

Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest

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Abstract: Studies of mixed-species bird flocks have found that ‘nuclear’ species, those important to flock coherence, are either intraspecifically gregarious or are ‘sentinel’ species highly sensitive to predators. Both types of species are present in flocks of a Sri Lankan rain forest: orange-billed babblers (*Turdoides rufescens* Blyth) are highly gregarious, whereas greater racket-tailed drongos (*Dicrurus paradiseus* Linnaeus) are less so, but more sensitive and reliable alarm-callers. We hypothesized that flock participants would be attracted to the playback of both species more than to the clearly non-nuclear yellow-fronted barbet (*Megalaima flavifrons* Cuvier). Further, we hypothesized that insectivores would prefer babbler vocalizations, as babblers could facilitate their foraging in several ways. We found that the response of insectivores was three times greater during babbler or drongo playback, and eight times greater during playback of these two species together, than during barbet playback or silence. Insectivores did not show, however, any difference in their response to babbler as compared to drongo playback; omnivores and frugivores responded relatively equally to all treatments. Our results show that birds with high propensity to flock, such as insectivores, use the vocalizations of nuclear species to locate flocks and that a sentinel species may be as attractive as a highly gregarious species.

Key Words: avian community ecology, *Dicrurus paradiseus*, heterospecific attraction, mixed-species flocks, nuclear species, playback, sentinel species, Sri Lanka, *Turdoides rufescens*

INTRODUCTION

Mixed-species flocks are a striking feature of tropical avifaunas (Powell 1985, Thiollay 1999). The rising number of descriptions of flocks throughout the world allows ecologists to look for general patterns in flock composition and organization and to deduce the forces that structure these non-trophic communities. In the study of flock organization, researchers have repeatedly found that some ‘nuclear’ species seem important to the formation or maintenance of the flocks, whereas other ‘adherent’ species add little except their presence (Dolby & Grubb 1998, Moynihan 1962, Winterbottom 1943). Species are considered nuclear if they are found in a high percentage of flocks, are rarely found outside of flocks, and lead flocks, being joined by other species more than they follow other birds (Hutto 1994, Moynihan 1962).

Two types of nuclear species have been observed. The first type includes intraspecifically gregarious species, such as tits (family Paridae) in temperate regions (Morse 1970), or babblers (family Timaliidae) in Asia (Kotagama & Goodale 2004). The second type includes those species not particularly gregarious but highly sensitive to the presence of predators, and hence called ‘sentinel’ species (Greig-Smith 1981, Munn 1984). This sensitivity to predators may be related to foraging technique: in the tropics, sentinel species usually capture insects in the air (by ‘sallying’), and their visual scanning for prey may allow them to see predators more quickly than species that search for food off of the substrate (by ‘gleaning’; Goodale & Kotagama 2005, Munn 1984). These two types of nuclear species are both found in a flock system of a Sri Lankan rain forest: orange-billed babblers (*Turdoides rufescens* Blyth) are highly gregarious leaf-gleaners, whereas the sallying greater racket-tailed drongos (*Dicrurus paradiseus* Linnaeus, family Dicruridae) are less gregarious but more sensitive and reliable alarm-callers (Table 1). Babblers and drongos tend to be closely associated in the front of flocks, making it difficult to

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Table 1. Behavioural characteristics of the orange-billed babbler, the greater racket-tailed drongo and the yellow-fronted barbet. Data on flock composition and organization (rows 1–5) from Kotagama & Goodale (2004); data on alarm calling (rows 6–7) from Goodale & Kotagama (2005).

	Babber	Drongo	Barbet
1. Percentage of flocks (n = 476)	92	89	48
2. Propensity to flock (% individuals seen in flocks)	92 (n = 2440)	92 (n = 395)	68 (n = 157)
3. Individuals per flock	16.2 (n = 268)	2.7 (n = 316)	2.0 (n = 181)
4. Crossings led (n = 83 road crossings) ¹	54	9	1
5. Crossing score ²	0.44	0.49	0.76
6. Alarm calls to predators ³	7	9	0
7. 'False' alarm calls to non-predators ⁴	19	5	0

¹ Both babblers and drongos led more crossings than would be expected randomly based on their numbers of individuals per flock.

