## The composition and spatial organisation of mixedspecies flocks in a Sri Lankan rainforest

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We made a total of 476 observations on the composition and spatial organisation of flocks in lowland to mid-elevation rainforest in Sinharaja World Heritage Reserve, Sri Lanka, during 1981–1984 and 1995–1998. Flocks contained 10.9 species and 41.3 individuals on average. The composition of flocks was generally stable over time, changing little over the annual cycle or between the 1980s and the 1990s, although the abundance of some species appears to have changed following regeneration after logging in the 1970s. Flocks were larger, more diverse, and had a different composition (including more endemic and threatened species) compared to those described from the montane zone of Sri Lanka. They were typical of near-equatorial mixed-species flocks in that they included few migrants and were generally dominated by insectivores. They were unusual, however, in the numerical dominance of a single species, Orange-billed Babbler *Turdoides rufescens*, which averaged more than 16 individuals per flock and which was found in c.90% of flocks. This species and Greater Racket-tailed Drongo *Dicrurus paradiseus* are both possible 'nuclear species' for these mixed-species flocks, providing foraging and/or anti-predation benefits to other flocking species.

## INTRODUCTION

Mixed-species flocks are a prominent form of social organisation of foraging birds, particularly in the tropics (Powell 1985). In general, the occurrence of such flocks has been explained in terms of adaptations to reduce predation and increase foraging efficiency (reviewed in Morse 1977, Terborgh 1990). Flock systems vary widely in the numbers of species and individuals involved, with some of this variation explained by factors related to predation, including the openness of the vegetation and the density of avian predators (Thiollay 1999). More studies from different regions and habitats in the world are needed to further document the diversity of flock systems and better understand the applicability of the hypotheses that explain flocking.

In Sri Lanka, mixed-species flocks have been studied in the montane region (Partridge and Ashcroft 1976). A distinct and more diverse system, however, can be observed in the low to mid-elevation rainforests of the wet south-west part of the country, where avian diversity and endemism are higher. Here the flock system centres around the endemic, highly gregarious Orange-billed Babbler Turdoides rufescens. Several authors have commented on the tendency of babblers Timaliini to lead mixed-species flocks in the Indian subcontinent (Ali and Ripley 1987, Grimmett et al. 1999). Such flock systems have yet to be described systematically, although some of the flocks described by King and Rappole (2001a) in Myanmar were characterised by a very high number of laughingthrushes.

Here we describe mixed-species bird flocks in Sinharaja World Heritage Reserve, one of the largest rainforest tracts remaining in Sri Lanka, focusing on their composition and spatial organisation. We first took observations on flocks during the early 1980s, following logging in the reserve during the 1970s, and we then repeated the observations in the late 1990s. Our original objective was to use flocks as an indicator of how the avifauna had changed over this fifteen-year period of forest regeneration. Intrigued by the phenomenon of mixed-species flocking, however, we expanded our aims to include (a) comparing the size

and composition of the Sinharaja flocks to those described from the montane zone of Sri Lanka, and from other parts of the forested tropics, and (b) investigating the benefits that birds accrue in flocks and identifying which species are most essential to flock structure. In pursuit of this latter objective, we investigated how closely species foraged together in flocks, focusing on the relationship between the Orange-billed Babbler and other species. Such information is important because proximity is relevant in assessing whether species gain foraging benefits from associating with other flock members (Hutto 1994). We also collected information on which species lead flocks, as this is a principal characteristic of 'nuclear species', those that are important for the formation and/or maintenance of mixed-species flocks (Movnihan 1962, Hutto 1994).

## **STUDY SITE**

The study was conducted in the north-western sector of Sinharaja World Heritage Reserve, Sri Lanka (6°26′N 80°21′E, 450–600 m). The vegetation consists of dense, evergreen rainforest, dominated by *Mesua* spp. and *Shorea* spp. trees in the canopy (Gunatilleke and Gunatilleke 1981). Annual rainfall averages c.4 m with distinct dry (January–March) and wet seasons (April–December); diurnal temperatures range from 20°C to 25°C (Gunatilleke and Gunatilleke 1981).

The north-western sector of the reserve was logged in the 1970s (De Zoysa and Raheem 1987). The effects of the logging in the reserve were heterogeneous, so that some areas on steep ridges were completely uncut, whereas gaps were created near the logging roads. During the 1980s, we walked a network of logging roads near the Sinharaja Research Centre, formerly the centre of the logging operation, looking for flocks. By the 1990s most of these roads were overgrown, with the exception of a 3.5 km stretch that led from the entrance of the reserve, past the Research Centre, towards the Sinhagala lookout.