

**Structure, composition and heterospecific associations in
mixed-species flocks of birds in a lowland tropical rainforest in
northeastern India**

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By

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Declaration

I declare that the thesis entitled "Structure, composition and heterospecific associations in mixed-species flocks of birds in a lowland tropical rainforest in northeast India" comprises research work done by me under the guidance of Dr. Suhel Quader, and co-guidance of Dr. Rashid Raza. The work is original and has not been done earlier by anyone else. Part of this work, which is related to or similar to work done by other researchers, has been cited in this thesis at appropriate places. The results presented in this thesis have not been submitted previously to this or any other university for an M.Sc. or any other degree.

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(Dr. Suhel Quader)

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Certificate

I declare that the thesis entitled "Structure, composition and heterospecific associations in mixed-species flocks of birds in a lowland tropical rainforest in northeast India" comprises research work carried out by Umesh Srinivasan at the Centre for Wildlife Studies under my guidance, and the co-guidance of Dr. Rashid Raza, during the period 2007-2008, for the Degree of Master of Science in Wildlife Biology & Conservation of the Manipal University. The results presented in this thesis have not been submitted previously to this or any other university for an M.Sc. or any other degree.

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SUMMARY

Mixed-species flocks of birds are a regular feature of tropical and temperate forests worldwide, and have been the subject of detailed study, especially in the neotropics. Such flocks are composed of ‘nuclear’ species, crucial for the initiation and cohesion of mixed-species flocks, and ‘attendant’ species, which join and follow nuclear species. Species may benefit from joining mixed-species flocks either from an increase in foraging efficiency, a decrease in predation risk, or both. These benefits are likely to vary both qualitatively as well as quantitatively for different species participating in mixed-species flocks. This study was undertaken to:

1. investigate the participation of species and functional guilds of birds in mixed-species flocks in lowland tropical forest in northeastern India.
2. identify the species traits that influence heterospecific association in mixed-species flocks, in the context of the costs and benefits accruing to species from participating in mixed-species flocks.

Fieldwork was carried out in the Namdapha Tiger Reserve, Changlang district, Arunachal Pradesh, from December 2007 to March 2008. Twenty three line transects varying in length from 180 m to 500 m (a total effort of 30.36 km) were each walked four or five times to obtain data on species abundances and flock composition. Opportunistic sampling was also used to obtain data on flock composition. Randomisation procedures were used to simulate flocks with species composition expected in the absence of (a) differential tendencies of species to participate in mixed-species flocks, and (b) positive or negative species associations, and a comparison of observed flocks with simulated

flocks yielded measures of (a) the tendency for each species to participate in mixed-species flocks, and (b) pair-wise association between species.

Three distinct mixed-species flock types (i.e. understorey, canopy and large-bodied species flocks) were found in the same habitat type in the study area. Vertical stratification and body mass were found to be possible factors influencing non-random species composition in mixed-species flocks. A major finding of the study is the positive relationship between the number and strength of heterospecific associations in flock members, which provides a novel method for assessing the importance of each species participating in mixed-species flocks. Species gregariousness and foraging method were found to influence various aspects of heterospecific association in understorey mixed-species flocks. Gregarious species and sallying species separately had strong heterospecific associations. Canopy mixed-species flocks did not show clear trends in heterospecific association strength, suggesting that other factors than group size and foraging method may influence costs and benefits accruing to species from participating in canopy flocks.

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INTRODUCTION

Animals may form groups for a variety of reasons, including anti-predator, foraging, and reproductive benefits (Morse 1977). In a non-reproductive, foraging context, group formation is thought to confer two main benefits – increased foraging efficiency, and decreased predation risk. Group participants may simultaneously incur costs such as competition between group members and kleptoparasitism (Morse 1977).

Groups may consist of individuals of a single species (monospecific groups) or of multiple species (heterospecific groups). Participation in single-species groups is likely to be associated with costs and benefits that differ compared to participation in complex multi-species groups. For instance, foraging in heterospecific groups is likely to result in decreased competition between group members relative to monospecific groups since niche overlap between individuals of different species is much lower than that between conspecifics (Powell 1989). A species is expected to participate in heterospecific groups only if it benefits from doing so. If these benefits and costs are provided mainly by particular group members, positive and negative heterospecific associations are expected with these group members. Mixed species flocks, therefore, present a model system in which to understand varying patterns of grouping by evaluating the underlying costs and benefits to potential group participants.

Mixed-species flocks of birds occur in tropical and temperate habitats worldwide (Moynihan 1962, McClure 1967, King & Rappole 2001, Hart & Freed 2003, Kotagama & Goodale 2004) and comprehensive studies have been conducted on various aspects of mixed-species flocks in the neotropics (Munn & Terborgh 1979, Powell 1989, Graves &

Gotelli 1993, Jullien & Thiollay 1998, Jullien & Clobert 2000). Despite such detailed research, only few field studies have addressed questions of fundamental importance in mixed-species flocking. For instance, the participation of various functional groups in mixed-species flocks, and the processes influencing differential participation of different groups is yet unstudied. Further, the nature of, and the mechanisms underlying interspecific associations in mixed-species flocks are poorly understood, and have received mainly theoretical attention.

This study was conducted between December 2007 and March 2008 in the Namdapha Tiger Reserve, Changlang district, Arunachal Pradesh. This thesis consists of two chapters. The first chapter, titled “The structure and composition of mixed-species flocks of birds in a lowland tropical rainforest in northeastern India” examines and discusses the participation of various functional guilds of birds in mixed-species flocks, and identifies areas for future research. The chapter also introduces a new approach for assessing the propensity of a species to occur in mixed flocks. The second chapter is titled “Birds of many feathers: the effects of group size and foraging method on nuclearity and interspecific associations in avian mixed-species flocks”. In this chapter, certain predictions (which follow from hypotheses that have been advanced to explain interspecific association in mixed-species flocks) are framed. These predictions are then tested using data collected during the course of this study. In particular, the role of intraspecific gregariousness and foraging method in influencing interspecific associations is investigated. These associations are assessed in a rigorous and quantitative framework for the first time, allowing an evaluation of predicted association patterns based on the hypothesised costs and benefits of grouping. This chapter is in the form of a draft manuscript, and has been prepared for submission to the *Journal of Animal Ecology*.

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Figure 1: Sultan Tit *Melanochlora sultanea*, a possible 'nuclear species' in canopy mixed-species flocks.



Figure 2: Beautiful Nuthatch *Sitta formosa*, a regular canopy mixed-species flock participant.



Figure 3: Lowland tropical rainforest in Namdapha Tiger Reserve, Arunachal Pradesh.

CHAPTER – 1: The structure and composition of mixed-species flocks of birds in a lowland tropical rainforest in northeastern India

Introduction

Animals group together for diverse benefits, including anti-predator, foraging, and reproductive advantages. In a non-reproductive, foraging context, group formation is thought to confer two main benefits – increased foraging efficiency, and decreased predation risk (Morse 1977). Group participants may simultaneously incur costs such as competition between group members and kleptoparasitism (Morse 1977). Further, the costs and benefits from participating in simple monospecific groups are likely to differ qualitatively and quantitatively from those incurred from joining complex multi-species groups. For instance, niche overlap between members of multi-species groups is much lower than that between conspecifics in single-species flocks, resulting in lower competition levels in heterospecific groups (Powell 1989). Species are expected to participate in heterospecific groups only if they gain a net benefit from doing so.

Mixed-species flocks of birds have been described from tropical and temperate habitats in North, Central and South America (Davis 1946, Munn & Terborgh 1979, Powell 1979, Hutto 1987, Hart & Freed 2003), Europe (Fernandez-Juricic 2000), Africa (Winterbottom 1949, Hino 2002) and Asia (McClure 1967, King & Rappole 2001, Chen & Hsieh 2002, Kotagama & Goodale 2004). Detailed and intensive research on mixed-species flocks has been conducted in the neotropics where heterospecific flocks persist year-round, and flock participants defend territories communally (Munn & Terborgh 1979, Jullien & Thiollay 1998). Further, studies from South America have shown that members of stable heterospecific flocks possess significantly higher survival relative to solitary foragers (Jullien & Clobert 2000).

Several studies, both comparative and experimental field manipulations, have focussed on the relative costs and benefits faced by individual birds or bird species participating in mixed-species flocks in terms of predator-avoidance (Gaddis 1980, Popp 1988, Yaukey 1995, Thiollay 1999, Ragusa-Netto 2000) and foraging efficiency (Morse 1967, LaGory *et al.* 1984, Alatalo *et al.* 1985, Klein 1988, Waite & Grubb 1988, Veena & Lokesha 1993, Cimprich & Grubb 1994), or both (Morse 1977). Recent research has addressed the difference in the roles played by different species in mixed-species flocks in terms of flock initiation and warning against predators (Dolby & Grubb 1998, Goodale & Kotagama 2005, 2006).

Comparative studies have been conducted on the effects that anthropogenic pressures such as habitat fragmentation (Fernandez-Juricic 2000, Maldonado-Coelho & Marini 2000, Sridhar & Sankar 2008) and developmental disturbances (Rollfinke & Yahner 1991, Lee *et al.* 2005) have on the species composition and territorial dynamics of mixed-species flocks.

This study was carried out to examine species and functional guild participation in mixed-species flocks. The degree of participation by various species and functional guilds in mixed-species flocks was determined by comparing their observed participation in mixed-species flocks with an expectation of participation based on species abundances estimated during the study period. Such an approach in determining the degree of participation by species or guilds by taking the abundances of species into consideration has not been attempted in studies on mixed-species flocks previously.

The specific findings presented are:

1. The differences in species composition of mixed-species flock types in lowland tropical forest in northeast India.
2. The structure (number of species and number of individuals) of mixed-species flocks.
3. The composition of mixed-species flocks in terms of frequency of participation by different bird species and functional guilds in mixed-species flocks.

Study area

I carried out fieldwork in the Namdapha Tiger Reserve (27°23'30" to 27°39'40"N and 96°15'2" to 96°58'33"E) in Changlang district, eastern Arunachal Pradesh, India, from early December 2007 to mid March 2008. Namdapha is situated in the Eastern Himalaya, a global Biodiversity Hotspot, and is an Important Bird Area with over 425 bird species (Islam & Rahmani 2004). The tiger reserve is 1,985 km² in area and encompasses altitudes ranging from 200 to 4500 m ASL. Habitats include alpine and temperate forests at higher altitudes, and subtropical and tropical forests at lower elevations. Annual rainfall varies from 1500 to 3500 mm, most of which falls during the south-west monsoon months of April to October (Datta 2007).

Sampling was conducted in the Hornbill and Musathi areas in the buffer zone of the reserve, at altitudes ranging from 500 to 650 m ASL. The habitat in this area is composed of dipterocarp-dominated lowland tropical evergreen forest (Datta 2007).

Methods

Sampling methods

Bird sampling for abundances

Twenty-three line transects were established ranging in length from 180 to 500 m, and oriented to varying azimuths. The minimum distance between adjacent transects was 500 m, to maximise independence between transects. Each transect was walked on four occasions, and in the case of four transects, on five occasions, thereby totalling 92 walks of 23 transects. For every bird cluster detected, the species, cluster size (number of individuals), azimuth to the cluster (using a compass), and the detection distance to the centre of the cluster (using a laser rangefinder - 1000 Yardage Pro, Bushnell Corporation, Kansas, USA) was recorded. For clusters with a detection distance below 15 m, detection distance was estimated visually to the nearest metre. For gregarious species with large cluster sizes, cluster size was recorded in most cases as a range from a minimum to a maximum number of individuals, since an accurate count was not possible in all cases. The midpoint of this range was used in subsequent analyses. Transects were walked between 0830 and 1230 hours, when mixed-species flock activity was the highest.

Mixed-species flock sampling

Mixed-species flocks were sampled on the established line transects (during sampling for bird abundances), and opportunistically along pre-existing trails from 1300 to 1530hrs. When encountered on transects, for each mixed-species flock, species composition, as well as the cluster size, detection azimuth and detection distance for each species cluster in the mixed-species flock were recorded. These data were incorporated during species abundance estimation. During opportunistic sampling, the species composition of the mixed-species flock and the group size of each participating species were recorded.