² The average position of a bird in a road crossing (first, second, third, etc.) divided by the total number of birds that crossed (scores averaged first within a crossing, then among crossings). The crossing scores of babblers and drongos were not significantly different, but they were both significantly lower than the scores of barbets.

³ Number of alarm calls made to a raptor during 10 h of recordings of flocks and five opportunistically recorded hawk attacks.

⁴ Number of alarm calls in the same sample made to large or fast-flying non-predators.

determine from observational data with which species other flock participants prefer to associate.

Few data have been collected to determine why nuclear species are attractive to other species. Two (non-mutually exclusive) hypotheses are possible: first, nuclear species may be good indications of a flock and their active movements and vocalizations may make them easy to follow (Hutto 1994, Moynihan 1962). Second, behaviour of nuclear species may directly benefit adherent species. Sentinel species may increase other species' awareness of predators, a benefit likely to outweigh the costs of their occasional stealing of food ('kleptoparasitism'; Munn 1986). The large numbers of individuals of gregarious species may dilute the risk of predation (Terborgh 1990), and they may give warning to nearby kin or mates of predator attacks, which other species can overhear (Gaddis 1980, Sullivan 1984). In contrast to sentinel species, gregarious nuclear species can also positively affect the foraging efficiency of other flock participants. They may disturb insects as the flock moves through the forest ('beating', Hino 1998, Swynnerton 1915), or serve as models for other species to copy foraging locations or techniques ('social learning', Krebs 1973). Thus, species in the Sri Lankan flock system could obtain more foraging benefits from babblers than from drongos, which are interspecifically aggressive and kleptoparasitic (Hino 1998, King & Rappole 2001).

To test whether Sri Lankan birds outside of flocks were attracted more to babbler or drongo vocalizations, we performed a playback experiment, comparing them to the vocalizations of the non-nuclear, frugivorous yellow-fronted barbet (*Megalaima flavifrons* Cuvier, family Capitonidae). Barbets are less frequent in flocks and less exclusive to them, and are usually in the back of flocks as they follow other species (see Table 1). We prepared random samples of all three species' vocalizations and

hypothesized that flock participants would be more attracted to the vocalizations of babblers and drongos because they are both good indications of a flock. We also hypothesized that insectivores increase their foraging from associating with the babblers, and would thus be most attracted to babbler vocalizations. In contrast, we hypothesized that species that eat a significant amount of fruit ('omnivores and frugivores') would respond evenly to babblers and drongos.

STUDY SITE AND SPECIES

The study was conducted in the Sinharaja World Heritage Reserve (6°21'N, 80°21'E), located in the humid south-west lowlands of Sri Lanka. The vegetation within the reserve is broadly classified as evergreen, dipterocarp rain forest (Gunatilleke & Gunatilleke 1981). The north-western sector of the reserve in which we worked was selectively logged in the late 1970s (de Zoysa & Raheem 1987). Open areas remain at some major junctions of logging roads or in areas prone to landslides; otherwise the vegetation is dense and the canopy continuous.

The mixed-species bird flocks at the study site average 11 species and more than 40 individuals (Kotagama & Goodale 2004). Species names follow Grimmett *et al.* (1999).

METHODS

Recording of vocalizations and construction of playback exemplars

Between June and August 2000, we made 25 h of recordings, encountering flocks while walking a 15-km circuit of roads inside the reserve. Recordings were

Table 2. Vocal characteristics in flocks of the orange-billed babbler, the greater racket-tailed drongo and the yellow-fronted barbet, and descriptions of the vocalizations represented on the playback exemplars.

