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Group size does not influence territory size and overlap in a habituated population of a cooperative breeding Himalayan Galliforme species

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Understanding the factors that influence territorial behaviour is essential for determining whether fragmented habitats are able to support the spatial ecological conditions that maintain cooperative breeding systems of threatened bird species. Here, we examine territorial behaviour of the cooperative breeding Buff-throated Partridge *Tetraophasis szechenyii* in patchy tree-line habitats of the Pamuling Mountains in western China. This population has been habituated to humans through supplementary feeding by Tibetan Monks. We studied 18 groups during three consecutive breeding seasons and two non-breeding seasons from March 2007 through July 2009, using direct tracking of colour-marked individuals. Territories were occupied by stable family groups, and were centred on the interface of two or more different tree-line habitats. Groups occupied the same close area near the nest from one year to the next. However, territory sizes, estimated using radio-telemetry, were smaller compared to those of other non-cooperative breeding montane Galliformes. Both territory size and overlap were greater during the non-breeding season. Group size did not influence territory size, in either the breeding or non-breeding season. Territorial behaviour was influenced by supplementary food given at two offering sites during both seasons, in proximity to both nesting and roost sites. Further research should focus on examining the interactions between supplementary feeding and family group composition, with direct comparisons of data from non-supplementary fed partridge populations outside of Buddhist Sacred Sites.

Key words: *Tetraophasis szechenyii*, general linear mixed models, cooperative breeding, territorial behaviour, tree-line habitats, habituation

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Avian cooperative breeding systems appear to arise when environmental constraints severely limit opportunities for younger birds to breed independently (Ehrlich et al. 1988). These limitations may include a shortage of territory openings because higher quality habitats are saturated with established breeders. Studies have shown that for most cooperative breeding bird species, individuals are year-round residents and defend their territories throughout the breeding and non-breeding seasons (Russell & Rowley 1993, Ekman 2006). Larger cooperative breeding groups tend to inhabit better, higher-quality territories and have greater reproductive success (see Brown 1987, Stacey & Koenig 1991). In recent years, considerable attention has gone into understanding which factors influence territory size in threatened cooperative breeding species that occupy

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fragmented habitats (Pasinelli *et al.* 2001, Bellis *et al.* 2004, Doucette 2010), primarily to help determine whether such fragmented habitats are able to support the spatial ecological requirements that maintain cooperative breeding systems.

This study examines whether group size influences territory size and territory overlap, in a threatened cooperative breeding Galliforme species occupying fragmented Himalayan tree-line habitats. The Buff-throated Partridge *Tetraophasis szechenyii* is a large Galliforme species endemic to China (Lu 2006). The species is resident in coniferous forest, alpine shrublands and tundra habitat of tree-line ecotones at 3,350–55,000 m elevation (Machinnon *et al.* 2000, Potapov 2002) that are often subject to severe weather conditions (Xu *et al.* 2008). The buff-throated Partridge is a cooperative breeder (Xu *et al.* 2010, 2011), which is especially rare amongst Galliformes, since for the overwhelming majority of species the young are precocious and there is limited parental care (Ligon & Burt 2004). In addition, the species is currently listed as vulnerable according to the Red Book of China (Wang & Xie 2004), due to severe habitat loss and degradation and illegal hunting.

Himalayan Galliformes are notoriously difficult to study since they live in highly complex montane environments (see Gaston *et al.* 1983). We selected a localized population of Buff-throated Partridge that has been habituated through supplementary feeding by Tibetan Monks within a culturally protected tree-line landscape. This population offers a unique opportunity to study aspects of territorial behaviour that can be used for the study of other non-habituated Himalayan populations. Our objectives are: (1) to determine seasonal territory size and degree of overlap between neighbouring groups; (2) investigate relationships between group size, territory size, and overlap between neighbouring breeding groups; (3) assess breeding site fidelity. We hypothesized that larger breeding groups would require more resources and would occupy larger territories, and that larger breeding groups with more individuals would show less territorial overlap than smaller groups.