Analytical methods

Abundance estimation

To estimate the detection function and detection probability of bird species without the bias of differing detectability across species, species were divided into three ‘detection classes’ based on their median detection distances, each class containing an equal number of species. This approach assumes intra-class homogeneity in species detection functions and models multi-species data more parsimoniously by exploiting species’ similarity in detectability (Allredge *et al.* 2007). The detection function for each of these three classes was estimated separately using the program Distance (Thomas *et al.* 2005), and these detection functions were used to estimate the species-specific cluster abundance by post-stratification, surrogating each species as a stratum level.

Mixed-species flock types

It was apparent during sampling that there were at least two flock types that differed in species composition. Hierarchical agglomerative cluster analysis (using Jaccard’s similarity index with UPGMA linkage) was used in the program PCord (McCune & Mefford 1999) to identify different flock types based on species composition of these flocks.

Species participation in mixed-species flocks

For each flock type, a candidate pool of species potentially contributing to flock species composition was identified. This pool included all species which had participated in at least one flock of that flock type. The program R (R Development Core Team 2008) was used to simulate mixed-species flocks by drawing species from the candidate species pool as a function of the abundance of each species alone. The number of species drawn in

each simulated flock was equal to the observed mean flock size. This yielded null flocks with a composition expected in the absence of (a) differences in the tendency of species to join mixed-species flocks, and (b) positive or negative associations between flock participating species. As many null flocks were obtained as the observed number of flocks for each flock type. In this set of null flocks, the number of flocks in which a particular species occurred was computed. This process was repeated 10,000 times to obtain a species-specific distribution of abundance-weighted expected occurrence in mixed-species flocks. The non-parametric 95% confidence intervals (0.025 and 0.975 quantiles) of these distributions were obtained, and species were categorised into three classes in the following manner (Fig. 1):

- a. **Core species:** species for which the observed number of occurrences in mixed-species flocks exceeded the upper 95% confidence interval of their occurrences expected by chance.
- b. **Regular attendants:** species for which the observed number of flock occurrences fell within the 95% confidence intervals of the distribution of their expected occurrences.
- c. **Irregular attendants:** species for which the lower 95% confidence interval of the distribution their expected occurrences exceeded the observed number of occurrences in mixed-species flocks.

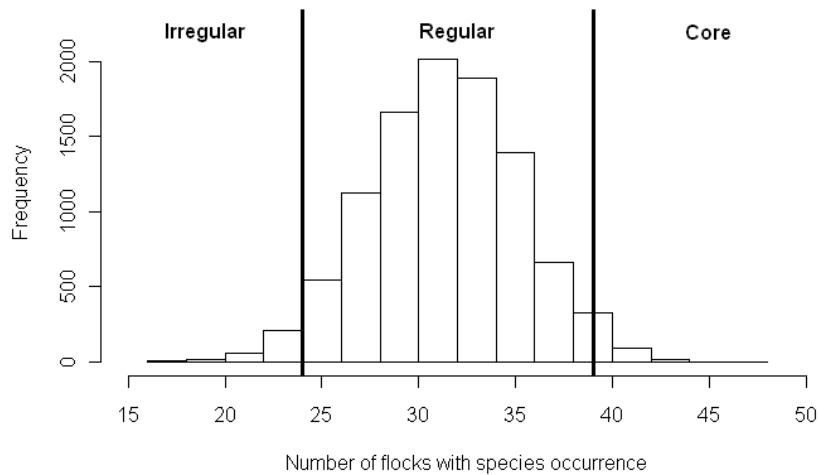


Figure 1: Example of a species-specific distribution of expected occurrence in mixed-species flocks based on abundance of the species. The bold black lines indicate the lower and upper non-parametric 95% confidence intervals of this distribution.

Some species occurred as irregular attendants in one flock type but were either core species or regular attendants in the other flock type. For comparisons between flock types, these species were not considered members of the flock type in which they occurred as irregular attendants.

Species characteristics

Species were classified as gleaners, bark surface gleaners, hoverers, salliers, predators and fruit pickers based on the predominant foraging method of each species as reported in secondary sources (Ali 1977, Ali & Ripley 1983, Grimmett, Inskipp & Inskipp 1998) and from observations made during the study. The definitions of gleaning, hovering and sallying are based on descriptions in Robinson & Holmes (1982), and are as follows:

Gleaners: species that forage mainly by picking stationary prey items off a substrate such as foliage or tree bark when either stationary or hopping; hence foliage gleaners and bark-surface gleaners.

Hoverers: species that forage predominantly by picking stationary prey items from a substrate while in flight.

Salliers: species that forage mainly by pursuing flying prey and capturing these when in flight (described as ‘hawking’ by Robinson & Holmes (1982)).

Species were classified as insectivores, omnivores, nectarivores, frugivores, granivores and carnivores based on the degree of predominance of a particular food component in the diet of a species as given in secondary sources (Ali 1977, Ali & Ripley 1983, Grimmett *et al.* 1998). Species were classified as residents and altitudinal migrants based on information available in the literature (Ali 1977, Ali & Ripley 1983, Grimmett *et al.* 1998). Body mass of species was obtained from Ali & Ripley (1983).

Results

Mixed-species flocks types

The species composition of 101 mixed-species flocks was recorded from observations made on line transects and during opportunistic sampling. Cluster analysis with five groupings identified three major flock types in addition to two groups of atypically composed ‘outlier’ flocks. Each of the latter two groups was represented only by two flocks. Multi-response Permutation Procedure (MRPP), which tests whether there is a significant difference between two or more groups of sampling units, indicated clear differences between groups (chance-corrected within-group agreement, $A = 0.122$, probability of obtaining smaller or equal $\delta < 0.0001$).

The mixed-species flock types identified were:

- a. Understorey and midstorey flocks of predominantly small-bodied bird species (n = 60 flocks) and composed of species such as *Alcippe nipalensis* (Nepal Fulvetta),

Alcippe castaneiceps (Rufous-winged Fulvetta), *Rhipidura albicollis* (White-throated Fantail), *Erpornis zantholeuca* (White-bellied Erpornis), *Abroscopus albogularis* (Rufous-faced Warbler), *Phylloscopus reguloides* (Blyth's Leaf-warbler), *Seicercus castaneiceps* (Chestnut-crowned Warbler), *Culicicapa ceylonensis* (Grey-headed Canary Flycatcher) and *Dicrurus remifer* (Lesser Racket-tailed Drongo). These are henceforth referred to as understorey flocks.

- b. Canopy and midstorey foraging flocks (n = 26 flocks) composed of species such as *Melanochlora sultanea* (Sultan Tit), *Pericrocotus flammeus* (Scarlet Minivet), *Heterophasia annectans* (Rufous-backed Sibia), *Coracina melaschistos* (Black-winged Cuckoo-shrike), *Sitta castanea* (Chestnut-bellied Nuthatch), *S. formosa* (Beautiful Nuthatch) and *Dicrurus remifer*. These are henceforth referred to as canopy flocks.
- c. Understorey and midstorey foraging flocks of predominantly large-bodied species (n = 11 flocks) composed of species such as *Garrulax* spp. (laughingthrushes), *Cissa chinensis* (Green Magpie), *Harpactes erythrocephalus* (Red-headed Trogon) and *Alophoixus flaveolus* (White-throated Bulbul). The species and guild participation in these flocks was not analysed due to low sample size.

Both flock types 'a' and 'c' were understorey-midstorey foraging flocks, with species in flock type 'a' being significantly smaller than those in flock type 'c' (Fig. 2). Flock type 'b', which foraged predominantly in the canopy, did not differ from the other flock types in the body masses of its participant species.

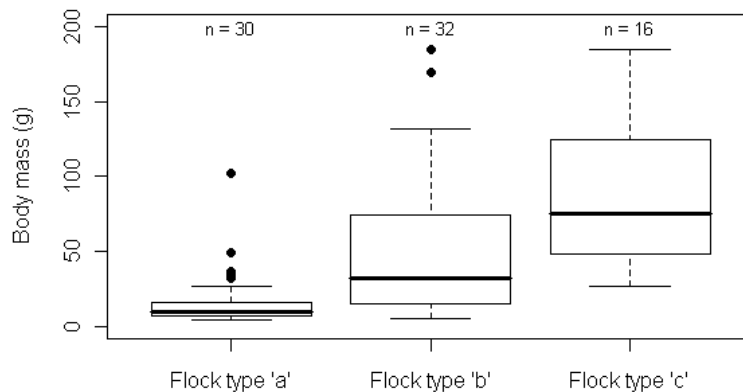


Figure 2: Body mass distribution of participant species of three mixed-species flock types. Flock type 'c' is composed of species that are significantly larger than species comprising Flock type 'a'.

The structure of mixed-species flocks

Mean species richness (derived from a raw count of the number of species) of understorey flocks was 6.37 species (range from 3 to 12 species, SD = 2.16) (Fig. 3a). The mean number of individuals in understorey flocks was 32.4 (range from 4 to 64, SD = 15.21) (Fig. 4a). Mean species richness of canopy flocks was 7.15 species (range from 3 to 14 species, SD = 2.48) (Fig. 3b). The mean number of individuals in canopy flocks was 31.14 (range from 12 to 79, SD = 16.18) (Fig. 4b).

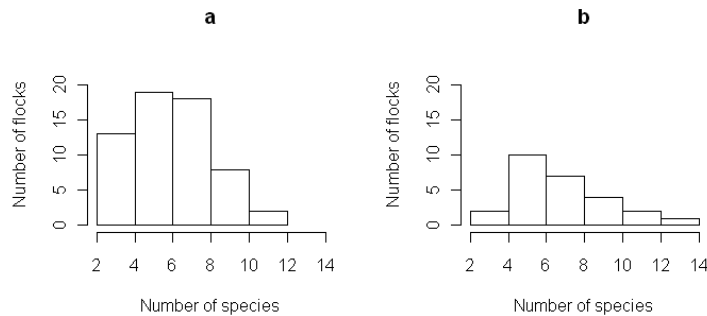


Figure 3: Frequency distribution of species richness in (a) understorey flocks and (b) canopy flocks.

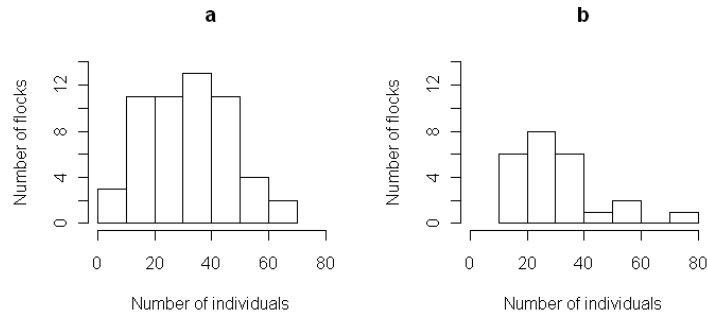


Figure 4: Frequency distribution of number of individuals in (a) understory flocks and (b) canopy flocks.

Patterns of species participation in mixed-species flocks

Flocking and non-flocking species

Fifty-three species participated in varying degrees in both understory or canopy mixed-species flocks. Thirty-four species did not participate in mixed-species flocks. These species are henceforth referred to as non-flocking species. Appendix 1 lists these species. A majority of flocking species (83.0%) were insectivores compared to only 47.1% of non-flocking species. Omnivores and nectarivores were also represented in flocking species, unlike carnivores, frugivores and granivores, which never occurred in mixed-species flocks. Both the nectarivores occurring in the study area were flock participants (Fig. 5).

