

ARE WHITE-BROWED BABBLERS TERRITORIAL?

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White-browed Babblers *Pomatostomus superciliosus* had overlapping home ranges during the non-breeding season. During the breeding season these home ranges were restricted in area and there was little overlap between groups. There were three types of interaction associated with this spacing behaviour. Foraging interactions involved the aggregation of two or more groups to forage in a common area, and were more common during the non-breeding season. Calling displays involved members of two groups calling to each other. This occasionally led to the third interaction, chases, where one bird from each group chased each other. Calling displays and chases resulted in the separation of groups and occurred almost exclusively during the breeding season.

The most parsimonious explanation for the behaviour of these White-browed Babbler groups was that they held territories during the breeding season, but became non-territorial for the rest of the year. The lack of territorial behaviour during the non-breeding season may be related to limited food supplies during the summer.

INTRODUCTION

Hinde (1956), following Noble (1939), defined a territory as 'any defended area'. He identified two components essential to territorial behaviour; the restriction of all or some types of behaviour to a specific area, and the defence of that area. He also argued that self-advertisement within the area was commonly associated with territorial behaviour but was not essential. This definition includes a wide diversity of spacing behaviours but excludes behaviours related to the defence of mates as these are not restricted to a specific area (Hinde 1956).

It has generally been assumed that White-browed Babblers *Pomatostomus superciliosus*, like Grey-crowned Babblers *Pomatostomus temporalis* and Hall's Babblers *Pomatostomus halli*, are territorial (Counsilman and King 1977; Boles 1988); however, little evidence has been presented to support this claim. Boles (1988) assumed they were territorial, because Gould (1865) found them performing a display (huddle display *sensu* King 1980), which King (1980) later observed being performed by Grey-crowned Babblers during territorial disputes. However, King also observed this behaviour when the group was alone and sometimes when the female was incubating, so it was not exclusively a territorial display.

In the central wheatbelt of Western Australia, White-browed Babblers lived in groups of up to 13 birds in which there was only one breeding pair (Cale 1999). Their breeding season extended from July to November, but the majority of breeding occurred before the end of October. These groups occupied home ranges that were restricted to remnant vegetation, although, unlike many other remnant-dependent species, they lived in a wide range of remnants including linear strips (Lynch and Saunders 1991). White-browed Babblers are predominantly ground and bark foragers and they were never recorded feeding more than 20 metres away from remnant vegetation (Cale 1994; Lynch *et al.* 1995).

In this paper I describe interactions between White-browed Babbler groups within remnant vegetation of the central wheatbelt of Western Australia. I then address the specific question; are White-browed Babblers territorial?

METHODS

Study area

This study was carried out within a 1 680 square kilometre area just north of Kellerberrin, which is approximately 200 kilometres east of Perth, Western Australia. This area is part of the Western Australian wheatbelt that has undergone extensive clearing for the purposes of agriculture. Over 500 remnants of the original vegetation remain within the study area, 77 per cent of these are less than 20 hectares in size and only 4 per cent are larger than 100 hectares (Arnold and Weeldenburg 1991). White-browed Babbler groups were monitored in 20 remnants varying in size from 2 to 70 hectares.

Monitoring of groups

From 1994 to 1996 I caught and colour-banded 357 White-browed Babblers. Most were caught using mist nets, by attracting the group to the nets with the taped call of a fledgling. I also banded nestlings before they fledged and occasionally caught newly fledged young by hand. Each bird was given a unique colour band combination consisting of a colour band over the metal band on one leg and two colour bands on the other leg. Where possible all birds from the same group were given the same colour band over metal combination and adjacent groups were given a different combination. This made it easier to identify groups and to determine when adjacent groups were aggregating.

For all babbler groups found in the study sites I defined a *Habitat Patch* based on the distribution of vegetation considered suitable for the permanent occupation of a group (Cale 1999). The boundaries of these habitat patches were determined from a hardcopy of the 1994 Landsat image and were then verified on the ground. Areas of suitable vegetation were considered to be discrete habitat patches if they were separated by more than 100 metres of unsuitable vegetation.