	Babbler	Drongo	Barbet
Frequency of vocalizations in flocks (n = 263 15-s segments) ¹	88%	27%	22%
Types of non-alarm vocalizations included in exemplars	'Babble' (contact call) 'Regular chatter' (group assembly)	Song sung individually or in chorus	Trilled song
Types of alarm vocalizations included in exemplars	'Cuk' (aerial alarm) 'Stacatto chatter' (given to ground predators)	High-pitched notes	No alarm call
Percentage of 20 exemplars that included alarm vocalizations (percentage of notes in such exemplars that were alarm type)	20% (9%)	60% (70%)	0% (n/a)

¹ Percentage of tape segments sampled in which species could be heard in the foreground. Segments chosen to sample recordings of different flocks throughout the recording area.

made with an audiocassette recorder (Marantz PMD 222, Marantz America, Itasca, IL, USA), an omnidirectional microphone (Sennheiser ME 62, Sennheiser Electronic Corp., Old Lyme, CT, USA) and a parabolic dish (Telenga universal mount, Telenga Microphones, Tobo, Sweden). In listening to these recordings we found all segments of 1 min or more in which one of the three species of interest was in the foreground of the tape with a high signal-to-noise ratio. The species differed in the amount of vocalizations they made in flocks: babblers were almost always making their contact calls, whereas drongos and barbets vocalized less frequently (Table 2).

We then randomly selected segments to make 20 playback tapes ('exemplars') for each species. Random selection resulted in one complication: the species differed in the amount of alarm vocalizations represented in the exemplars (Table 2; for further descriptions of alarm vocalizations see Goodale & Kotagama 2005). Barbets are not known to make alarm calls, and babblers had only a few alarm calls included on the exemplars. In contrast, a large proportion of the drongo vocalizations were of alarm type, although enough (8) drongo exemplars did not include alarm vocalizations that we could determine whether the inclusion of alarms affected response (see below).

Each exemplar consisted of a 1-min natural recording repeated 10 times to make a 10-min playback tape. To edit out the vocalizations of other species, we used the digital filter of the sound analysis package Avisoft (Version 3.9, Avisoft Bioacoustics, Berlin, Germany). After construction of the tapes, we used a sound level meter (RadioShack 33-4050, RadioShack Corp., Fort Worth, TX, USA) to measure their amplitude and adjusted the volume of the playback speakers (SME-AFS, Mineroff Electronics, Elmont, NY, USA) so that the tapes were all played at the same volume, a peak amplitude of 76 dB, measured 5 m from the speaker in the direction it was pointed (the three species are roughly similar in the natural amplitude of their calls).

Treatments and trial protocol

To simulate a flock, we broadcast two playback tapes simultaneously. There were six treatments consisting of the possible intraspecific and heterospecific combinations of the three species, and a seventh treatment of silence. In preliminary trials, we tested some non-avian sounds (high-pitched crickets and low-pitched frogs), but there was less response to these trials (two birds approaching within 15 m of the speaker in 10 trials) than to silence (four responses in 10 trials), thus demonstrating that the playback of natural sounds alone does not attract birds to the speaker.

Between June and August 2002, we conducted playback trials from 07h00 to 16h00 daily at 20 playback sites near the Sinharaja Field Research Station, averaging four trials per day. Sites were selected to be 250 m from each other, and it is highly likely that the pool of potential respondents at one site was different from the pools at other sites, based on our experience counting birds from line transects. As variation in response was due to both diurnal factors (greatest response in early morning) and some differences between sites (sites in gaps had more visible response), we decided to minimize the within-site variation by visiting each site at a particular time of day.

Trials at a particular site were performed in random order, every other day, until all seven treatments had been conducted there. To avoid pseudoreplication (Kroodsma 1989), exemplars were not played more than once per treatment (e.g. tape 1 of species A was combined with the vocalizations of species B in only one trial), except in the intraspecific treatments (where each tape was used twice, each time in combination with a different tape of the same species). Nor were exemplars played more than once at a particular site.

At a site, two speakers were placed 3 m apart on either side of the road, and two observers were located approximately 20 m from each other on either side of the axis between the two speakers. Importantly, trials were

not started if a flock could be heard from the playback site (should a flock approach the playback site it would be impossible to know whether species were following the flock or reacting to the playback). During playback the observers noted any species they heard or saw approach within 15 m of the speaker. The entire trial was tape-recorded, using the recording equipment described above.