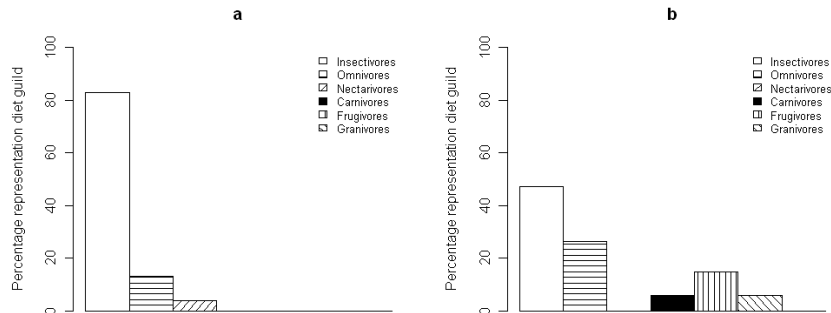


Figure 5: Diet guild representation in (a) flocking and (b) non-flocking species.

Both flocking and non-flocking species were mainly species that predominantly use gleaning (off foliage or leaf litter) as a foraging method. No predatory or fruit picking species participated in mixed-species flocks, whereas all species that hover-fed were flock participants (Fig. 6).

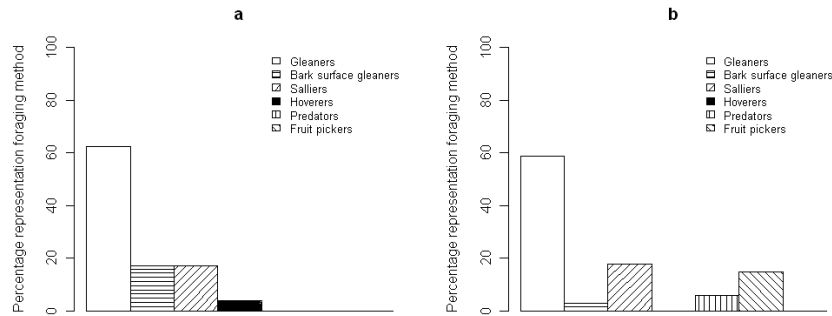


Figure 6: Foraging group representation in (a) understorey and (b) canopy mixed-species flocks.

Flock types and species participation

Forty species participated in understorey flocks. Of these, 13 species were core participants, 17 species were regular attendants, and 10 species were irregular attendants. Of the 10 irregular attendants, 5 species were regular attendants in canopy mixed-species flocks (Appendix 2). Thirty-eight species participated in canopy flocks. Of these, 8 species were core participants, 24 species were regular attendants, and 6 species were irregular attendants. Of the 6 irregular attendant species, 3 were core species and 1 was a regular attendant in understorey mixed-species flocks (Appendix 3).

Twenty-five species participated in both understorey and canopy flocks. Two species – *Aethopyga saturata* (Black-throated Sunbird) and *Alophoixus flaveolus* (White-throated Bulbul) were irregular attendants in both understorey and canopy flocks. The latter

appeared to prefer understorey mixed-species flocks composed of large-bodied species, but this preference was not analysed.

Core and attendant species

All core species in understorey and canopy flocks were insectivorous. In understorey flocks all regular attendant species were insectivores. Although regular attendant species in canopy flocks were dominated by insectivores, omnivores and nectarivores also participated regularly in canopy mixed-species flocks (Fig. 7).

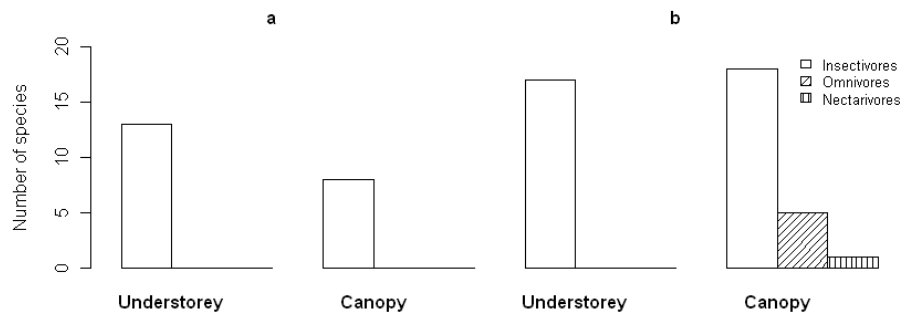


Figure 7: Diet guilds in (a) core and (b) regular attendant species. All core species in mixed-species flocks are insectivores.

Core species in both flock types showed a relatively even representation of different foraging method groups compared to regular attendant species. The low number of bark-surface feeders (one) in core species of understorey flocks is since only one species, *Alcippe castaneiceps* (Rufous-winged Fulvetta) used mainly bark gleaning as a foraging method among all species that are understorey flock participants. Only one hovering species *Seicercus castaneiceps* (Chestnut-crowned Warbler) occurred in canopy flocks (as a regular attendant). This species, however, was a core species in understorey flocks. Regular attendants in both flock types were dominated by foliage gleaners, followed by bark-surface feeders, salliers and hoverers (Fig. 8).

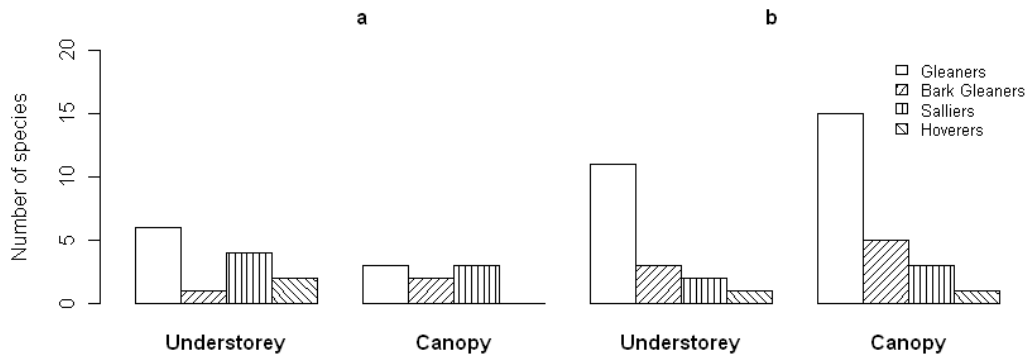


Figure 8: Foraging method groups in (a) core and (b) regular attendant species. Core species show a relatively even representation of different foraging method groups compared to attendant species.

Seasonal status of core and attendant species

Altitudinal migrants outnumbered year-round resident species (residents) in core species of understorey flocks (Fig. 9), and this pattern was reversed in regular attendants. Core and regular attendant canopy species were approximately equally represented by residents and altitudinal migrants.

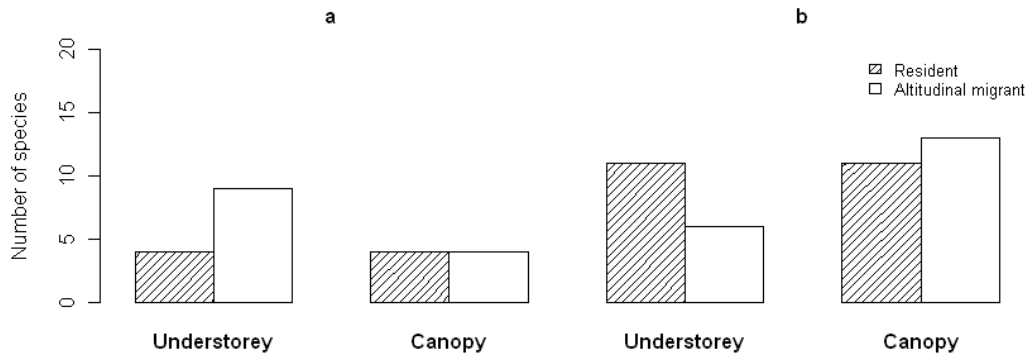


Figure 9: Seasonal status of (a) core and (b) regular attendant species.

Discussion

Mixed-species flock types

Although mixed-species flocks have been described in detail from tropical and temperate regions from South America, Europe, Africa and Asia, the co-existence of three distinct flock types in the same habitat has been recorded from elsewhere only in north-central Myanmar, also in dipterocarp-forest (King & Rappole 2001). Three compositionally distinct mixed-species flock types occurred in the lowland tropical dipterocarp-dominated evergreen forest of Namdpaha Tiger Reserve. These flocks were roughly segregated in terms of foraging height and body size. The mixed-species flocks composed of *Alcippe nipalensis* (Nepal Fulvetta) and associated species foraged mainly in the understorey (with some participant species in the midstorey), whereas flocks composed of *Melanochlora sultanea* (Sultan Tit), *Pericrocotus flammeus* (Scarlet Minivet) and other species foraged mainly in the canopy. The third type of mixed-species flocks was composed of species which foraged in the understorey as well as the midstorey. These, however, differed from the first flock type in being composed of species that had significantly higher body masses than species participating in the first flock type (Fig. 2). The third flock type was usually composed of *Garrulax* spp. (White-crested, Greater and Lesser Necklaced laughingthrushes), *Cissa chinensis* (Green Magpie), *Dicrurus remifer* (Lesser Racket-tailed Drongo) and *Harpactes erythrocephalus* (Red-headed Trogon).

In the study area, the two mixed-species flock types that occupied the same vertical stratum (the understorey) showed a significant difference in the body masses of their constituent species, whereas the third (canopy) flock participants, which occupied a different vertical stratum, did not differ from either of the understorey flocks in this respect (Fig. 2). Body mass and vertical stratification are possible factors determining

non-random patterns of species participation in flocks. Differently sized species may exploit resources that differ to such a degree that large species might be unable to facilitate the foraging of small species and vice versa. Similarly, differently sized species might have different predators, and for a species, joining a flock with members that are much larger or smaller than itself might not provide the same anti-predator benefits that joining similarly sized species affords. The foraging niches of flock participants and separation of resource utilization by participant species of different flock types requires investigation, as do the patterns of predation pressure operating on different flock participants.

The mechanisms that permit the co-existence of a high diversity of flocking insectivores require further study. It has been hypothesised that permanent mixed-species bird flocks might be one factor maintaining high bird species diversity in the neotropics. The participation of small-bodied species in flocks with large territories, leading to under-utilisation of resources by small-bodied species, is hypothesised to allow species with a high degree of niche overlap to co-exist, thereby increasing species richness (Powell 1989). An alternative mechanism (Graves & Gotelli 1993) responsible for high species richness in the neotropics may be the checkerboard pattern seen among congeneric flock participant species with similar ecologies (i.e. likely competitors). This has the effect of increasing local species diversity by “generating different combinations of species in different flocks” (Graves & Gotelli 1993).

Mixed-species flock structure

The number of species (\pm SE) participating in understory mixed species flocks, of which *Alcippe nipalensis* (Nepal Fulvetta) was a core constituent (6.37 ± 0.28 species), was

similar to flock species richness of other southeast Asian flocks led by another fulvetta species, *Alcippe morrisoniana* (Grey-cheeked Fulvetta) (5.8 ± 0.2 species) (Chen & Hsieh 2002). The number of individuals participating in flocks (32.4 ± 1.96 individuals) was appreciably lower than those recorded by Chen & Hsieh (2002) (51.4 ± 2.7 individuals).

Flocking and non-flocking species

Flocking species were dominated by insectivores (over 80%), and included omnivores and nectarivores. Granivores, frugivores and carnivores never participated in flocks (Fig. 5), reinforcing the observation that mixed-species flocks are composed mainly insectivorous bird species (Moynihan 1962). The other two diet guilds that participated in mixed-species flocks also include insects in their diet (omnivores and nectarivores), but to a lesser degree. Insectivorous species that did not participate in mixed-species flocks in the study area included species occupying bamboo or secondary forest, and occur in mixed-species flocks in those habitats (Ali & Ripley 1983, Rasmussen & Anderton 2005). These were species such as the *Xiphirhynchus superciliaris* (Slender-billed Scimitar-babbler), *Pomatorhinus erythrocnemis* (Spot-breasted Scimitar-babbler) and *Macronous gularis* (Striped tit-babbler). Other insectivorous species which did not participate in mixed-species flocks were flycatchers (genus *Militia* and *Ficedula*) and wren-babblers (genus *Pnoepyga* and *Napothera*). Species of the genus *Niltava* are irregular participants in mixed-species flocks (Chen & Hsieh 2002); the other genera are not known flock participants. Flycatchers might not participate in mixed-species flocks since they are specific to certain microhabitats such as the vicinity of streams and ravines (Ali & Ripley 1983), and might be unable to follow or remain with fast-moving flocks. Similarly, it is possible that wren-babbler species, owing to their specific microhabitat preferences (such

as moss covered rocks and logs and very dense undergrowth [Ali & Ripley 1983]), are unable to follow flocks.