METHODS

Study area

Buff-throated Partridge were studied across a tree-line ecotone in the Pamuling Mountains (30°06'N 101°11'E), Ganzi Tibetan Autonomous Prefecture, Sichuan Province. The 340 ha study site is situated at an elevation of 3,900–4,200 m and is dominated by Holly-leaf Alpine Oak *Quercus aquifolioides* forest, which is distributed mainly along the southern-most slopes of the region, but also occurs in a more stunted and scrubby stature along the western slopes. Other tree-line habitats include: Flaky Fir forest dominated by Flaky Fir *Abies squamata* and Masters Larch *Larix mastersiana*; Rhododendron scrub habitat (approximately 50 cm in height), composed of violet purple flowering Rhododendron *Rhododendron nitidulum*; and Alpine Meadow, primarily composed of Sichuan Kobresia *Kobresia setchwanensis* meadow. The semi-humid climate is typical of the Qinghai-Tibetan plateau tree-line, with spring occurring from April to June, summer only in July, autumn from August to September, and winter from October to March. Flowering of dominant plants (e.g. *Rhododendron nitidulum*) occurs predominantly from May to June, and snow typically covers the ground from November to April. Consequently, birds living at the tree-line are confronted with particularly long cold winters of 6–7 months duration.

Study population and marking birds

We studied the Buff-throated Partridge during three consecutive breeding seasons and two non-breeding seasons, from March 2007 until July 2009. The population at the Pamuling Tibetan Monastery has been offered daily supplementary food (rice and corn) for a number of years and is given cultural protection as a Sacred Site by Tibetan culture. Birds search for food at two 'offering' sites each morning for one hour. Buddhist cultural protection and supplementary feeding is an integral component of local conservation management across many areas of Asia for a variety of taxa (Lu & Zheng 2002, Wang *et al.* 2005, Shen 2008). Sadly, this form of conservation management has largely been ignored or under-valued by international ecologists, and empirical research on such taxa has generally not occurred because of academic concerns over how representative such data may be for the species' ecology.

Habituation to humans enabled us to do direct behavioural observations of these groups over extended periods of time (e.g. Lu & Zheng 2002) and approach groups to within 10 m without observers influencing their behaviour. Buff-throated partridges were deemed to be members of a family group based on behavioural traits, where group members searched for food together and shared the same roosting tree (Xu *et al.* 2008). Individual birds were captured using drop-netting and a rice bait in March and December of each study year (Yang *et al.* 2009). We gave 35 individuals a unique colour ring combination and made observations for 18 breeding groups during three consecutive breed-

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ing seasons, and 12 breeding groups (including ten of the previous 18) during two non-breeding seasons. Non-breeders were also present within each family group during the breeding seasons, acting as helpers in brooding, vigilance and territory defense, and also showing food to the young (Xu *et al.* 2011).

Locating groups and data collection

A combination of habituation and observer familiarity with the species roosting and foraging ecology and vocalizations, permitted us to locate groups in dense tree-line forest habitat within a 1 km distance and to count all individual birds within our study area, without the need for radio-telemetry. All colour-marked birds were located and directly tracked for one day at three-day intervals. The position of each group was recorded using a handheld GPS receiver (Garmin Etrex Vista) with an accuracy of ±8 m when they were estimated to have ranged >30 m from the previous location fix. Thus, we were able to record 5–10 location fixes per family group per day. Beginning in 2007, 28 nests were monitored during the breeding season, when all breeding and non-breeding members within each family group remain in close proximity to the nest.

Territory size, overlap, and site fidelity

At Pamuling, the Buff-throated Partridge breeding season occurs from April (spring) to July (summer) and the non-breeding season from August (autumn) to March (winter). Copulation occurs during the second half of March, egg-laying commences mid-March towards the end of May, and incubation occurs from early April to mid-June. We defined territories as the area birds occupy and defend against other groups for the purpose of reproduction, and which provides foraging resources for all breeding and non-breeding individuals and nestlings within the same group year-round (Cramp 1998).

BIOTAS software v.2.0 (Ecological Software Solutions, Florida) was used to estimate breeding and non-breeding seasonal territory size, degree of territory overlap and breeding site fidelity of each family group. Territory size was determined using the fixed-kernel (FK) method with least-squares cross-validation (Worton 1989) which generally yields far more accurate and informative estimates than other contemporary methods (Seaman & Powell 1996, Barg *et al.* 2005). Only groups with >30 fixes were used for the analysis (Seaman *et al.* 1999). We calculated the fixed kernel (FK) territory size with the probability density of 95%, 75%, and 50% for family groups that included all members that survived +3 months, and non-breeding season territory sizes for family groups that survived +6 months. We excluded territory estimates with insufficient number of fixes, with the exception of overlap determination and site fidelity. ArcGIS (Environmental Systems Research Institute, Inc. 2005) was used to map the 95% FK estimated territories of each family group within the study area.