Statistical analysis

The response variable was the number of species that approached the speaker during the playback period, not including the species whose vocalizations were played (referred to hereafter as 'heterospecific attraction'). We conducted analysis separately for insectivores and for omnivores/frugivores. Diets were classified by a literature search (Ali & Ripley 1987, Grimmett *et al.* 1999, Henry 1971, Legge 1880).

In comparing treatments, we used a simple frequency table, conducting Fisher's exact test on the 7×2 table that summarized the number of trials in each treatment in which there was at least one heterospecific response and the number of trials in which there was no response. This approach avoids the problems encountered when running Friedman's test on data with many non-responses (F. J. Rohlf, *pers. comm.*). The frequency table approach does lose information on the location of the trial in the original blocked design; however, the relative response among the treatments was consistent among the locations (see below). To compare between treatments, we subsequently performed Fisher's exact test on all treatment pairs, correcting the α level by the Dunn-Sidak method (Sokal & Rohlf 1995).

We also investigated which species were attracted to playback. In this analysis we did count multiple responses per trial, provided that the bird (1) did not directly follow another bird's movement within 1 min and (2) did not arrive near the speaker within 1 min of another bird actively vocalizing in the playback arena. We then asked whether those species that responded most to babbler and/or drongo vocalizations were species with high propensity to flock, with propensity to flock defined as the percentage of individuals of that species seen in flocks (Thiollay & Jullien 1998), and with the data on propensity taken from Kotagama & Goodale (2004, and unpubl. data for two species). To measure a species' attraction towards babbler and drongo vocalizations, we divided the number of responses in treatments that included these two species by the number of responses during the entire experiment (we refer to this ratio as the 'specificity to babbler and drongo vocalizations'). We used simple linear regression to test whether species' specificity to babbler and drongo vocalizations was related to their propensity to flock.

Lastly, we tested whether exemplars that included alarm calls differed in response from those that did not, using Fisher's exact tests as above.

RESULTS

Heterospecific attraction: effects of playback treatments

The majority of responses to playback were by heterospecific birds. Excluding the three species modelled in the playback, 23 species responded to playback (a total of 87 responses), including nine insectivores, 13 omnivores or frugivores, and one *Accipiter* hawk (Table 3). The modelled species responded 26 times during trials that included their vocalizations, and five times when they were considered heterospecifics.

As hypothesized, more heterospecific birds were attracted to the vocalizations of the nuclear species, the babbler and the drongo, than to the adherent species, the barbet, or to silence. The pattern was shown most strongly by insectivorous birds (Fisher's exact test for all treatments, $n = 140$, one-tailed $P < 0.002$; Figure 1a), which included four fly-catching species and seven gleaning or probing species. Insectivorous species were attracted significantly more to the babbler/drongo treatment than to the barbet/barbet treatment (Fisher's exact test, $n = 40$, Dunn-Sidak corrected two-tailed $P < 0.05$), or to silence (Fisher's Exact Test, $n = 40$, Dunn-Sidak corrected two-tailed $P < 0.01$). Results were consistent among locations, as the babbler/drongo treatment received the most response in 10 of the 20 locations. However, heterospecific omnivores and frugivores were not strongly affected by playback (Fisher's exact test for all treatments, $n = 140$, one-tailed $P > 0.70$), responding almost as much to the barbet/barbet treatment as to those treatments with babbler or drongo vocalizations (Figure 1b).

The attraction of birds towards the speaker during playback of babbler and drongo vocalizations was more than momentary, as shown by some birds staying close to the speaker and by flock formation after playback. In 23 trials heterospecific birds stayed within 15 m of the speaker for at least 5 min. This occurred mostly during the babbler/drongo treatment (6 trials), the babbler/babbler treatment (5 trials) and the drongo/drongo treatment (5 trials). In eight trials a new flock had formed within 15 m of the speaker by the end of the playback period.

Babbler and drongo vocalizations were similarly attractive to other species. Rather than preferring the babbler vocalizations as hypothesized, insectivores responded almost as much to drongo vocalizations as to babbler vocalizations; omnivores and frugivores also showed little difference in their response to the two species (see Figure 1).