I visited most habitat patches regularly (approximately 1–4 times per month) throughout the breeding seasons (July–October) of 1994 to 1996. Visits during the non-breeding season were less frequent, but given the longer period, the total number of visits was approximately the same as for the breeding season. During visits to a habitat patch I attempted to locate all groups of babblers occupying it. The locations of all groups were mapped using aerial photographs for analysis of home range size and shape.

Sometimes members of several groups were observed together. In these cases I considered both groups to be present if I recorded at least two banded birds from each group, the total number of birds was consistent with the expected number in both groups, and I could find no sign of these groups elsewhere. I considered these periods of group mixing as interactions if group composition was not clear or some physical or acoustic behaviour occurred. Differences in the frequency of interactions between the breeding and non-breeding (combined pre-breeding and post-breeding) seasons was tested using Chi-square analysis with correction for continuity (Zar 1996). Calling displays and chases were combined in this analysis, because of the low expected frequencies for chases.

Home ranges

The home range of a group was defined by the smallest polygon that encompassed all observed locations of that group. The boundaries of this home range were restricted to native vegetation. All locations recorded for a group throughout the three years of the study were combined to estimate its home range size. Estimates of home range size were calculated for groups that were followed through at least one full year. Because the size of most home ranges was determined from accumulating data over several years, they are slight over-estimates of the area used by a group in any one year. However, the purpose of these home range estimates is to compare the change in area used between the breeding and non-breeding season, and since both are biased in the same way this comparison remains valid.

Two measures, linear dimension and area, were used to describe the size of home ranges. The linear dimension was defined as the straight line distance between the farthest two points on the boundary polygon of the home range. The area of each home range was measured to the nearest 0.1 hectare, while the linear dimension was measured to the nearest 10 metres. These measurements were made for the total area occupied by each group and for the area each group occupied during the breeding season (defined as July to October).

RESULTS

Home range size

Home ranges varied in size from 1.5 to 15.3 hectares, with an average of 6.6 hectares (Table 1). The total home range of a babbler group was on average 65 per cent larger in size and 85 per cent longer than the area they occupied during the breeding season (Table 1). A group's total home range frequently overlapped with those of adjacent groups but there was very little overlap between home ranges during the breeding season.

TABLE 1

The average area and linear dimensions of the total home range and the breeding home range of 30 groups of White-browed Babblers. The values are presented as mean \pm S.E.

	Area (ha)	Linear Dimension (m)
Total home range	6.6 \pm 0.6	853 \pm 69
Breeding home range	4.0 \pm 0.4	462 \pm 48

Interactions between groups

I observed 38 interactions between groups of White-browed Babblers. All except two of these interactions were between groups in the same habitat patch. The two exceptions involved groups from adjacent habitat patches, which were connected by remnant vegetation and were only a few hundred metres apart. Most interactions were between two groups (35 interactions), but two interactions involved three groups and one involved four groups.

Interactions between groups occurred at all times of the year (Table 2). However, the types of interactions occurring during the breeding season and the non-breeding season differed significantly ($\chi^2_{(1)} = 4.65$ $p = 0.031$). The most common type of interaction was for members of two or more groups to forage as a single group (*Foraging interaction*). These interactions could last for several hours. The end of a foraging interaction was never obvious, because individuals slowly coalesced back into their respective groups. Most foraging interactions occurred during the non-breeding period. Three of the eight foraging interactions I observed during the breeding season occurred between groups that had finished nesting and had young juveniles. Therefore, these cases could be considered post-breeding interactions. Another four of the foraging interactions during the breeding season involved newly budded groups interacting with their original group. These interactions occurred while the budded groups were establishing their new territory and building their first nest.

TABLE 2

Types of group interactions and their frequency of occurrence at different times of the year. See text for descriptions of interaction types.