We estimated an index in order to distinguish differences of overlap between neighbours in different sized groups. We calculated the minimum percentage overlap of two intersecting neighbouring groups based on all three fixed kernel territory estimators since these percentages are based on territory size, which differs between groups. Degree of overlap was calculated using the following index (Atwood & Weeks 2003, Doucette 2010):

$$[(area_{\alpha\beta}/territory_{\alpha})\times(area_{\alpha\beta}/territory_{\beta})]^{0.5}.$$

$Area_{\alpha\beta}$ corresponds to the area of overlap, and both $territory_{\alpha}$ and $territory_{\beta}$ correspond to the territories of the subsequent groups α and β, respectively. To assess site fidelity we determined the degree in overlap between the 95%, 75% and 50% fixed kernel territories used by seven family groups tracked during two consecutive breeding seasons (following Doucette 2010). The first breeding season territory was used as the numerator, with the second breeding season territory used as the base for calculation of the degree of breeding site fidelity.

Statistical analyses

Within and across-seasons territory size and overlap analyses were conducted with general linear mixed models (GLMM). We included group size, number of fixes, year, and season as fixed factors; family group identity was included as a random effect because some groups were recorded over consecutive breeding and non-breeding seasons (2008 and 2009). All three fixed kernel territory size estimators (95% FK, 75% FK and 50% FK) and the degree of overlap were entered as dependent variables. All statistical tests were conducted using SPSS for windows release 17.0 (SPSS Inc 2001). All tests were two-tailed ($\alpha = 0.05$). Mean values are given ± SE unless stated otherwise.

RESULTS

Location of territories and territory size

Sizes of all family group territories were independent of the number of fixes for 95% FK during the breeding ($F_{1,17} = 0.65$, $P = 0.44$) and non-breeding seasons ($F_{1,1}1 = 0.03$, $P = 0.88$). Territory size based on 95%

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FK for all family groups was independent of the group size during the breeding ($F_{3,17} = 1.36$, $P = 0.27$) and non-breeding season ($F_{4,11} = 0.7$, $P = 0.43$). Territory size was still independent of the group size for 75% FK and 50% FK (Table 1). All fixed kernel mean breeding territory size estimations were significantly smaller than that of the non-breeding season (95%FK: $F_{1,29} = 30.69$, $P < 0.01$; 75%FK: $F_{1,29} = 43.07$, $P < 0.01$; 50%FK $F_{1,29} = 26.98$, $P < 0.01$, Table 1). Territory size did not differ between years during breeding ($F_{2,17} = 4.38$, $P = 0.06$) and non-breeding seasons ($F_{1,11} < 0.01$, $P = 0.99$) for 95% FK estimations.

Territorial overlap and site fidelity

All territories overlapped with that of neighbouring groups. The degree overlap of territory for all three FK estimations was not correlated with group sizes during the breeding and non-breeding season (Table 2). Overall mean territory overlap for 95% FK estimations between neighbouring groups was significantly greater during the non-breeding seasons (29.8 ± 2.4%, $n = 12$) than in the breeding season (20.7 ± 2.38%, $n = 18$, $F_{1,29} = 6.55$, $P = 0.02$). Overall mean territory overlap was still significantly larger for 75% FK ($F_{1,29} = 10.67$, $P < 0.01$), but not for 50% FK ($F_{1,29} < 0.01$, $P = 0.94$, Table 2).

Seven groups were selected to detect site fidelity during two successive years (H14, H5, WH1, H6, H7, H8 and H9 in 2008, and H12, WH3 and H13 in 2009; Fig. 1A). Among the seven groups, group structure was stable for four groups (H8, H9, H14 and WH1) and this included two groups with insufficient number of fixes (H14 in 2008 and 2009, and WH1 in 2008), whereas the structure of helpers (not of breeding pairs) differed between the remaining three groups (H5 vs. H12, H6 vs. WH3, and H7 vs. H13). In all three cases, one helper (either male or female) left the breeding group the following year (2009), and in one instance a new female joined in 2009 following the departure of a male helper (from group H7 in 2008 to group H13 in 2009). All seven groups maintained a similar territory for roosting or nesting, with territory size remaining

Table 1. Effect of group size, number of fixes and year on territory size (ha) of Buff-throated Partridge in the Pamuling Mountains. General linear mixed models (GLMM) were conducted using 95%, 75% and 50% fixed kernel (FK) estimations as dependent variables and family group identity included as a random effect.