Core and attendant species

Diet guilds

All core species in both understorey and canopy mixed-species flocks were insectivores, reinforcing the importance of insectivory in influencing species participation in flocks. In addition, regular attendants in understorey flocks were also all insectivores (Fig. 7). Although most regular attendants in canopy flocks were insectivorous, a small number of omnivores and nectarivores also regularly participated in these flocks. These species may join and follow mixed-species flocks only part of the time to satisfy their dietary requirement of insects, accounting for their status as regular attendants, rather than as core species.

Foraging method groups

Core species of mixed-species flocks were more evenly represented by different foraging method groups than are regular attendants, which are dominated by foliage gleaners (Fig. 8). Different foraging groups, due to specialised behaviours, contribute qualitatively and quantitatively different benefits to heterospecifics in mixed-species flocks. For instance, gregarious foliage gleaners are likely to flush insects or other active prey making these accessible to heterospecifics (Swynnerton 1915), and salliers, because they scan for insect prey are likely to detect predators and provide early warning (Munn 1984, Goodale & Kotagama 2005). The expected patterns of interspecific association that follow from these hypotheses are examined in the next chapter of this thesis. These specialized functional contributions might have the consequence of balancing foraging method representation in

the 'core' of a mixed-species flock. In other words, core species composition of a mixed-species flock is likely to be stable due to the exchange between core species of specialized, possibly complementary benefits. King & Rappole (2001) observed "substantial species-specific variation in foraging behaviour" among flock participants. They concluded that foraging facilitation was not a major benefit accruing to flock members since species with a particular foraging method would be unable to facilitate the foraging of species with a different foraging method. However, as has been stated above, it is the *difference* in foraging behaviour between participant species that is likely to offer foraging benefits, either directly through mechanisms such as beating of prey, or indirectly through reducing the time spent on vigilance (allowing more time for foraging).

Seasonal status of participant species

Altitudinal migrants outnumbered year-round residents in core species of understory flocks whereas the number of altitudinal migrants and residents was equal in core species of canopy flocks (Fig. 9). Both these findings are interesting in terms of the year-round stability of mixed-species flocks. In the neotropics, mixed-species flocks are known to be compositionally stable year-round (Munn & Terborgh 1979, Jullien & Thiollay 1998). Broad scale temporal patterns in mixed-species flock composition are unknown from Namdapha, and it is possible that these flocks do not occur during the breeding season. However, if species participate in heterospecific flocks throughout the annual cycle, the species composition of mixed-species flocks at different times of the year is likely to differ. Following movement to higher breeding grounds, the altitudinal ranges of different species will overlap in some parts of the altitudinal gradient but will not coincide exactly (Ali 1977). The composition of mixed-species flocks in different parts of the altitudinal gradient following seasonal movement is, however, expected to be similar in terms of the

functional guilds associating in flocks, since species are expected to associate with each other in a non-random manner based on the costs and benefits they incur from heterospecific association.

Conclusions

In areas with several different flock types co-existing in the same habitat, as in the dipterocarp forests of tropical Asia, vertical stratification and bird species body mass are possible factors determining non-random patterns of flock participation by species. Body mass is likely to play an important role in influencing species associations (and therefore flock composition) since similar sized species are expected to exploit similar resources (compared to species of very different body masses) and be at risk from similar predators. Core participants of mixed-species flocks show a relatively even representation of different foraging methods compared to attendant species. This suggests that the specialised behaviours displayed by these groups may influence the benefits received by other group members, and that the exchange of qualitatively different benefits mediated by specialised behaviours might be complementary to each other. Core species include a high proportion of altitudinal migrants, and the functional guild composition of mixed-species flocks following seasonal movements up or down the altitudinal gradient requires further study. Finally, a novel method of quantifying the differential tendencies of species to participate in mixed-species flocks in the context of the abundance of each species is presented.

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CHAPTER – 2: Birds of many feathers: the effect of group size and foraging method on nuclearity and interspecific associations in avian mixed-species flocks

Summary

1. Species participating in mixed-species flocks have stronger interspecific associations with increasing numbers of species associating with them. This trend is true separately for participant species in two distinct mixed-species flock types (understorey and canopy flocks). This indicates that the more attractive a species is to heterospecifics (or, the more ‘nuclear’ a species becomes), the stronger its associations become, since it is likely to provide a large benefit to other species which join it.
2. Intraspecific group size (or gregariousness) and foraging method are species traits that explain interspecific association strength in understorey flocks. These are traits that are likely to largely determine the foraging and anti-predator benefits provided by mixed-species flock participants to heterospecifics. In particular, gregarious gleaners and salliers separately have the strongest associations with other foraging groups in understorey flocks. These groups are expected to provide the greatest benefit to heterospecifics in terms of feeding advantages and early warning against predators respectively.
3. Gregarious gleaners and salliers have the strongest association with each other compared with any other pair of foraging groups in understorey flocks. This association is likely to be mutualistic in terms of the feeding advantage gained by salliers and the predator avoidance acquired by gleaners.
4. Traits which determine heterospecific associations in understorey flocks may not influence the same in canopy flocks, possibly due to the more open nature of the

forest canopy compared to the understorey, which allows easier detection of canopy bird species predators.

Key-words: *foraging efficiency, heterospecific association, mixed-species flock, nuclear species, predator avoidance*

Introduction

Animals may form groups for a variety of reasons, including anti-predator, foraging, and reproductive benefits (Morse 1977). In a non-reproductive, foraging context, group formation is thought to confer two main benefits – increased foraging efficiency, and decreased predation risk. Group participants may simultaneously incur costs such as competition between group members and kleptoparasitism (Morse 1977).

Groups may be monospecific or heterospecific, and participating in single-species groups is likely to be associated with costs and benefits that differ compared to participation in complex multi-species groups. For instance, foraging in heterospecific groups is likely to result in decreased competition between group members relative to monospecific groups since niche overlap between individuals of different species is much lower than that between conspecifics (Powell 1989). Also, individuals of different participant species may also introduce the benefits of certain specialized behaviours to the group as a whole (e.g. in multi-species bird flocks, gregarious foliage gleaning species may beat or flush active prey making these accessible to other flock members).

Mixed-species bird flocks have been described from tropical and temperate habitats worldwide (Moynihan 1962, McClure 1967, Powell 1979, Hutto 1994, Latta & Wunderle

1996, Fernandez-Juricic 2000, Chen & Hsieh 2002, Hino 2002, Hart & Freed 2003, Kotagama & Goodale 2004). Although detailed information regarding the species composition of mixed-species flocks is available, the nature of (and mechanisms determining) interspecific associations within mixed-species flocks has not received more than theoretical attention.

Two major sets of hypotheses have been advanced to explain the benefits accruing to species from participating in mixed-species flocks: increased foraging efficiency and greater predator avoidance (review in Morse 1977). Feeding advantages can be achieved through one or more independent mechanisms such as beating for insects or other active prey (Swynnerton 1915, Winterbottom 1943, 1949) and facilitation of food finding through social learning (Moynihan 1962). Likewise, predation risk can be lowered by multiple processes such as early detection of predators, the confusion effect, and dilution (Morse 1977). These advantages are not mutually exclusive, and the nature and degree of benefit gained by flock members is likely to vary for each participant species (Morse 1977, Herrera 1979).

Empirical observations and experimental results have provided separate support for each of the two major benefits hypothesised to explain the formation and existence of mixed-species flocks (Morse 1967, Gaddis 1980, LaGory *et al.* 1984, Alatalo *et al.* 1985, Klein 1988, Popp 1988, Waite & Grubb 1988, Veena & Lokesha 1993, Cimprich & Grubb 1994, Yaukey 1995, Thiollay 1999, Ragusa-Netto 2000). Recent research has focused on the benefits provided by different species in mixed-species flocks in terms of lowering predation risk, as well the role of different species in flock initiation (Dolby & Grubb 1998, Goodale & Kotagama 2005a, 2006).

Mixed-species flocks of birds are composed of ‘nuclear’ species, responsible for the initiation and cohesion of these flocks, and ‘attendant’ species, which join and follow nuclear species (Moynihan 1962). Nuclear species are therefore expected to play important roles in providing benefits to attendant species in terms of foraging efficiency or predator avoidance, or both. As a result, nuclear species are likely to have a large number of stable heterospecific associations. The ability of a species to provide benefits to other species is influenced by its traits. In particular, group size (or gregariousness) and foraging method are traits expected to determine to a large extent the nature and degree of the benefit provided. Species that forage by sallying (and, to a lesser extent, by hovering), because they scan for insect prey, detect predators early and provide sentinel benefits (Munn 1984, Goodale & Kotagama 2005b). Intraspecifically gregarious species are likely to provide feeding benefits through beating for active prey (especially foliage and bark gleaners) and food finding through social learning, and anti-predator advantages through dilution, predator confusion and early warning (Morse 1977).

Group size being equal, salliers are expected to provide greater anti-predator benefits than either foliage or bark surface gleaners because they scan for insect prey and can detect predators early. Salliers, regardless of group size are unlikely to increase the foraging efficiency of heterospecifics. The anti-predator as well as foraging advantages provided by gleaners to heterospecifics should increase with increasing gregariousness. Predator avoidance mechanisms such as dilution, early warning and predator confusion should be positively influenced by increasing gregariousness, as should be processes that facilitate foraging such as beating for active prey and food finding through social learning.

In this study, certain predictions that follow from the premises above were posed and tested:

1. The greater the benefits provided by a species, the greater the number of stable interspecific associations it will have, and the stronger these associations will be. Therefore there is predicted to be a positive relationship between the number and strength of interspecific associations across flock participants.
2. Interspecific association strength is related to group size and foraging method. In particular, intraspecifically gregarious gleaners and salliers will have the strongest interspecific associations since these foraging groups are likely to provide the greatest benefits to heterospecifics.
3. Associations between gregarious gleaners and salliers will be stronger than associations between other pairs of foraging groups, since the association is likely to be highly mutualistic.

Materials and Methods

Study area

Fieldwork was carried out in the Namdapha Tiger Reserve (27°23'30" to 27°39'40"N and 96°15'2" to 96°58'33"E) in Changlang district, eastern Arunachal Pradesh, India, from early December 2007 to mid-March 2008. Namdapha is situated in the Eastern Himalaya, a global Biodiversity Hotspot, and is an Important Bird Area with over 425 bird species (Islam & Rahmani 2004). The tiger reserve is 1,985 km² in area and encompasses altitudes ranging from 200 to 4500 m ASL. Habitats include alpine and temperate forests at higher altitudes to subtropical and tropical forests at lower elevations. Annual rainfall

varies between 1500 and 3500 mm, most of which falls during the south-west monsoon months from April to October (Datta 2007).

Sampling was conducted in the Hornbill and Musathi areas in the buffer zone of the reserve, at altitudes ranging from 500 to 650 m ASL. The habitat in this area is composed of dipterocarp-dominated lowland tropical evergreen forest (Datta 2007).

Sampling methods

Bird sampling for abundances

Twenty-three line transects were established ranging in length from 180 to 500 m and oriented to varying azimuths. The minimum distance between adjacent transects was 500 m, to maximise independence between transects. Each transect was walked on four occasions, and in the case of four transects, on five occasions, thereby totalling 92 walks of 23 transects. For every bird cluster detected, the species, cluster size (number of individuals), azimuth to the cluster (using a compass), and the detection distance to the centre of the cluster (using a laser rangefinder - 1000 Yardage Pro, Bushnell Corporation, Kansas, USA) were recorded. For clusters with a detection distance below 15 m, detection distance was estimated visually to the nearest metre. For gregarious species with large cluster sizes, cluster size was recorded in most cases as a range from a minimum to a maximum number of individuals, since an accurate count was not possible in all cases. The midpoint of this range was used in subsequent analyses. Transects were walked between 0830 and 1230 hours, when mixed-species flock activity was the highest.

