The seasonality of mixed-species bird flocks in a Sri Lankan rainforest in relation to the breeding of the nuclear species, Orange-billed Babbler *Turdoides rufescens*

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Introduction

The seasonality of mixed-species bird flocks varies dramatically across the world. At one extreme are temperate flock systems that only form during the winter months or during migration (Morse 1970), and even some flocks in the subtropics appear to be formed mostly of migrant species (Ewert & Askins 1991, Gram 1998). At the other extreme are tropical systems that occur throughout the year and in which migrant species play a small role (Kotagama & Goodale 2004). Interestingly, however, there are some tropical systems that do show seasonal fluctuations in flock size and composition (Davis 1946, Develey & Peres 2000). These fluctuations could be influenced by the underlying density of arthropods and/or by the breeding season of the species involved (Develey & Peres 2000).

One open question is how flock systems are affected by the breeding season of a 'nuclear species', defined as a species that is important to the formation and/or maintenance of flocks (Moynihan 1962). Munn (1984) studied this question in Peru (see also Munn & Terborgh 1979) and found that flocks continue to function throughout the breeding season of the nuclear species—Bluish-slate Antshrike *Thamnomanes schistogynus*—with breeding individuals flying far from their nests in order to join flocks. Munn's system was somewhat atypical, however, in that the nuclear species was not particularly gregarious; in most flock systems, nuclear species are highly gregarious (Goodale & Beauchamp 2010), and in some Asian systems one species can compose a large percentage of the flock (Chen & Hsieh 2002). What happens to flocks that form around such gregarious species when these species breed?

In previous work on a flock system of a tropical rainforest in Sri Lanka, we have shown that flock size is seasonally stable, with only a few migrant species joining flocks in the winter months (Kotagama & Goodale 2004). However, we never measured seasonal changes in the density of flocks, so it is possible that flocks might actually still show seasonal fluctuations. This flock system is led by the nuclear species, the Orange-billed Babbler *Turdoides rufescens*, for which little breeding information is available. Therefore, we had two objectives in this study: (a) to measure seasonal changes in the density of flocks, and (b) to see if that seasonality was related to the breeding of the Orange-billed Babbler. We also aimed to chronicle some aspects of the nesting of this little-studied babbler (Henry 1998).

Study site

This study was conducted in the north-western sector of the Sinharaja World Heritage Reserve (6.433°N 80.350°E), Sri Lanka's largest remaining patch of lowland rainforest (450–600 m). This sector of the reserve was logged in the 1970s and the effects, including large gaps, are still visible near the main logging road, along which we walked. Annual rainfall is about 4 m with distinct dry (January to March) and wet seasons (April to December) (Kotagama & Goodale 2004).

Methods

To determine whether the density of flocks changes seasonally, we walked along 8 km of the main logging road that leads from the town of Kudava towards the mountain of Sinhagala. From November 2004 to December 2006, we walked this route three times a month at 07h30–11h00. The months of May and June were only sampled in one year each, because of extremely wet conditions.

We recorded all flocks seen or heard within 50 m of this transect, and estimated the number of Orange-billed Babblers present in the flock. Returning along the same route, we watched for any indication of breeding by Orange-billed Babblers, including mating, nesting or feeding of fledged chicks.

In conducting two-tailed t-tests, we used a method that does not assume equal variances (Ruxton 2006). Means are given ± one standard deviation.

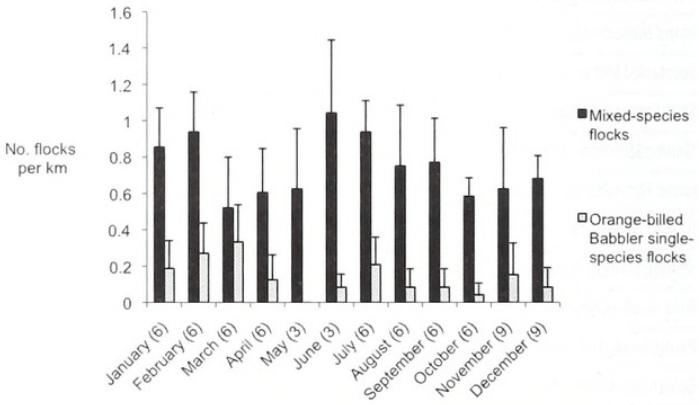
Results

Seasonal density of flocks

We recorded 492 flocks during the sampling period. In all of these, Orange-billed Babblers were present. Apparently, our transect method, which required relatively fast walking, failed to detect the approximately 8% of flocks that do not contain Orange-billed Babblers (Kotagama & Goodale 2004)—these flocks that do not include the noisy Orange-billed Babblers can be quite cryptic and difficult to detect.

The density of mixed-species flocks did not differ seasonally (Figure 1). The highest density of flocks (1.04 flocks per km) was recorded in June, and the lowest (0.52 flocks per km) was recorded in March. There was no significant difference between the density of flocks in the dry season from January to March (18 days sampled) and the rest of the year from April to December (54 days sampled), (t-test, $t_{27.37} = 0.71$, $P = 0.48$).