Variables		GLMM		Territory size (ha)	
		F	*P*	Means	Range
Breeding season ($n = 18$)					
95% FK	Group size	1.36	0.27	10.6 ± 0.3	8.6–13.5
	Fixes	0.65	0.44		
	Year	2.52	0.12		
75% FK	Group size	2.22	0.16	5.7 ± 0.2	4.5–7.5
	Fixes	0.05	0.83		
	Year	4.06	0.04		
50% FK	Group size	1.93	0.19	3.1 ± 0.1	2.4–3.9
	Fixes	0.32	0.58		
	Year	0.45	0.65		
Non-breeding season ($n = 12$)					
95% FK	Group size	0.7	0.43	13.7 ± 0.5	11.4–16.9
	Fixes	0.03	0.88		
	Year	<0.01	0.99		
75% FK	Group size	0.36	0.56	7.8 ± 0.3	6.5–9.5
	Fixes	<0.01	0.97		
	Year	0.13	0.73		
50% FK	Group size	0.01	0.81	4.2 ± 0.2	3.5–5.8
	Fixes	0.19	0.68		
	Year	0.93	0.36		

Table 2. Effects of group size, number of fixes and year on the degree of territory overlap (%) in Buff-throated Partridge in tree-line habitats, Pamuling Mountains. General linear mixed models (GLMM) were calculated using 95%, 75% and 50% fixed kernel (FK) estimations as dependent variables and family group identity included as a random effect.

Variables		GLMM		Degree territory overlap (%)	
		F	*P*	Means	Range
Breeding season ($n = 18$)					
95% FK	Group size	0.09	0.78	20.7 ± 2.4	6.9–36.9
	Fixes	0.07	0.82		
	Year	0.63	0.59		
75% FK	Group size	0.56	0.47	20.7 ± 1.8	0–23.5
	Fixes	4.08	0.07		
	Year	0.23	0.8		
50% FK	Group size	0.59	0.46	10.2 ± 5.2	0–28.9
	Fixes	2.19	0.16		
	Year	1.65	0.23		
Non-breeding season ($n = 12$)					
95% FK	Group size	1.26	0.29	29.8 ± 2.4	15.8–42.6
	Fixes	1.12	0.32		
	Year	24.58	<0.01		
75% FK	Group size	3.5	0.1	20.9 ± 1.9	11.5–30.2
	Fixes	7.41	0.03		
	Year	15.39	<0.01		
50% FK	Group size	1.08	0.33	10.3 ± 1.7	0–22.1
	Fixes	0.31	0.59		
	Year	2.32	0.17		