Mixed-species flock sampling

Mixed-species flocks were sampled on the established transects (during sampling for bird abundances), and opportunistically along pre-existing trails from 1300 to 1530 hours. When encountered on transects, for each mixed-species flock, species composition, as well as the group size, detection azimuth and detection distance for each species cluster in the mixed-species flock were recorded. These data were incorporated in species abundance estimation. During opportunistic sampling, the species composition of the mixed-species flock and the group size of each participating species were recorded.

Analytical methods

Abundance estimation

To estimate detection functions and detection probabilities of bird species without the bias of differing detectability across species, species were divided into three detection classes based on their median detection distances, each class containing an equal number of species. This approach assumes intra-class homogeneity in species' detection functions, and models multi-species data more parsimoniously by exploiting species' similarity in detectability (Allredge *et al.* 2007). Detection function for each of these three classes was then estimated separately using the program Distance (Thomas *et al.* 2005). These detection functions were used to estimate species-specific cluster densities through post-stratification by surrogating each species as a level of stratification.

Mixed-species flock types

It was apparent during sampling that there were at least two flock types that differed in species composition. Hierarchical agglomerative cluster analysis (using Jaccard's

similarity index with UPGMA linkage) in the program PCord (McCune & Mefford 1999) was used to identify different flock types based on their species composition.

Measuring flocking propensity and species associations

For each flock type, a candidate pool of species potentially contributing to flock species composition was identified, composed of all species that had participated in at least one flock. The program R (R Development Core Team 2008) was used to simulate mixed-species flocks by drawing species from the candidate species pool as a function of the estimated abundance of clusters of each species alone. The number of species drawn in each simulated flock was equal to the observed mean flock size. This yielded null flocks with a composition expected in the absence of (a) differences in species tendency to participate in mixed-species flocks, and (b) positive or negative interactions between species.

Cluster abundance was used as a probability weight instead of individual abundance since species join mixed-species flocks in units of species-specific groups rather than as individuals (for gregarious species, individuals are subsets of clusters, and for solitary species are the same as clusters).

Species participation in mixed-species flocks

A species was categorised as participating in mixed-species flocks significantly more than expected if the observed number of occurrences in mixed-species flocks exceeded the upper 95% confidence interval of the distribution of its species-specific expected occurrence (i.e. the distribution of its occurrences in the simulated flocks). Where for a species the observed number of flock occurrences fell within the 95% confidence

intervals of this distribution, it was classified as participating in flocks as expected. Where the lower 95% confidence interval exceeded the observed number of occurrences, the species was classified as participating in flocks significantly less than expected. Non-parametric confidence intervals (0.025 and 0.975 quantiles) were used as cut-offs. Appendix tables S1 and S2 list the upper and lower confidence intervals of the species-specific expected occurrence distribution and the observed number of occurrences in mixed-species flocks.

Species associations and association strengths

Interspecific associations and association strengths were derived from a comparison of species co-occurrences in simulated flocks and observed species co-occurrences in mixed-species flocks. As many null flocks were simulated as the observed number of flocks for each flock type. In this set of simulated flocks, for each possible pair-wise combination of species, the number of flocks in which both species co-occurred was computed. This process was repeated 10,000 times to obtain a frequency distribution of expected pair-wise co-occurrence in simulated flocks. A pair of species was defined as being positively associated if the observed number of flocks in which they co-occurred exceeded the upper 95% confidence interval of the distribution of the number of co-occurrences in the simulated flocks (Fig. 1). The non-parametric confidence interval (0.975 quantile) was used as a cut-off.

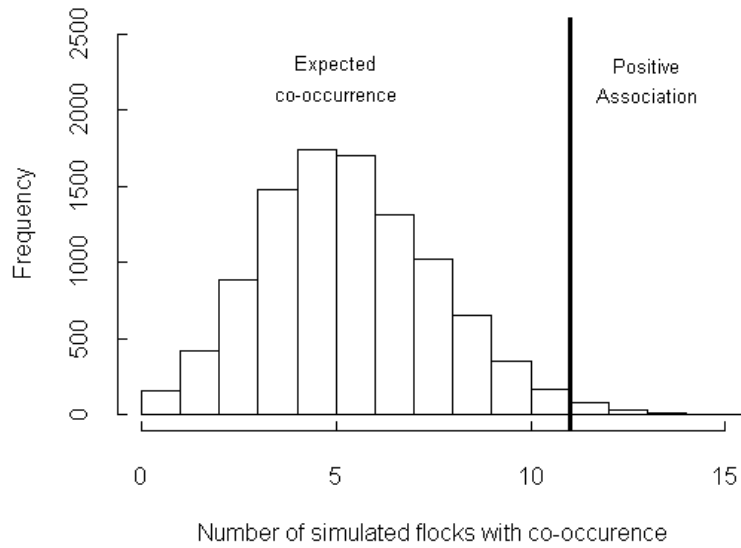


Figure 1: Example of an abundance weighted frequency distribution of co-occurrences of a species pair in simulated flocks. The solid black line indicates the non-parametric upper 95% CI of the distribution. An observed number of co-occurrences falling to the right of the line was defined as a positive association. The association strength was computed as a standardised measure indicating how much to the right of the mean of the distribution the observed number of co-occurrences was.

For significant associations, the association strength was calculated as a standardised measure equal to the difference between the observed number of co-occurrences and the mean of the distribution of co-occurrences in the simulated flocks, scaled by the standard deviation of the distribution.

Therefore, the association strength is given by:

$$\text{Association strength} = (O - \mu) / \sigma$$

Where,

O = observed number of co-occurrences

μ = mean of the abundance-weighted frequency distribution

σ = standard deviation of the abundance-weighted frequency distribution

Species characteristics

Species were classified as foliage gleaners, bark surface gleaners, hoverers, and salliers, based on the predominant foraging method, as reported in secondary sources (Ali 1977, Ali & Ripley 1983, Grimmett, Inskipp & Inskipp 1998) and from observations made during the study.

Feeding methods were defined based on Robinson & Holmes (1982) with modifications, as follows:

Gleaners: species that forage mainly by picking stationary prey items off a substrate such as foliage or tree bark when either stationary or hopping. Hence foliage gleaners and bark surface gleaners.

Hoverers: species that forage predominantly by picking stationary prey items from a substrate when in flight.

Salliers: species that forage mainly by pursuing flying prey and capturing these when in flight (described as 'hawking' by Robinson & Holmes (1982)).

Appendix tables S1 and S2 list the foraging methods of flock participant species. Foliage and bark surface gleaners were subsequently treated together as gleaners, and hoverers and salliers were treated together as non-gleaners for analysis. Species nomenclature follows Grimmett *et al.* (1998) with modifications from Rasmussen & Anderton (2005).

Results

Mixed-species flock types

3,974 individuals (887 clusters) representing 99 species were recorded on line transects. The species composition and species-specific cluster sizes of 101 mixed-species flocks were recorded from line transects and opportunistic sampling. Cluster analysis with five groupings identified three major flock types and two groups of atypically composed

‘outlier’ flocks. Each of the latter two groups was represented by only two flocks. Multi-response Permutation Procedure (MRPP), which provides a test of whether there is a significant difference between two or more groups of sampling units, was used to test the significance of the grouping (chance-corrected within-group agreement, $A = 0.122$, probability of obtaining smaller or equal $\delta < 0.0001$). The mixed-species flock types identified were understorey mixed-species flocks, canopy-mixed species flocks and flocks of large-bodied species (Chapter 1).

Species associations in mixed-species flocks

As predicted, in understorey and in canopy flocks separately, the mean interspecific association strength of a species (average of association strengths of a given species for all its heterospecific associations) related positively with the number of significant positive interspecific associations for the species (Fig. 2). Understorey flocks: $R^2 = 0.654$, $p < 0.001$; canopy flocks: $R^2 = 0.446$, $p < 0.001$.

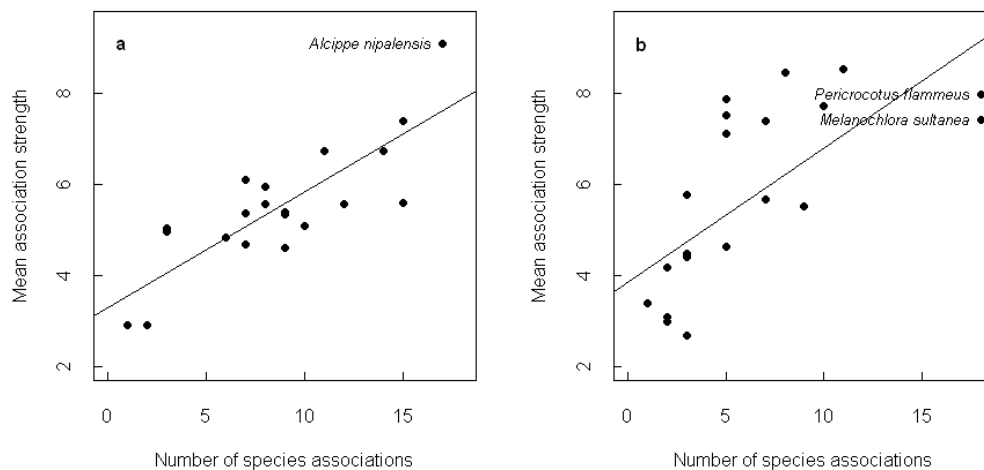


Figure 2: Mean interspecific association strength increases with increase in number of significant interspecific associations in (a) understorey and (b) canopy flocks.

For each flock type, species which participated significantly less than expected were excluded from the analysis. Species which participated in both flock types were assigned to that flock type in which participation was greater.

Interspecific associations and species traits

Intraspecific group size and foraging method were expected to predict the association strengths of participant species of mixed-species flocks. Species that habitually foraged by gleaning (either foliage or bark surface) outnumbered non-gleaners in both flock types (Fig. 3). In understorey flocks (Fig. 3a), there was wide variation in the mean intraspecific group sizes of gleaning species; non-gleaning species, however showed little variation in intraspecific group size. Mean group size was variable for both gleaners and non-gleaners in canopy flocks (Fig. 3b).

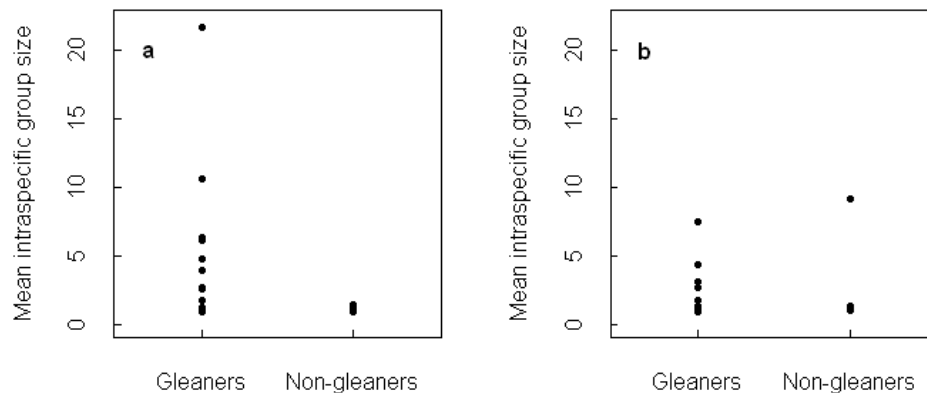


Figure 3: Mean intraspecific group size in gleaners and non-gleaners in (a) understorey and (b) canopy mixed-species. Gleaners show greater variation in gregariousness than non-gleaners in understorey flocks.

In understory flocks, mean association strength showed an increasing trend with increase in log intraspecific group size for gleaners (adjusted $R^2 = 0.314$) (Fig. 4a). For non-gleaners, mean association strength ranges from 4.68 to 7.41, whereas mean intraspecific group size ranges only from 1 to 1.5. On inclusion of non-gleaners in the analysis, no clear relationship emerges between mean association strength and intraspecific group size (adjusted $R^2 = 0.066$) (Fig. 4a). Since group size and foraging method were expected to predict species associations, I examined these covariates in the framework of linear modelling and model selection. The small sample size corrected Akaike's Information Criterion ($AICc$) was used as a basis for model selection (Burnham & Anderson 2002). The $AICc$ values, model weights (w_i) and adjusted coefficients of determination of the candidate models considered are presented in Table 1. The additive model of foraging method and group size had the best support in terms of $AICc$ and model weights as well as the highest adjusted R^2 (Table 1).