Table 3. The species that responded, and their response by treatment, in order of the total number of approaches towards the speaker. Abbreviations: B: orange-billed babbler; D: greater racket-tailed drongo; Y: yellow-fronted barbet; S: silence.

	Propensity to flock (%)	Trials per treatment in which species approached speaker						
		BD	BY	BB	DD	DY	YY	S
Heterospecific insectivores								
Black-naped monarch	67	7	1	2	2	2	0	1
<i>Hypothymis azurea</i> Boddaert								
Indian scimitar babbler	71	4	1	0	1	1	1	0
<i>Pomatorhinus horsfieldii</i> Sykes								
Dark-fronted babbler	35	1	3	0	1	0	1	0
<i>Rhopocichla atriceps</i> Jerdon								
Malabar trogon	96	1	2	2	0	1	0	0
<i>Harpactes fasciatus</i> Pennant								
Scarlet minivet	62	3	0	1	1	0	0	0
<i>Pericrocotus flammeus</i> Forster								
4 other species		0	0	1	3	1	0	0
Heterospecific omnivores and frugivores								
Yellow-browed bulbul	36	5	2	6	4	4	5	3
<i>Iole indica</i> Jerdon								
Pale-billed flowerpecker	28	3	2	1	0	3	2	0
<i>Dicaeum erythrorhynchos</i> Latham								
Sri Lanka blue magpie	31	1	2	0	0	0	1	0
<i>Urocissa ornata</i> Wagler								
Sri Lanka mynah	13	0	1	0	0	1	1	1
<i>Gracula ptilogenys</i> Blyth								
9 other species		4	5	1	3	1	1	1

Flocking propensity of respondents

The difference in response between insectivores and fruit-eating birds was also reflected in a positive relationship between a species' propensity to flock and its attraction to babbler and/or drongo vocalizations ($F_{1,7} = 17.0$, $P < 0.005$, $R^2 = 0.71$; Figure 2). Propensity was related to diet: the four species in the correlation analysis that had the highest propensities were insectivores, whereas the three species that had the lowest propensities were omnivores and frugivores.

Effects of alarm notes in exemplars

The attraction to drongo vocalizations did not depend on whether alarm notes were included in the playback exemplar or not. In two of the three treatments that included drongo vocalizations, exemplars without alarm calls were more attractive to insectivorous birds than exemplars with alarm calls. In none of the treatments was there any significant effect of the presence of alarm calls on response of insectivores (or other species; six Fisher's exact tests, each $n = 20$, all one-tailed $P > 0.25$). The

few babbler exemplars that included alarm notes likewise showed no consistent trend to be more or less attractive than other exemplars.

DISCUSSION

We found that birds outside of flocks in this Sri Lankan rain forest were attracted to heterospecific vocalizations, and that insectivorous species were particularly attracted to the playback of the nuclear species of the flock system, the babbler and the drongo. The difference in response between insectivorous and fruit-eating birds, which did not show a preference for any of the playback treatments, was related to insectivores having a higher propensity to flock than other species (Kotagama & Goodale 2004). All species responded equally to babbler as compared to drongo vocalizations. The response to playback did not depend upon whether the exemplar had alarm calls or not, indicating that the simulation of the species, and not merely the playback of alarm calls, was attractive to other birds.

Heterospecific response to playback was low (≤ 1.5 species per trial in all treatments) in part because response