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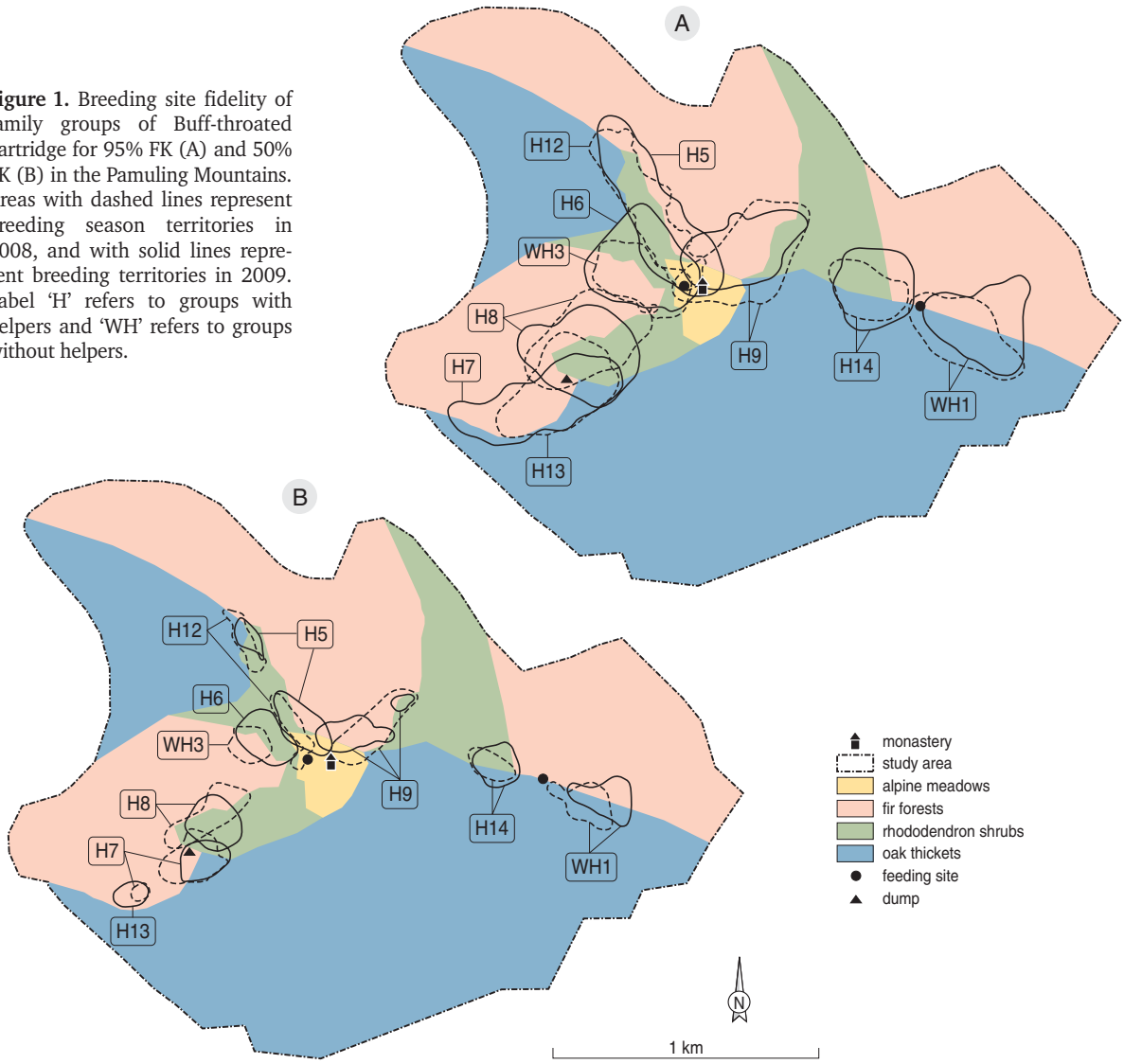


Figure 1. Breeding site fidelity of family groups of Buff-throated Partridge for 95% FK (A) and 50% FK (B) in the Pamuling Mountains. Areas with dashed lines represent breeding season territories in 2008, and with solid lines represent breeding territories in 2009. Label 'H' refers to groups with helpers and 'WH' refers to groups without helpers.

stable and defended year-round. All helpers from all groups took part in vigilance and territory defence, and they also provided protection to the young, particularly from attack by Thick-billed Crows *Corvus macrorhynchus*. Breeding females rarely participated in territory defense. The mean territorial overlap of these seven family groups between 2008 and 2009 was 56.9 ± 4.4% (range 47.2–76.2%) for 95% FK, and 66 ± 3.1% (range 52.7–72.6%) for 75% FK, and 72.7 ± 1.8% (range 64.9–78.7%) for 50% FK (Fig.1B).

All Buff-throated Partridge territories encompassed two or more tree-line habitat types (Fig. 2) during both seasons. The locations of both supplementary feeding sites and that of the local Monastery dumpsite appeared to influence the spatial configuration of partridge territories between seasons. Four neighbouring territories (H7, H13, and H8 in both 2008 and 2009) enclosed the monastery dump within their territorial boundary. Three breeding groups (H10, H11 and WH1) enclosed one of the supplementary feeding sites at the edges of their territory. Four breeding groups (H3, H6, H9 and WH2 in 2008) enclosed one of the supplementary feeding sites at the edge of their territory during the breeding season, whereas they converged toward, but did not overlap with that of the feeding site during the breeding season. Territories of the two remaining breeding groups (H1 and H2) did not correlate with supplementary feeding during the breeding