Table 1

$AICc$ values, model weights and adjusted R^2 values for candidate models explaining species association strengths in understory flocks. GS indicates log intraspecific group size; FM denotes foraging method (glean and non-glean).

<i>Model</i>	<i>AICc</i>	$\Delta AICc$	w_i	<i>adj. R²</i>
Null	106.9	5.7	0.0392	
GS + FM + GS x FM	103.7	2.5	0.1962	0.317
GS + FM	101.2	0	0.6941	0.329
GS	106.9	5.8	0.0389	0.066
FM	107.3	6.2	0.0315	0.049

Table 2 presents the $AICc$ values, model weights and adjusted coefficients of determination for the candidate models considered to explain species association strengths in canopy flocks.

Table 2

AICc values, model weights and adjusted R^2 values for candidate models explaining species association strengths in canopy flocks. GS indicates log intraspecific group size; FM denotes foraging method (glean and non-glean).

<i>Model</i>	<i>AICc</i>	$\Delta AICc$	w_i	<i>adj. R</i> ²
Null	107.78	0	0.4162	
GS + FM + GS x FM	111.15	6.7	0.0146	-0.038
GS + FM	109.18	3.2	0.0824	0.018
GS	107.21	0.2	0.3808	0.068
FM	109.77	2.7	0.1059	-0.052

In contrast to the understorey flocks, no pattern with group size and foraging method was apparent (Fig. 4b), and the null model was a better candidate than any of the other models which incorporated either group size and foraging method separately, or together (additively or interactively).

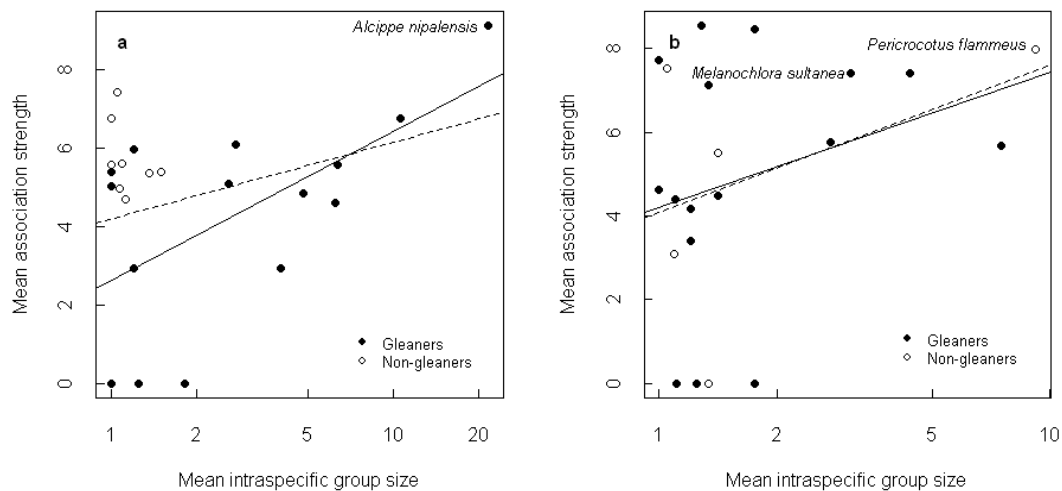


Figure 4: Relationship between group size and association strength in (a) understorey and (b) canopy mixed-species flocks. The dashed line indicates the relationship between group size and association strength for all species (both gleaners and non-gleaners) and the solid line indicates the relationship between group size and association strength for gleaners only. Association strength of gleaners rises with increasing gregariousness in understorey flocks. Note that the x-axis is in the natural log scale.

Species which participated significantly less than expected in each flock type were excluded from the analysis.

Trends in interspecific association strength

For this analysis, the mean and standard error was computed for each foraging group by averaging the association strengths of all species belonging to a foraging group and deriving the standard error of this value. As predicted, gleaners with high intraspecific group size (mean group size > 3) had greater association strengths than solitary or pair-forming gleaners as well as hoverers. In addition, gregarious gleaners had association strengths which were comparable with that of salliers, as expected. The association strengths of salliers were comparable with that of gleaners in general but higher than that of hoverers (Fig. 5a). In canopy flocks, the association strengths of large and small group size gleaners and salliers (canopy flocks lack hoverers) were comparable (Fig. 5b), contrary to expectation.

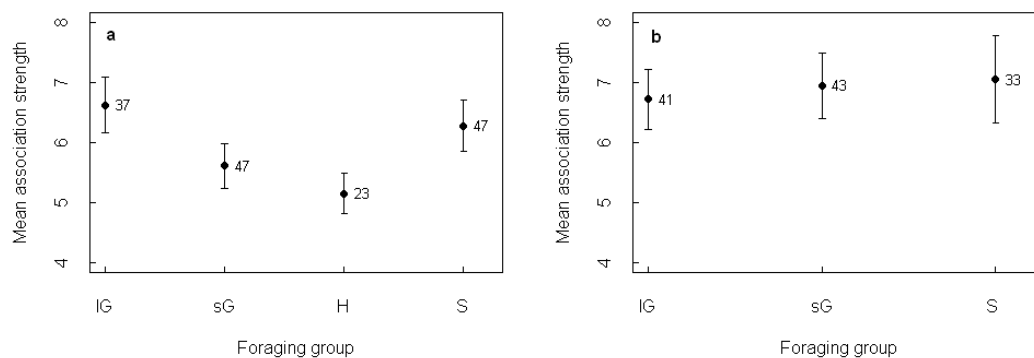


Figure 5: Mean and standard errors of association strengths of different foraging groups in (a) understorey and (b) canopy mixed-species flocks. IG: gleaners with large (>3) intraspecific group size; sG: gleaners with small (<=3) intraspecific group size; H: hoverers; S: salliers. Numbers alongside the data points indicate the number of pair-wise associations for each foraging group.

Association strengths: foraging group pairs

For all species in a foraging group, all species association strengths with species belonging to the other foraging group were averaged regardless of species identity, and the standard error for this value was computed (Fig. 6). Association strengths within the groups of gleaners with large intraspecific group size in understorey flocks (i.e. associations between gregarious gleaners and gregarious gleaners) and within the group salliers (i.e. between salliers and salliers) in canopy flocks was not computed due to low sample size (three instances in each case). Hoverers did not positively associate with each other in understorey flocks, and did not occur in canopy flocks.

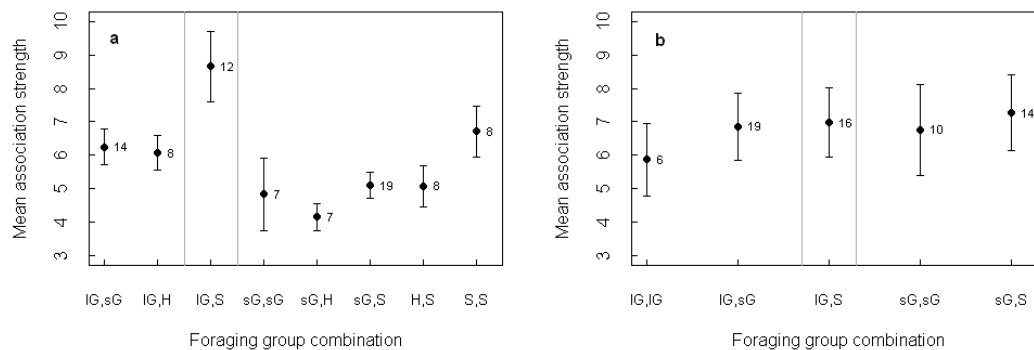


Figure 6: Mean and standard errors of association strengths between foraging groups in (a) understorey and (b) canopy mixed-species flocks. IG: gleaners with large (>3) intraspecific group size; sG: gleaners with small (≤ 3) intraspecific group size; H: hoverers; S: salliers. The data point enclosed within light grey lines represents the association strength between gregarious gleaners and salliers. Numbers alongside the data points indicate the number of pair-wise associations for each foraging group.

The strongest association in understorey flocks was between gleaners with large intraspecific group size and salliers (Fig. 6a), as expected. Association strengths of all pairs of foraging groups were comparable in canopy flocks (Fig. 6b).

Discussion

Heterospecific association numbers and association strength

Participant flocking species had, on average, stronger interspecific associations with increasing numbers of species associating with them. This trend was true separately for participant species in both understorey and canopy flocks. Within mixed-species flocks, some species will provide greater benefits to associate heterospecifics than others in terms of foraging efficiency, or predator avoidance, or both. The larger the benefit provided by a species, the greater the number of species that will associate with it consistently, and the stronger the association between benefit-providing species and benefit-seeking species. As a result, along a continuum of benefit provided, as species move higher along the continuum, not only do they become attractive to more species, they also become more attractive to each of the attracted species.

‘Nuclear’ species, responsible for flock cohesion in mixed-species flocks are likely to fall in the high end of this continuum, and species with the most number of associations (and the strongest ones) are likely to be nuclear species. These are *Alcippe nipalensis* (Nepal Fulvetta) in the understorey flocks (Fig. 2a), and *Melanochloa sultanea* (Sultan Tit) and *Pericrocotus flammeus* (Scarlet Minivet) in the canopy flocks (Fig. 2b). The relationship between the number and strength of heterospecific associations in mixed-flock participants thus provides a continuum from ‘most nuclear’ to ‘least nuclear’ species within a flock type.

Group size and foraging method as predictors of association strength

In understorey flocks, intraspecific group size and foraging method correlates well with the strength of heterospecific associations of participant flocking species. Different

foraging groups are likely to provide different benefits to associate heterospecifics. For a constant group size, species that habitually capture insect prey in flight (non-gleaners such as salliers, and to a lesser extent, hoverers) provide greater 'sentinel' benefits than gleaners due to their visual scanning for prey, allowing them to detect predators more quickly than gleaners (Munn 1984, Goodale & Kotagama 2005a). With gleaners, an equal benefit in predator avoidance due to early warning may be acquired only at larger group sizes. In addition, intraspecifically gregarious gleaners are capable of providing other benefits such as beating for prey (Swynnerton 1915, Winterbottom 1943, 1949), dilution and predator confusion (Morse 1977).

Several flock types therefore contain 'nuclear' species which are either intraspecifically gregarious gleaners (Morse 1970) or solitary salliers (Greig-Smith 1981, Munn 1984). Goodale & Kotagama (2005b) using playback experiments in Sri Lanka reported that flocking species responded equally to *Dicrurus paradiseus* (Greater Racket-tailed Drongo) and *Turdoides rufescens* (Orange-billed Babbler) calls. The former is a solitary sallier and a 'sentinel' species, and is highly sensitive to predator presence, whereas the latter is a gregarious gleaner.

As predicted, in this study, the association strengths of non-gleaners and gleaners follow different trends. With increasing gregariousness, heterospecific association strength of gleaner species rises significantly. This is consistent with the expectation that the more individuals in the group, the greater the benefit provided to flock participants. Non-gleaners, which showed very little variation in group size (Fig. 3a), had higher association strengths than gleaners with comparable (low) group sizes (Fig. 4a). This may be explained based on the fact that non-gleaners are much better sentinels than gleaners

(holding group sizes constant); in addition, gleaners with low group sizes are highly unlikely to be providers of other benefits (e.g. beating for active prey, dilution) that gregarious gleaners provide.

The expected relationship between association strength, and group size and foraging method did not emerge in canopy flocks. This lack of predicted pattern may be due to the fact that predators of canopy bird species may be more easily detected than predators of understorey species due to the relative openness of the canopy (Thiollay 1999), making gleaners and non-gleaners equally likely to detect predators. There, is however, no evidence in support of this hypothesis, and other mechanisms may be responsible for the association patterns observed in canopy mixed-species flocks.