Time of year	Interaction type			Number of Interactions
	Foraging	Calling displays	Chases	
Breeding (July–Oct)	8	10	3	21
Post-breeding (Nov–Feb)	8	1	0	9
Pre-breeding (Mar–June)	8	0	0	8

Almost all of the other interactions occurred during the breeding season (13 of 14 observations) and all involved calling between members of different groups (*Calling displays*) (Table 2). Calling displays generally involved more than one bird from each group, but not all members of groups were involved on all occasions. Calling displays sometimes led to the third type of interaction (*Chases*) where two birds, one from each group, chased each other. I was never able to determine which individuals were involved in chases. During calling displays and chases it was common for some members of the different groups to forage together. However, in contrast to foraging interactions these interactions were short (less than 20 minutes) and always led to both groups moving some distance away from each other.

DISCUSSION

Some of the observed interactions (*calling displays* and *chases*) between groups of White-browed Babblers resulted in these groups separating from each other. These behaviours were also associated with a reduction in the overlap between group home ranges during the breeding season. These observations are consistent with Hinde's (1956) definition of territorial behaviour, and are broadly similar to the territorial disputes described for the Grey-crowned Babbler (Counsilman 1977; King 1980) and Hall's Babbler (Balda and Brown 1977). However, calling displays and chases in White-browed Babbler groups were only evident during the breeding season, and though calling displays often involved many group members, chases only involved individuals. This differed from the territorial

disputes described for the other Australian babblers (Balda and Brown 1977; Counsilman 1977; King 1980). In these species most individuals from each group were involved in disputes and for at least Grey-crowned Babblers disputes occurred throughout the year (Counsilman 1977).

The observed behaviour of White-browed Babblers could be interpreted in two ways. Firstly, the size of home ranges during the breeding season may be restricted by the location of the nest and this could result in groups occupying mutually exclusive areas without invoking territorial behaviour. Given that there was competition for breeding positions in both sexes of this species and males guarded females (Cale 1999), calling displays and chases may be related to mate defence and not territorial behaviour. I believe this explanation is unlikely, because some calling disputes involved a large proportion of the birds in both groups and this would not be expected if these interactions were related to mate defence.

I believe the most parsimonious explanation for the observed behaviour of babbler groups is that they hold breeding territories, but are not territorial during the non-breeding season. This is similar to the behaviour of some other co-operatively breeding species, such as the White-winged Chough *Corcorax melanorhamphos* (Rowley 1978) and the Hoatzin *Opisthocomus hoazin* (Strahl and Schmitz 1990). These species leave their territories during the non-breeding season and sometimes aggregate in large flocks. The lack of territorial behaviour in these two species during the non-breeding season was associated with the limited availability of an essential resource (i.e. food, Rowley 1978; and water, Strahl and Schmitz 1990). The foraging aggregations of White-browed Babbler groups may be similar to this behaviour. Supporting this view are observations of babbler groups moving during the summer. These group movements were associated with a low abundance of invertebrates in their habitat patches and invertebrate resources tended to be highly aggregated within remnants (Cale 1999).

Heinsohn *et al.* (2000) described the coalition of White-winged Chough groups after an extensive drought. These coalitions provided an opportunity for the amalgamation of small groups and the authors proposed that this was an important component of the species' social behaviour. Although White-browed Babbler groups did not amalgamate, foraging interactions during the non-breeding season were associated with a major period of dispersal by male babblers (Cale 1999). Foraging interactions therefore, provided opportunities for these males to have social interaction with potential new groups. I have argued elsewhere (Cale, in press) that social interaction is an important requirement for male dispersal, and this may be an alternative reason for the prevalence of groups coalescing during the non-breeding season.

These observations on the territorial behaviour of White-browed Babblers were made in the degraded remnants of a highly fragmented landscape. What impact these changes in habitat have had on the behaviour of this species is unknown, because of the lack of observations on spacing behaviour in other parts of its range. Baldwin (1975) stated that White-browed Babblers in the Inverell district of New

South Wales became nomadic after breeding, but she did not give any details of this behaviour. This suggests that at least some groups in this area were not territorial during the non-breeding season. However, this area has also been modified by agricultural activity, though the extent of this modification is likely to be less extreme than in the current study area.

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