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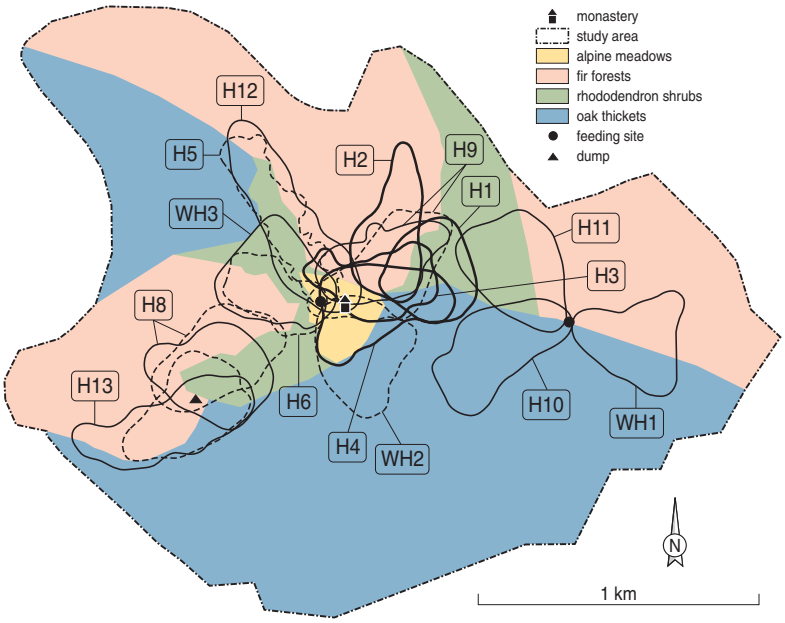


Figure 2. Location of territories of Buff-throated Partridge in tree-line habitats in the Pamuling Mountains, China. Solid bold lines represent breeding season territories in 2007, dashed lines represent breeding territories in 2008; and solid lines represent breeding territories in 2009. Label 'H' refers to groups with helpers and 'WH' refers to groups without helpers.

season. The distance from the geometric centre of each breeding group territory to the nearest supplementary feeding site or dump ranged 130–310 m for all groups. During the non-breeding season, two neighbouring groups enclosed the monastery dump within their territory boundary. Nine groups enclosed the supplementary feeding site near the monastery within their territorial boundaries, and the territory of the one remaining group enclosed one of the supplementary feeding sites.

DISCUSSION

This study provides the first quantitative data on the territorial behaviour of a cooperative breeding Galliforme species. Buff-throated Partridge territorial behaviour changed between seasons, and breeding groups utilized a much larger area during the non-breeding season. We cannot be certain as to how representative these data are of partridge populations that occur outside of Buddhist Sacred Sites. Our estimates of territory size are smaller than those estimated (using radio-telemetry) for the closely related and non-cooperative breeder Chestnut-throated Partridge *T. obscures* (43 ha and 59 ha) during the spring and summer months (Klaus *et al.* 2003). They are also smaller than territory sizes estimated for female (17.4 ha) and male (19.0 ha) Ruffed Grouse *Bonasa umbellus* (Whitaker *et al.* 2007), female (24.5 ha) and male (39.2 ha) Hazel Grouse *B. bonasia* (Rhim & Lee 2004) and also for Blood Pheasant *Ithaginis cruentu* (15.5 ha) a species known to inhabit the same tree-line habitats in the region (Jia *et al.* 2004). Our estimates are however larger than the 3-ha territories estimated for the threatened Chinese Grouse *B. sewerzowi* (Sun & Fang 1997).

Interactions between competing neighbours could influence Buff-throated Partridge territory size in the Pamuling Mountains, as has been suggested for other bird species (e.g. Adams 2001, Valcu & Kempenaers 2010) particularly as so many groups are habituated to supplementary feeding. A greater number of conspecifics within an area is known to reduce overall territory size in some bird species (Schoener 1968), possibly leading to greater competitive pressure between neighbours, resulting in relatively smaller territories. In order to gain access to mates, however, breeding individuals would have to expand their home range or territory (Whitaker *et al.* 2007). A pilot study of the same colour-marked habituated population revealed that each breeding pair forms a tight bond, which can last several years (Yang, unpubl. data), suggesting that this reduces the need for males or females to expand their range to look for potential mates.