Figure 1. Seasonal variation in the density of mixed-species flocks and single-species Orange-billed Babbler flocks. Numbers in parentheses show the number of days sampled for each month during the study. Error bars indicate +1 standard deviation (data from November 2004 to December 2006).



In contrast, the occurrence of single-species flocks of Orange-billed Babblers was higher in the dry months (January–March) than during the rest of the year (Figure 1). The density of such single-species flocks was higher in these three months pooled together (n = 18) than during the rest of the year (n = 54, t-test, $t_{23.03} = 3.56$, $P = 0.0017$).

These single-species flocks, presumably composed of small breeding groups, were small, averaging 7.2 ± 2.6 babblers (n = 82). In contrast, mixed-species flocks usually included 20.0 ± 8.8 babblers (n = 397). One might hypothesise that if small groups of babblers occur in monospecific flocks during the dry season (January–March), then the average number of babblers in mixed flocks would be smaller during that time. This was indeed found to be the case (15.0 ± 8.7 babblers in the dry season, n = 116, versus 22.1 ± 8.0 babblers in the rest of the year, n = 281; t-test, $t_{200.78} = 7.65$, $P < 0.0001$).

Breeding behaviour of Orange-billed Babbler

Most of the Orange-billed Babbler breeding records (19 of 22) were during the months of January–March (Table 1). A total of 10 nests

Table 1. Independent observations of breeding in Orange-billed Babblers

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Nests	3	3	2									2
Fledgings	2	3	2				1					
Matings	2	2										

were found; these were placed at a variety of heights (range 5.5–35 m, mean = 15.4 m), in trees of several different species including large species such as *Syzygium rubicundum*, *Mesua thwaitesii* and *Shorea trapezifolia*, and fruiting trees such as rambutan *Nephelium lappaceum* in gardens near the forest edge. Nests consisted of a bowl made of fine vines, including the roots of ferns, on top of a small platform constructed from a few twigs. One nest examined after it was abandoned measured 83 × 90 mm inside, with an interior depth of 65 mm, and 153 × 172 mm outside, with a depth of 85 mm. Eggs were blue-green in colour, and one that was found broken on the ground measured 16.6 × 22.8 mm. The number of eggs was usually unknown, except for one nest that was observed to have five eggs; three nestlings hatched in another nest and two chicks fledged in a third.

Orange-billed Babblers were clearly cooperative in their breeding habits. For example, at three separate nest sites, three or more adults were observed to help with construction. At another site, four adults fed the chicks, and at another the fledglings were observed being fed by three adults. Given that the birds were not marked, the number of adults feeding young was probably even greater. Even in records where only one or two adults were attending the nest, or were seen to feed the chicks, there was usually a group of babblers within 25 m, and often within 10 m. The average size of babbler groups close to nests was 4.5 individuals (n = 9).

Discussion

We found that the density of mixed-species flocks did not change seasonally, although the density of small single-species Orange-billed Babbler groups, which are presumably breeding groups, did increase during the dry season in January to March, when babblers were nesting. Our survey method did not detect flocks without Orange-billed Babblers, and this could bias the result if the percentage of such flocks itself varies seasonally. However, reanalysing the 1990s seasonal data from Kotagama & Goodale (2004), we found that the proportion of such flocks did not change between the dry season (1 of 31 flocks) and the wet season (16 of 139 flocks), (Fisher's Exact Test, $P = 0.21$).

These flocks observed in the humid lowland rainforest of Sri Lanka are among the most aseasonal flock systems described in the world. Previous work showed that the number of species in flocks did not change seasonally and that the composition of flocks was also quite stable, with the exception of several migrant species that are found in flocks, only one of which is a regular member (Kotagama & Goodale 2004). This study demonstrates that the density of flocks also does not change seasonally. This lack of seasonal change is very different from temperate and subtropical systems that have been described (Morse 1970, Gram 1998), and the system appears to be more stable even than others in the tropics (Davis 1946, Develey & Peres 2000). It appears that even during the Orange-billed Babbler's breeding season there are enough non-breeding babblers to act as leaders for mixed-species flocks, so that these mixed-species flocks continue unabated.

This study adds to the evidence that the core of mixed-species flocks in the lowlands of Sri Lanka are small groups of Orange-billed Babblers. These groups most likely comprise closely related individuals, consisting of a mated pair of adults and their previous year's offspring, and they breed cooperatively, as has been described for other species of *Turdoides* babblers (Gaston 1978, Zahavi 1990, Ridley & Raihani 2007). Our observations suggest that these family groups roost together, and then join with other groups through the morning. Other species follow babblers (Kotagama & Goodale 2004), and larger babbler groups are clearly more attractive to other species than small groups. Usually the small groups of nesting babblers forage rather quietly in the proximity of the nest and do not attract other species. Further work is needed to understand the territoriality and use of space of both the babblers and other species in these mixed-species flocks.

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