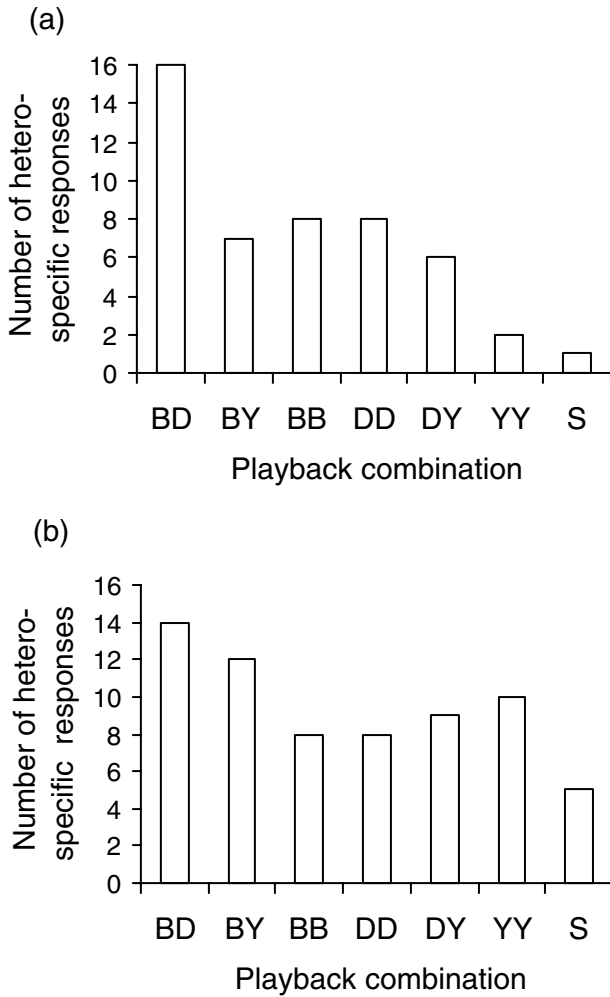


Figure 1. Response to playback, broken down by the diet of the responding species: (a) insectivores, (b) omnivores and frugivores.

was constrained by our conservative experimental design and analysis. We conducted playback trials only if a flock was not present in an area because when flocks were present it was unclear which species were responding to playback and which were simply following the flock. Conducting playback outside of flocks, however, greatly limited the number of birds that were available to respond. In previous studies we have found that more than half of the common species in this forest spend more time in flocks than outside of them and those species with very high propensities to flock (which would be expected to respond most strongly) are by definition rare outside of flocks. We also applied conservative rules in analysing the data to ensure that multiple responses within a trial were independent of each other (in total there were 157 responses, of which 115 were judged to be independent). Finally, our statistical analysis had low power due to the combination of non-parametric statistics

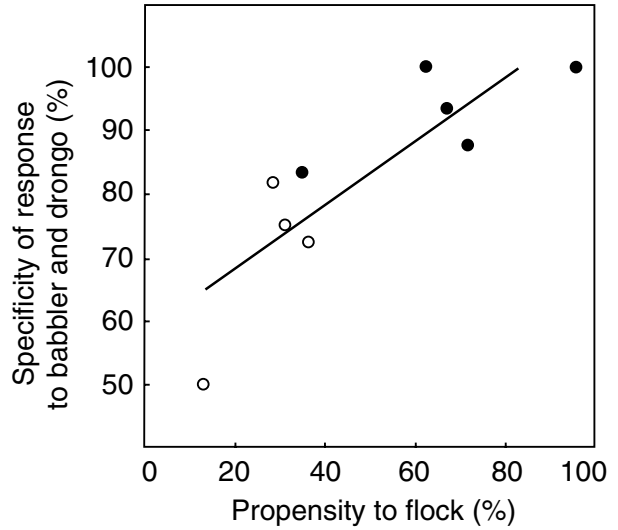


Figure 2. The relationship between species' propensity to flock (P), and their specificity to babler and drongo vocalizations (S; $P = 0.50S + 58$). Filled circles: insectivores; open circles: omnivores and frugivores. Nine species that responded at least four times were included in the regression (no species approached three times, and 17 species responded once or twice).

and the multiple comparisons necessary when dealing with seven treatments.

Despite these constraints, it is clear that attraction to heterospecific vocalizations is an important proximate mechanism by which birds locate flocks in this Sri Lankan rain forest. Although we demonstrated some flock formation after playback, flock formation is naturally complete by 07h30. Heterospecific attraction remains important throughout the day, however, because flocks move like waves through the forest, picking up territorial species when moving through their territories (Kotagama & Goodale 2004; see also Jullien & Thiollay 1998, Munn & Terborgh 1979 for similar observations). Indeed, the species that responded most to playback – the yellow-browed bulbul (*Iole indica* Jerdon, 29 responses), the black-naped monarch (*Hypothymis azurea* Boddaert, 15 responses), and the pale-billed flowerpecker (*Dicaeum erythrorhynchos* Latham, 11 responses) – are all species that defend small territories in disturbed patches near the logging roads. Our results are thus consistent with other studies that have shown animals use heterospecific vocalizations to locate flocks, shown by Mönkkönen *et al.* (1996) for mixed bird flocks of the temperate zone and Windfelder (2001) for mixed tropical primate troops.

