures of the rest nine groups were undetermined.

The overall mean group size in the two natural populations was not significantly different from that of the fed population at PML (Table II; *U*-tests, ZGS vs PML, $P = 0.41$; GXG vs PML, $P = 0.15$). The helper numbers of per cooperative group were also similar in fed and natural populations, without significant difference (Table II; *U*-tests, ZGS vs PML, $P = 0.16$; GXG vs PML, $P = 0.053$). However, group density and population density was lower in the two natural populations than in the population at PML (Table II). The two natural populations had also lower frequencies of cooperative breeding compared to PML (Table II), but we did not detect any statistical significance between them (Fisher's exact test, ZGS vs PML, $P = 0.39$; GXG vs PML, $P = 0.29$).

DISCUSSION

In this study, we found cooperative breeding behavior in two natural buff-throated partridge populations, revealing that facultative cooperative breeding is a breeding strategy occurring in all populations rather than a unique case in the habituated population (Xu *et al.*, 2011; Yang *et al.*, 2011). The group size of the buff-throated partridge (range=2-5) was smaller compared to the other cooperative breeding cases reported in Galliformes (2-15 for the hybrid population of white eared-pheasants *Crossoptilon crossoptilon* and Tibetan eared-pheasants *C. harmani*, Lu and Zheng, 2005; 2-9 for black-breasted wood-quail *Odontophorus leucolaemus*, Hale, 2006; 2-7 for kalij pheasant *Lophura leucomelanos*, Zeng, 2014). The cooperative behaviors reported in the cases of cooperative Galliformes, *e.g.* finding food for chicks, cooperative vigilance and territorial defense (Lu and Zheng, 2005; Hale, 2006; Xu *et al.*, 2011; Zeng, 2014), were also observed in the natural buff-throated partridge populations. Such behaviors are likely main means

of helpers providing aids to the breeding pairs in cooperative Galliforme breeders. However, in our study, it was not possible to determine the breeding status of each adult within cooperative groups through behavioral observations. We were not able to determine which adults were breeders or helpers that forwent reproduction opportunities or if all of them were breeders.

Our comparison among the three populations showed that group and population density were lower in the natural populations than in the habituated population. In particular, we compared the frequency of cooperative breeding among populations. Although the statistical analysis showed that there was no significant difference between each two populations, we found a trend of lower percentages of cooperatively breeding groups at the natural populations than at the habituated population. The three study sites have similar climate, altitude, topography and habitat, thus, year-round supplementary feeding at PML is likely the critical variable that differs among study sites. Consequently, food resources are richer and more easily obtained at PML. When faced with the choice of leaving or staying on natal territories, sexual mature offspring born on high-quality territories benefit from delayed dispersal and kin-based cooperative breeding (Stacey and Ligon, 1987, 1991; Hatchwell and Komdeur, 2004). Increase food availability thus facilitates cooperative breeding (Dickinson and McGowan, 2005; Baglione *et al.*, 2006). This relationship between resources and cooperative breeding may explain the observed differences in the frequency of this breeding strategy between the natural and habituated populations of the buff-throated partridge. If the partridge has difficulty obtaining sufficient resources as a member of a group in the natural populations, then they would be more likely to disperse from natal territories. Additionally, decreased resource availability among study sites may directly translate to lower population densities in natural populations (Hoodless *et al.*, 1999).

Ecological and demographic factors contribute to the development and occurrence of cooperative breeding (Brown, 1987), but no factor by itself causes delayed dispersal and cooperation (Koenig *et al.*, 1992). Our study demonstrated variation trends in demography and cooperative breeding between two natural populations and one habituated population, and we suspect resource availability as a potential factor influencing cooperative breeding in the buff-throated partridge. However, our study involved surveys at different sites in different years, so that potential year-to-year variations in breeding parameters are hard to avoid. And also, our small sample size is lack of statistical power to show significant differences. Therefore, we recommend more extensive monitoring and quantitative experiment to examine the dynamics of the relationship between resource availability and cooperative breeding.

CONCLUSION

To conclude, we found facultative cooperative breeding in two natural buff-throated partridge populations. However,

the key demographic parameters, including population density, group density, and the frequency of cooperative breeding, were lower in the two natural populations than in a population habituated to supplemental feeding by humans. Given that supplementary feeding in the habituated populations is the critical difference from the two natural ones, we suspect food availability as a potential factor that influenced demography and prevalence of cooperative breeding in the buff-throated partridge. Further studies, examining the dynamics of the relationship between resource availability and cooperative breeding by buff-throated partridges, are needed.

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Statement of conflict of interest

All the authors contributed in this paper declare that they have no conflict of interest.

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