Contrary to our hypothesis, we found that group size did not influence territory size. Griesser *et al.* (2009) reported that group size did not affect core territory sizes of the cooperative breeding Apostlebird *Struthidea cinerea*, but that group size did influence the species' home range size, probably because larger groups were able to regain dominance at their breeding

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sites. Moreover, it is likely that the ranging behaviour of Buff-throated Partridge at the Pamuling Tibetan Monastery is influenced by the supplementary food given by monks at two offering sites during both seasons, in proximity to both nesting and roost sites. Xu *et al.* (2008) reported that food availability at Buff-throated Partridge roost sites was poorer than at foraging sites, whereas other studies have demonstrated that the spatial configuration of foraging and roosting sites exerts a significant influence on the home range size of other Himalayan Galliformes (Lu & Zheng 2002).

Family groups with helpers exhibited less territorial overlap with neighbouring groups than single pairs, but only during the breeding season. This is of benefit to the larger partridge groups with helpers since they are able to obtain enough food to meet their energy and nutrient requirements for egg production (e.g. Robbins 1981, Nager *et al.* 2000), whereas expanding their territory may result in more competition with conspecifics and possibly higher predation rates (e.g. Whitaker *et al.* 2007).

Partridge groups occupied the same area in close proximity to the nest from one year to the next. Such breeding site fidelity would enable these groups to maintain an established territory and increase their knowledge of predation and competition in the area (e.g. Bergerud & Gratson 1988). In addition, family group members spent all of their time roosting and foraging together during the breeding season (Xu *et al.* 2008), and participated in territorial defense against neighbouring groups throughout the year. This pattern of territorial behaviour is very uncommon in Galliforme species. We suspect that this behavioural pattern for the Pamuling partridge population is again related to the monastery environment (i.e. supplementary feeding). Further observations are needed to determine if neighbouring groups coalesce.

Many studies have reported that food availability outside the breeding season can affect the maintenance of relationships and spatial behaviour of species living in family groups (e.g. Kraaijeveld & Dickinson 2001, Dickinson & McGowan 2005). Large groups will be more conspicuous to predators (Hebblewhite & Pletscher 2002) and per capita food availability could be decreased by exploitative competition within large groups (Fortin & Fortin 2009). We conclude that further research should focus on examining the interactions between supplementary feeding and family group composition, with direct comparisons of data from non-supplementary fed partridge populations outside of Buddhist Sacred Sites.

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SAMENVATTING

Het voorkomen van coöperatieve broedzorg bij vogels lijkt voornamelijk af te hangen van de mogelijkheid die jonge, geslachtsrijpe vogels hebben om zelf te gaan broeden. Als deze mogelijkheid afwezig is, sluiten zij zich vaak aan bij groepen territoriale dieren om zo hun kans op reproductie in de toekomst te vergroten. De grootte van die territoria hangt vaak samen met de kwaliteit van een groep. Onder de hoendervogels (Galliformes) is coöperatieve broedzorg een zeldzaam verschijnsel, aangezien de jongen van deze soorten snel onafhankelijk zijn en slechts weinig ouderlijke broedzorg ontvangen. In het hier beschreven onderzoek bestudeerden de auteurs wat de invloed is van groepsgrootte op territoriumgrootte bij het Roodkeelwigstaarthoen *Tetraophasis szechenyii*, een met uitsterven bedreigde endemische vogelsoort uit de Chinese Himalaya. Het onderzoek is uitgevoerd aan 18 coöperatieve groepen, die deel uitmaakten van een populatie die bijgevoerd werd door Tibetaanse monniken. De dieren zijn daardoor goed te observeren zonder gebruik te maken van zenders. De onderzoekers keken hoe plaatsgetrouw de groepen waren, hoeveel overlap er tussen de groepen was en wat de invloed van de bijvoerplaatsen was voor hun plaatskeuze. Zij vonden dat de grootte en mate van overlap van de territoria verschilde wanneer het gemeten werd binnen of buiten het broedseizoen. De grootte van de groep speelde daarbij geen rol. Wel belangrijk was hoe de plaatsen waar bijgevoerd werd, lagen ten opzichte van hun broed- en slaapplaatsen. (KvO)

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