As hypothesized, species with a high propensity to flock approached preferentially the vocalizations of the two species that had nuclear characteristics, the babler and the drongo, rather than the barbet or silence. The reaction towards the babler is not surprising, as babblers are continuously vocal in flocks and an immediate cue that a

flock is present. Babblers can be seen in the early morning in monospecific flocks, which if watched for long enough are inevitably joined by other species. The reaction to drongos, however, was higher than expected. Drongos are a good indication of a flock since they are rarely found outside of them; however, they are not continuously vocal like the babblers (see Table 2), and they are known to be kleptoparasitic in other flock systems (King & Rappole 2001). Our results indicate that other species will form flocks around drongos when drongos vocalize outside of flocks. Indeed, in four of the eight flocks formed after playback, a drongo was present, while babblers were not. In on-going studies, we have indeed found that drongos outside of babbler-led flocks are almost always found with other species. These flocks without babblers may be more common than we had previously thought, since they are relatively quiet and difficult to detect.

We are not able to deduce why birds are attracted towards nuclear species from our results. We had predicted that insectivores, especially fly-catching ones, would prefer babbler vocalizations over those of drongos, since they may be able to increase their foraging in association with babblers. We did not find such a preference, however. Instead, we see two possible explanations for the results: (1) both species are good indications of flocks since they so rarely occur outside of flocks, or (2) the two species both give benefits to species that associate with them, benefits most likely related to anti-predation (while babblers' alarm calls may not be as reliable as drongos, their large numbers reduce other species' risk). Both these explanations can explain the high attraction to the combined treatment because flocks with both species tend to be larger and benefits could be additive. Although we cannot distinguish between these two hypotheses, we can make one conclusion that was to us rather unexpected: a sentinel species can be as attractive to flock participants outside of flocks as a highly gregarious species.

The results of this study demonstrate that playback can be a useful technique to understand the roles of species in flocks (see Mönkkönen *et al.* 1996 for a study of a single nuclear species, and Munn 1986 and Sullivan 1984 for other uses of playback in studying mixed-species flocks). We hope that further studies can distinguish between whether nuclear species are attractive to other species because they are good indications of flocks or because of the benefits they confer on other species; such a study will need to use the vocalizations of an adherent species that is as frequent in flocks as a nuclear species, but is neither gregarious nor alarm-calling. It should also be emphasized that the study of nuclear species is not merely a theoretical problem: nuclear species also have an applied significance as they contribute to flock cohesion, and one of the first manifestations of tropical forest fragmentation is loss of mixed-species flocks along with the obligate

flocking species that attend them (Stouffer & Bierregaard 1995, Thiollay 1992).

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LITERATURE CITED

- ALI, S. & RIPLEY, S. D. 1987. *Compact handbook of the birds of India and Pakistan, together with those of Bangladesh, Nepal, Bhutan and Sri Lanka*. (Second edition). Oxford University Press, New Delhi. 737 pp.
- DE ZOYSA, N. & RAHEEM, R. 1987. *Sinharaja, a rain forest in Sri Lanka*. March for Conservation, Colombo. 61 pp.
- DOLBY, A. S. & GRUBB, T. C. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. *Animal Behaviour* 56:501–509.
- GADDIS, P. 1980. Mixed flocks, accipiters, and antipredator behavior. *Condor* 82:348–349.
- GOODALE, E. & KOTAGAMA, S. W. 2005. Alarm calling in Sri Lankan mixed-species bird flocks. *Auk* 122:108–120.
- GREIG-SMITH, P. W. 1981. The role of alarm responses in the formation of mixed-species flocks of heathland birds. *Behavioral Ecology and Sociobiology* 8:7–10.
- GRIMMETT, R., INSKIPP, C. & INSKIPP, T. 1999. *A guide to the birds of India, Pakistan, Bangladesh, Bhutan, Sri Lanka and the Maldives*. Princeton University Press, Princeton. 888 pp.
- GUNATILLEKE, C. V. S. & GUNATILLEKE, I. A. U. N. 1981. The floristic composition of Sinharaja – a rain forest in Sri Lanka with special reference to endemics and dipterocarps. *Malaysian Forester* 44:386–396.
- HENRY, G. M. 1971. *A guide to the birds of Ceylon*. (Second edition). Oxford University Press, Oxford. 457 pp.
- HINO, T. 1998. Mutualistic and commensal organization of avian mixed-species foraging flocks in a forest of western Madagascar. *Journal of Avian Biology* 29:17–24.