In understorey flocks, gregarious gleaners had stronger heterospecific associations than gleaners with small group size and hoverers. Association strengths of salliers were comparable with those of gregarious gleaners. This pattern is consistent with the hypothesis that gregarious gleaners and salliers provide the greatest benefits to flock participants. In canopy flocks, all foraging groups have comparable strengths of association, suggesting that foraging method is not an important trait determining benefit provided to canopy flock participants.

Mutualisms and association strengths

The association between gregarious gleaners and salliers is expected to be a mutualism since gregarious gleaners can flush or beat insect prey (Swynnerton 1915, Morse 1977) for salliers whereas salliers can provide early warning against predators (Goodale & Kotagama 2005a) to gleaners. No other association between pairs of species belonging to

different foraging methods is expected to be mutualistic to as high a degree as the association between gregarious gleaners and salliers. The prediction that the strongest associations will be between these two foraging groups is supported in understory flocks, in which this association is significantly stronger than all other pair-wise foraging group associations. Within mixed-species flocks, not all associations are likely to be mutualistic. Several heterospecific associations in mixed-species flocks are very possibly commensal, or parasitic to some degree e.g. nuclear species being joined and followed by ‘adherent’ species which probably do not provide any significant benefit to the nuclear species except a decrease in the statistical risk of predation. These associations are expected to be much weaker than a true mutualism which benefits both associating species.

In canopy mixed-species flocks, associations between different pairs of foraging groups do not differ significantly in their strengths, indicating that associations (and therefore costs and benefits) may be driven by traits other than foraging method.

Conclusions

The observation of empirical patterns expected from mechanisms hypothesised to explain species associations in heterospecific bird flocks provides support for the broad explanations invoked to explain mixed-species flocking. In heterospecific bird flocks, degree of gregariousness and foraging method are species traits that are likely to be important determinants of benefits provided by a species to associate heterospecifics; these benefits flow from specialised behaviours that different species exhibit. Benefits and costs accruing to participant species in canopy mixed-species flocks might be influenced by factors other than group size and foraging method, since predator detection,

and possibly foraging mechanisms might differ from those in the understorey due to structural differences between the two vegetation strata.

This study provides a novel method for identifying and quantifying heterospecific association in general, potentially applicable in the testing of complex interspecific interactions such as mutualism, facilitation and competition and. Further, an objective technique of identifying nuclear species in mixed-species flocks along a continuum from 'most nuclear' to 'least nuclear' is presented.

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Table S1
Understorey mixed-species flock participants

<i>Sl.no.</i>	<i>Scientific name</i>	<i>English name</i>	<i>Observed</i>	<i>LL</i>	<i>UL</i>	<i>FM</i>
1	<i>Abroscopus albogularis</i> ⁺	Rufous-faced Warbler	38	22	37	Glean
2	<i>Abroscopus supercilialis</i>	Yellow-bellied Warbler	3	1	10	Glean
3	<i>Aethopyga saturata</i>	Black-throated Sunbird	15	24	39	Glean
4	<i>Alcippe castaneiceps</i> ⁺	Rufous-winged Fulvetta	25	6	19	Bark glean
5	<i>Alcippe nipalensis</i> ⁺	Nepal Fulvetta	44	6	19	Glean
6	<i>Alcippe rufogularis</i> ⁻	Rufous-throated Fulvetta	1	4	16	Glean
7	<i>Alophoixus flaveolus</i> ⁻	White-throated Bulbul	1	9	22	Glean
8	<i>Arachnothera magna</i> ⁻	Streaked Spiderhunter	1	10	23	Glean
9	<i>Blythipicus pyrrhotis</i>	Bay Woodpecker	2	1	8	Bark glean
10	<i>Celeus brachyurus</i>	Rufous Woodpecker	1	1	10	Bark glean
11	<i>Culicicapa ceylonensis</i> ⁺	Grey-headed Canary Flycatcher	45	18	34	Sally
12	<i>Dendrocitta formosae</i> ⁻	Grey Treepie	1	2	10	Glean
13	<i>Dicrurus aeneus</i>	Bronzed Drongo	1	1	9	Sally
14	<i>Dicrurus remifer</i> ⁺	Lesser Racket-tailed drongo	36	9	22	Sally
15	<i>Erpornis zantholeuca</i> ⁺	White-bellied Erpornis	31	13	27	Glean
16	<i>Gampsorhynchus rufulus</i>	White-hooded Babbler	1	0	4	Glean
17	<i>Gecinulus grantia</i>	Pale-headed Woodpecker	1	0	4	Bark glean
18	<i>Harpactes erythrocephalus</i> ⁻	Red-headed Trogon	1	12	25	Glean
19	<i>Hemipus picatus</i> ⁺	Bar-winged Flycatcher Shrike	3	0	2	Sally
20	<i>Heterophasia annectans</i> ⁻	Rufous-backed Sibia	2	9	22	Bark glean
21	<i>Melanochlora sultanea</i>	Sultan Tit	2	2	12	Glean
22	<i>Minla ignotincta</i>	Red-tailed Minla	1	0	6	Bark glean
23	<i>Orthotomus cuculatus</i> ⁺	Mountain Tailorbird	3	0	2	Glean
24	<i>Paradoxornis atosuperciliaris</i>	Lesser Rufous-headed Parrotbill	1	0	1	Glean
25	<i>Paradoxornis gularis</i> ⁻	Grey-headed Parrotbill	1	2	12	Glean
26	<i>Pericrocotus flammeus</i>	Scarlet Minivet	2	2	11	Sally
27	<i>Phylloscopus cantator</i>	Yellow-vented Warbler	1	0	4	Glean
28	<i>Phylloscopus reguloides</i> ⁺	Blyth's Leaf Warbler	13	2	11	Glean
29	<i>Picus flavinucha</i> ⁻	Greater Yellownappe	1	2	12	Bark glean
30	<i>Pteruthius melanotis</i> ⁺	Black-eared Shrike Babbler	6	0	4	Glean
31	<i>Rhipidura albicollis</i> ⁺	White-throated Fantail	31	9	22	Sally
32	<i>Rhipidura hypoxantha</i>	Yellow-bellied Fantail	16	10	23	Sally
33	<i>Sasia ochracea</i>	White-browed Piculet	2	0	2	Glean
34	<i>Seicercus castaneiceps</i> ⁺	Chestnut-crowned Warbler	15	4	14	Hover
35	<i>Seicercus poliogenys</i>	Grey-cheeked Warbler	12	4	15	Hover
36	<i>Seicercus whistleri</i> ⁺	Whistler's Warbler	4	0	3	Hover
37	<i>Sitta castanea</i>	Chestnut-bellied Nuthatch	1	0	6	Bark glean
38	<i>Stachyris chrysaea</i>	Golden Babbler	6	0	7	Glean
39	<i>Stachyris nigriceps</i>	Grey-throated Babbler	10	5	16	Glean
40	<i>Yuhina nigrimenta</i> ⁻	Black-chinned Yuhina	1	2	11	Glean

Species are arranged in alphabetical order of their scientific names. Nomenclature follows Grimmett *et al.* (1998) with modifications from Rasmussen & Anderton (2005).

'Observed' indicates number of flocks (out of 60 flocks) in which the species occurred; 'LL' and 'UL' refer to the lower and upper 95 per cent confidence intervals of the species-specific distribution of expected occurrence (out of 60 flocks) in simulated mixed-species flocks; 'FM' refers to predominant foraging method of the species. A '+' superscript against the scientific name indicates greater participation in mixed-species flocks than expected and a '-' denotes lower than expected participation. Absence of a superscript indicates occurrence in flocks as expected.

Table S2
Canopy mixed-species flock participants

<i>Sl.no.</i>	<i>Scientific name</i>	<i>English name</i>	<i>Observed</i>	<i>LL</i>	<i>UL</i>	<i>FM</i>
1	<i>Abroscopus superciliaris</i>	Yellow-vented Warbler	1	0	7	Glean
2	<i>Aethopyga saturata</i>	Black-throated Sunbird	1	13	22	Glean
3	<i>Alcippe castaneiceps</i>	Rufous-winged Fulvetta	2	3	12	Glean
4	<i>Alcippe nipalensis</i>	Nepal Fulvetta	1	3	12	Bark glean
5	<i>Alophoixus flaveolus</i>	White-throated Bulbul	2	5	14	Glean
6	<i>Arachnothera magna</i>	Streaked Spiderhunter	9	5	15	Glean
7	<i>Blythipicus pyrrhotis</i>	Bay Woodpecker	3	0	6	Bark glean
8	<i>Celeus brachyurus</i>	Rufous Woodpecker	2	0	7	Bark glean
9	<i>Chloropsis hardwickii</i>	Orange-bellied Leafbird	3	0	4	Glean
10	<i>Cissa chinensis</i>	Green Magpie	4	0	6	Glean
11	<i>Coracina melaschistos</i> ⁺	Black-winged Cuckoo Shrike	8	0	5	Glean
12	<i>Culicicapa ceylonensis</i>	Grey-headed Canary Flycatcher	10	10	20	Sally
13	<i>Dendrocitta formosae</i>	Grey Treepie	2	1	7	Glean
14	<i>Dicrurus aeneus</i> ⁺	Bronzed Drongo	8	0	6	Sally
15	<i>Dicrurus hottentottus</i>	Spangled Drongo	1	0	7	Glean
16	<i>Dicrurus paradiseus</i>	Greater Racket-tailed Drongo	1	0	6	Sally
17	<i>Dicrurus remifer</i> ⁺	Lesser Racket-tailed Drongo	15	5	14	Sally
18	<i>Erpornis zantholeuca</i>	White-bellied Erpornis	9	7	17	Glean
19	<i>Heterophasia annectans</i>	Rufous-backed Sibia	13	5	14	Bark glean
20	<i>Melanochlora sultanea</i> ⁺	Sultan Tit	18	1	8	Glean
21	<i>Minla cyanuroptera</i>	Blue-winged Minla	3	0	3	Glean
22	<i>Minla ignotincta</i> ⁺	Red-tailed Minla	6	0	4	Bark glean
23	<i>Paradoxornis gularis</i>	Grey-headed Parrotbill	6	1	8	Glean
24	<i>Pericrocotus brevirostris</i>	Short-billed Minivet	1	0	3	Sally
25	<i>Pericrocotus flammeus</i> ⁺	Scarlet Minivet	18	1	8	Sally
26	<i>Phylloscopus reguloides</i>	Blyth's Leaf Warbler	2	1	8	Glean
27	<i>Picus chlorolophus</i>	Lesser Yellownape	4	1	8	Bark glean
28	<i>Picus flavinucha</i>	Greater Yellownape	5	1	8	Bark glean
29	<i>Pomatorhinus ochraceiceps</i>	Red-billed Scimitar Babbler	1	0	2	Glean
30	<i>Pomatorhinus schisticeps</i>	White-browed Scimitar Babbler	1	0	2	Glean
31	<i>Psarisomus dalhousiae</i>	Long-tailed Broadbill	1	0	5	Glean
32	<i>Pteruthius melanotis</i>	Black-eared Shrike Babbler	2	0	3	Glean
33	<i>Rhipidura albicollis</i>	White-throated Fantail	1	5	14	Sally
34	<i>Seicercus castaneiceps</i>	Chestnut-crowned Warbler	2	2	9	Hover
35	<i>Sitta castanea</i> ⁺	Chestnut-bellied Nuthatch	9	0	5	Bark glean
36	<i>Sitta formosa</i> ⁺	Beautiful Nuthatch	5	0	3	Bark glean
37	<i>Stachyris nigriceps</i>	Grey-throated Babbler	1	2	11	Glean
38	<i>Tephrodornis virgatus</i>	Large Woodshrike	2	0	3	Glean

Species are arranged in alphabetical order of their scientific names. Nomenclature follows Grimmett *et al.* (1998) with modifications from Rasmussen & Anderton (2005).