- HUTTO, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in Western Mexico. *Condor* 96:105–118.
- JULLIEN, M. & THIOLLAY, J.-M. 1998. Multi-species territoriality and dynamics of neotropical forest understorey bird flocks. *Journal of Animal Ecology* 67:227–252.
- KING, D. I. & RAPPOLE, J. H. 2001. Kleptoparasitism of Laughingthrushes by Greater Racket-tailed Drongos in Burma (Myanmar). *Forktail* 17:121–122.
- KOTAGAMA, S. W. & GOODALE, E. 2004. The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. *Forktail* 20:55–62.
- KREBS, J. R. 1973. Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). *Canadian Journal of Zoology* 51:1275–1288.
- KROODSMA, D. E. 1989. Suggested experimental designs for song playbacks. *Animal Behaviour* 37:600–609.
- LEGGE, W. V. 1880. *A history of the birds of Ceylon*. Self-published, London. 1624 pp.
- MÖNKKÖNEN, M., FORSMAN, J. T. & HELLE, P. 1996. Mixed-species foraging aggregations and heterospecific attraction in boreal bird communities. *Oikos* 77:127–136.
- MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecological Monographs* 40:119–168.
- MOYNIHAN, M. 1962. The organization and probable evolution of some mixed-species flocks of Neotropical birds. *Smithsonian Miscellaneous Collections* 143:1–140.
- MUNN, C. A. 1984. *The behavioral ecology of mixed-species bird flocks in Amazonian Peru*. Ph.D. thesis, Princeton University, Princeton. 160 pp.
- MUNN, C. A. 1986. Birds that 'cry wolf'. *Nature* 391:143–145.
- MUNN, C. A. & TERBORGH, J. W. 1979. Multi-species territoriality in Neotropical foraging flocks. *Condor* 81:338–347.
- POWELL, G. V. N. 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. *Ornithological Monographs* 36:713–732.
- SOKAL, R. R. & ROHLF, F. J. 1995. *Biometry: the principles and practice of statistics in biological research*. (Second edition). W. H. Freeman & Co., New York. 887 pp.
- STOUFFER, P. C. & BIERREGAARD, R. O. 1995. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76:2429–2445.
- SULLIVAN, K. A. 1984. Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour* 91:294–311.
- SWYNNERTON, C. F. M. 1915. Mixed bird parties. *Ibis* 67:346–354.
- TERBORGH, J. 1990. Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *American Journal of Primatology* 21:87–100.
- THIOLLAY, J.-M. 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. *Conservation Biology* 6:47–60.
- THIOLLAY, J.-M. 1999. Frequency of mixed-species flocking in tropical forest birds and correlates of predation risk: an intertropical comparison. *Journal of Avian Biology* 30:282–294.
- THIOLLAY, J.-M. & JULLIEN, M. 1998. Flocking behaviour of foraging birds in a neotropical rain forest and the antipredator defence hypothesis. *Ibis* 140:382–394.
- WINDFELDER, T. L. 2001. Interspecific communication in mixed-species groups of tamarins: evidence from playback experiments. *Animal Behaviour* 61:1193–1201.
- WINTERBOTTOM, J. M. 1943. On woodland bird parties in Northern Rhodesia. *Ibis* 85:437–442.