'Observed' indicates number of flocks (out of 26 flocks) in which the species occurred; 'LL' and 'UL' refer to the lower and upper 95 per cent confidence intervals of the species-specific distribution of expected occurrence (out of 26 flocks) in simulated mixed-species flocks; 'FM' refers to predominant foraging method of the species. A '+' superscript against the scientific name indicates greater participation in mixed-species flocks than expected and a '-' denotes lower than expected participation. Absence of a superscript indicates occurrence in flocks as expected.

CONCLUSIONS

In habitats such as the dipterocarp forests of tropical Asia, several compositionally different mixed-species flock types co-exist. Preferential participation of bird species in different flock types may be influenced by body mass, since similarly sized species are likely to be subject to similar foraging limitations and predation pressures. Core species in mixed-species flocks may exchange complementary benefits in foraging and predator-avoidance, the nature of these benefits arising from the specialised behaviours peculiar to different foraging methods groups. Such complementarity in benefits provided to heterospecifics may explain the relatively even representation of different foraging groups in core flocking species.

Species in mixed-species flocks are likely to be nuclear in relation to other flock participants, rather than simply either nuclear or attendant. In other words, nuclearity is more likely context-specific rather than simply species-specific. This study provides a novel method in assessing nuclearity of flock members along a continuum from most to least nuclear. Nuclear species possess a large number of strong positive heterospecific associations. Empirically observed patterns of association between different foraging groups with different group sizes in understorey flocks lend support to the mechanisms hypothesised to influence interspecies associations in mixed-species groups in birds. In particular, gregarious gleaners and salliers, which were expected to provide the greatest benefits to heterospecifics in terms of foraging and predator-avoidance respectively had the strongest associations with other flock participants.

This study identifies a new approach through which heterospecific associations in animals can be identified, and the strength of these associations quantified. This is potentially for the testing of broad hypotheses related to complex interactions between animal species, such as competition, facilitation and mutualism.

Appendices

Appendix 1: Non-flocking species

<i>Scientific Name</i>	<i>English Name</i>
<i>Accipiter trivirgatus</i>	Crested Goshawk
<i>Aceros nipalensis</i>	Rufous-necked Hornbill
<i>Annorhinus tickelli</i>	Brown Hornbill
<i>Arborophila rufogularis</i>	Rufous-throated Partridge
<i>Dendrocitta frontalis</i>	Collared Treepie
<i>Ficedula hyperythra</i>	Snowy-browed Flycatcher
<i>Ficedula strophliata</i>	Rufous-gorgeted Flycatcher
<i>Hemixos flavala</i>	Ashy Bulbul
<i>Heterophasia picaoides</i>	Long-tailed Sibia
<i>Hypsipetes leucocephalus</i>	Black Bulbul
<i>Irena puella</i>	Asian Fairy Bluebird
<i>Leiothrix argentauris</i>	Silver-eared Mesia
<i>Macronous gularis</i>	Striped Tit-babbler
<i>Megalaima asiatica</i>	Blue-throated Barbet
<i>Megalaima australis</i>	Blue-eared Barbet
<i>Megalaima virens</i>	Great Barbet
<i>Mulleripicus pulverulentus</i>	Great Slaty Woodpecker
<i>Myiomela leucura</i>	White-tailed Robin
<i>Myophonus caeruleus</i>	Blue Whistling Thrush
<i>Napothera brevicaudata</i>	Streaked Wren Babbler
<i>Napothera epilepidota</i>	Eyebrowed Wren Babbler
<i>Niltava grandis</i>	Large Niltava
<i>Niltava macgrigoriae</i>	Small Niltava
<i>Niltava sundara</i>	Rufous-bellied Niltava
<i>Nyctyornis athertoni</i>	Blue-bearded Bee-eater
<i>Pnoepyga pusilla</i>	Pygmy Wren Babbler
<i>Polyplectron bicalcaratum</i>	Grey Peacock Pheasant
<i>Pomatorhinus erythrocnemis</i>	Spot-breasted Scimitar Babbler
<i>Tesia olivea</i>	Slaty-bellied Tesia
<i>Treron apicauda</i>	Pin-tailed Green Pigeon
<i>Xiphirhynchus superciliaris</i>	Slender-billed Scimitar Babbler
<i>Yuhina flavicollis</i>	Whiskered Yuhina
<i>Yuhina gularis</i>	Stripe-throated Yuhina
<i>Zoothera mollissima</i>	Plain-backed Thrush

Species are arranged in alphabetical order of scientific names. Nomenclature follows Grimmett *et al.* (1998) with modifications from Rasmussen & Anderton (2005).

Appendix 2: Understorey flock participants

<i>Status</i>	<i>Scientific name</i>	<i>English name</i>	<i>Participation</i>
C	<i>Abroscopus albogularis</i>	Rufous-faced Warbler	61.90
C	<i>Alcippe castaneiceps</i>	Rufous-winged Fulvetta	41.27
C	<i>Alcippe nipalensis</i>	Nepal Fulvetta	71.43
C	<i>Culicicapa ceylonensis</i>	Grey-headed Canary Flycatcher	73.02
C	<i>Dicrurus remifer</i>	Lesser Racket-tailed Drongo	57.14
C	<i>Erpornis zantholeuca</i>	White-bellied Erpornis	52.38
C	<i>Hemipus picatus</i>	Pied Flycatcher Shrike	4.76
C	<i>Orthotomus cuculatus</i>	Mountain Tailorbird	6.35
C	<i>Phylloscopus reguloides</i>	Blyth's Leaf Warbler	22.22
C	<i>Pteruthius melanotis</i>	Black-eared Shrike Babbler	9.52
C	<i>Rhipidura albicollis</i>	White-throated Fantail	49.21
C	<i>Seicercus castaneiceps</i>	Chestnut-crowned Warbler	23.81
C	<i>Seicercus whistleri</i>	Whistler's Warbler	6.35
RA	<i>Abroscopus superciliaris</i>	Yellow-bellied Warbler	4.76
RA	<i>Blythipicus pyrrhotis</i>	Bay Woodpecker	4.76
RA	<i>Celeus brachyurus</i>	Rufous Woodpecker	1.59
RA	<i>Dicrurus aeneus</i>	Bronzed Drongo	1.59
RA	<i>Gampsorhynchus rufulus</i>	White-hooded Babbler	1.59
RA	<i>Gecinulus grantia</i>	Pale-headed Woodpecker	1.59
RA	<i>Melanochlora sultanea</i>	Sultan Tit	3.17
RA	<i>Minla ignotincta</i>	Red-tailed Minla	1.59
RA	<i>Paradoxornis atrosuperciliaris</i>	Lesser Rufous-headed Parrotbill	1.59
RA	<i>Pericrocotus flammeus</i>	Scarlet Minivet	3.17
RA	<i>Phylloscopus cantator</i>	Yellow-vented Warbler	1.59
RA	<i>Rhipidura hypoxantha</i>	Yellow-bellied Fantail	25.40
RA	<i>Sasia ochracea</i>	White-browed Piculet	3.17
RA	<i>Seicercus poliogenys</i>	Grey-cheeked Warbler	19.05
RA	<i>Sitta castanea</i>	Chestnut-bellied Nuthatch	1.59
RA	<i>Stachyris chrysaea</i>	Golden Babbler	9.52
RA	<i>Stachyris nigriceps</i>	Grey-throated Babbler	15.87
IA	<i>Aethopyga saturata</i>	Black-throated Sunbird	23.81
IA	<i>Alcippe rufogularis</i>	Rufous-throated Fulvetta	1.59
IA	<i>Alophoixus flaveolus</i>	White-throated Bulbul	1.59
IA	<i>Arachnothera magna</i>	Streaked Spiderhunter	1.59
IA	<i>Dendrocitta formosae</i>	Grey Treepie	1.59
IA	<i>Harpactes erythrocephalus</i>	Red-headed Trogon	1.59
IA	<i>Heterophasia annectans</i>	Rufous-backed Sibia	3.17
IA	<i>Paradoxornis gularis</i>	Grey-headed Parrotbill	1.59
IA	<i>Picus flavinucha</i>	Greater Yellownappe	1.59
IA	<i>Yuhina nigrimenta</i>	Black-chinned Yuhina	1.59

Species are arranged based on degree of participation in mixed-species flocks. Nomenclature follows Grimmett *et al.* (1998) with modifications from Rasmussen & Anderton (2005).

C: Core species

RA: Regular attendant

IA: Irregular attendant

Participation: percentage of flocks in which the species participated

Appendix 3: Canopy flock participants

<i>Status</i>	<i>Scientific name</i>	<i>English name</i>	<i>Participation</i>
A	<i>Coracina melaschistos</i>	Black-winged Cuckoo Shrike	34.62
A	<i>Dicrurus aeneus</i>	Bronzed Drongo	26.92
A	<i>Dicrurus remifer</i>	Lesser Racket-tailed Drongo	53.85
A	<i>Melanochlora sultanea</i>	Sultan Tit	73.08
A	<i>Minla ignotincta</i>	Red-tailed Minla	23.08
A	<i>Pericrocotus flammeus</i>	Scarlet Minivet	69.23
A	<i>Sitta castanea</i>	Chestnut-bellied Nuthatch	34.62
A	<i>Sitta formosa</i>	Beautiful Nuthatch	19.23
RA	<i>Abroscopus superciliaris</i>	Yellow-bellied Warbler	3.85
RA	<i>Arachnothera magna</i>	Streaked Spiderhunter	34.62
RA	<i>Blythipicus pyrrhotis</i>	Bay Woodpecker	7.69
RA	<i>Celeus brachyurus</i>	Rufous Woodpecker	7.69
RA	<i>Chloropsis hardwickii</i>	Orange-bellied Chloropsis	11.54
RA	<i>Cissa chinensis</i>	Green Magpie	15.38
RA	<i>Culicicapa ceylonensis</i>	Grey-headed Canary Flycatcher	38.46
RA	<i>Dendrocitta formosae</i>	Grey Treepie	7.69
RA	<i>Dicrurus hottentottus</i>	Spangled Drongo	3.85
RA	<i>Dicrurus paradiseus</i>	Greater Racket-tailed Drongo	3.85
RA	<i>Erpornis zantholeuca</i>	White-bellied Erpornis	30.77
RA	<i>Heterophasia annectans</i>	Rufous-backed Sibia	50.00
RA	<i>Minla cyanuroptera</i>	Blue-winged Minla	11.54
RA	<i>Paradoxornis gularis</i>	Grey-headed Parrotbill	23.08
RA	<i>Pericrocotus brevirostris</i>	Short-billed Minivet	3.85
RA	<i>Phylloscopus reguloides</i>	Blyth's Leaf-warbler	7.69
RA	<i>Picus chlorolophus</i>	Lesser Yellownappe	15.38
RA	<i>Picus flavinucha</i>	Greater Yellownappe	19.23
RA	<i>Pomatorhinus ochraceiceps</i>	Red-billed Scimitar Babbler	3.85
RA	<i>Pomatorhinus schisticeps</i>	White-browed Scimitar Babbler	3.85
RA	<i>Psarisomus dalhousiae</i>	Long-tailed Broadbill	3.85
RA	<i>Pteruthius melanotis</i>	Black-eared Shrike Babbler	7.69
RA	<i>Seicercus castaneiceps</i>	Chestnut-crowned Warbler	7.69
RA	<i>Tephrodornis virgatus</i>	Large Woodshrike	7.69
IA	<i>Aethopyga saturata</i>	Black-throated Sunbird	3.85
IA	<i>Alcippe castaneiceps</i>	Rufous-winged Fulvetta	7.69
IA	<i>Alcippe nipalensis</i>	Nepal Fulvetta	3.85
IA	<i>Alophoixus flaveolus</i>	White-throated Bulbul	7.69
IA	<i>Rhipidura albicollis</i>	White-throated Fantail	3.85
IA	<i>Stachyris nigriceps</i>	Grey-throated Babbler	3.85

Species are arranged based on degree of participation in mixed-species flocks. Nomenclature follows Grimmett *et al.* (1998) with modifications from Rasmussen & Anderton (2005).

C: Core species

RA: Regular attendant

IA: Irregular attendant

Participation: percentage of flocks in which the species participated