

Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest

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The flow of information about predators in mixed-species groups is likely to influence the structure and organization of these communities. To map this flow, it is necessary to demonstrate in a playback experiment that animals use the information provided in heterospecific calls. We investigated the response of birds to conspecific and heterospecific calls in a mixed-species flock system of a Sri Lankan rainforest. We played back the aerial alarm calls of the species that produce the most alarms, the Orange-billed Babbler (*Turdoides rufescens*) and the Greater Racket-tailed Drongo (*Dicrurus paradiseus*), as well as natural choruses of alarm calls of several species, to 4 species of birds. We found that babblers moved quickly away from the playback speaker after hearing either babbler or drongo alarm calls. Ashy-headed Laughingthrushes (*Garrulax cinereifrons*) responded similarly to drongo alarm calls. Response by other species was less clear: Malabar Trogons (*Harporhynchus fasciatus*) stayed perched for longer during alarms of several species; drongos showed no difference in response to any treatment. We conclude that birds are listening to heterospecifics and suggest that their response is influenced by several factors, including their foraging technique. The fact that the babbler, the gregarious leading species of the flocks, gains information from another species is one of the first indications that such a “nuclear” species can benefit from its participation in mixed-species flocks, and the response of at least 2 species to drongo alarms emphasizes the importance sentinel species such as drongos may play in flock communities. *Key words*: alarm calls, alarm response, interspecific communication, mixed-species flocks, playback experiments, Sri Lanka. [*Behav Ecol* 19:887–894 (2008)]

Mixed-species groups are a prominent type of social organization in mammals (Terborgh 1990; Stensland et al. 2003) and especially in birds (Morse 1977; Greenberg 2000). The evidence continues to mount that these groups are in large part adaptations that reduce the risk of predation (Thiollay and Jullien 1998; Thiollay 1999), similar to single-species groups (Elgar 1989; Beauchamp 2004). One important component of predator vigilance in mixed groups is vocal alarm calls; birds in mixed-species flocks have been shown repeatedly to listen to other species’ aerial alarm calls (Munn 1984; Sullivan 1984). Generally, the pattern of information flow that has been described is asymmetric: the species that make alarm calls serve as core or “nuclear” species for the flocks, and other species do not make alarm calls but follow the nuclear species and respond to its calls (Gaddis 1980; Greig-Smith 1981; Sullivan 1985; Munn 1986; Ragusa-Netto 2002). Previously, we described an apparently more mutualistic system in the rainforests of Sri Lanka, where several species make aerial alarm calls (Goodale and Kotagama 2005a). These species differ in the information about predators encoded in their alarm calls, specifically in their reliability, the percentage of alarms which are made to actual threats (Koops 2004) and sensitivity, the percentage of threats detected. Thus, we suggested that an advantage of mixed-species flocking, as opposed to single-species flocking, is that the combination of different species’ alarm calls produces a greater overall amount of information about predators.

To investigate whether a system in which several species alarm call is indeed a mutualism, it is important to demonstrate that the species respond to each other. Observations of species being startled in the field after alarm calls are not sufficient to verify interspecific communication because birds could have seen the stimulus that elicited the alarm call or could be reacting to the movements of other birds (e.g., Lima 1995), rather than responding to vocal alarm calls. The effect of the vocalization can be isolated, however, in a playback experiment, like those performed by Munn (1986), although it should be noted that playback experiments cannot rule out the possibility that focal birds are responding to nonfocal birds which were themselves affected by the playback (see Discussion). A recent playback study (Magrath et al. 2007) demonstrated that there are situations in which birds of different species respond mutually to each other’s alarm calls. The 2 species of Australian passerines studied were not in mixed-species flocks, however, at the time of the experiment (although they do apparently co-occur in wintering mixed-species flocks). Similar studies are needed to determine whether vocal information about predators can flow mutualistically in mixed-species flocks or whether information flow in these communities is always as asymmetric as the older literature on mixed-species flocks suggests.

In the present study, our objective was to map the flow of information in the Sri Lankan flock system and determine whether species are responding to each other in a mutualistic manner. We had 2 hypotheses. First, we hypothesized that the Orange-billed Babbler (*Turdoides rufescens*) and the Greater Racket-tailed Drongo (*Dicrurus paradiseus*), the 2 species that produce alarm calls most frequently, would respond to each other’s aerial alarm calls and that some other flocking species like the Malabar Trogon (*Harporhynchus fasciatus*), which do not

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themselves alarm call, would also respond to the alarm calls of these 2 species. Second, we hypothesized that birds would respond more strongly to the calls of the drongo because the drongo's calls are more reliable, that is, more often associated with an actual alarm event, than the calls of the babbler (Goodale and Kotagama 2005a).

One further issue that we investigated was the influence of the acoustic characteristics of the alarm calls on the responses to them. The connection between the acoustic structure of alarm calls and their function has been well established since the work of Marler (1955), with most aerial alarm calls being of high-frequency and low-frequency bandwidth and thus difficult to localize (Klump and Shalter 1984). For this reason, the alarm calls of species are convergent, and birds in some mixed-species flock systems may have converged further to facilitate communication (Ficken 2000). Thus, for studies such as Magrath et al. (2007), in which the alarm calls of the 2 species studied were very similar to each other (although statistically distinguishable), the question arises whether birds are responding to any alarm call similar to their own. Likewise, when species' alarms do vary, the question becomes whether differences in responses to different species' alarms are a result of birds responding to the acoustic differences among the species. We therefore investigated the effects of the acoustic characteristics (peak frequency, frequency bandwidth, and frequency modulation) of the playback stimuli on response, focusing particularly on whether such variables could explain variation in responses in trials of one treatment class (e.g., the effect of peak frequency on responses to drongo alarm calls).

MATERIALS AND METHODS

Study system

The study was conducted in the Sinharaja World Heritage Reserve (6°21'N, 80°21'E), a lowland rainforest in Sri Lanka. The mixed-species flocks of this forest are large and complex, averaging 11 species and 41 individuals (Kotagama and Goodale 2004). The flocks are cohesive (although some territorial species enter the flock upon it coming into their territory and then drop out later), with most birds foraging actively within a 20 by 20 m area that moves steadily through the forest.

Playback tapes

The aerial alarm calls used here were recorded in a previous study, elicited by throwing a stick to one side of flocks (Goodale and Kotagama 2005a). We selected for playback the calls of the species which called most in response to this stimulus, the Orange-billed Babbler (which called in 35 of 73 trials) and the Greater Racket-tailed Drongo (which called in 21 of 73 trials), which are also the most frequent species in flocks (both are found in ca., 90% of flocks, although they differ in the numbers of individuals per flock—16 for babblers and 3 for drongos). Calls made in response to the thrown stick were similar to calls made in response to actual predators, in that the same call types were used, although they were of lesser duration (Goodale and Kotagama 2005a). Response to the prompted calls was similar to the response to calls made during real hawk attacks, used in later experiments (see below).

Sample spectrograms of the playback tapes are presented in Figure 1; acoustic characteristics of the calls are presented in Table 1 and in Results. As a control, we used the territorial song of the Yellow-fronted Barbet (*Megalaima flavifrons*), a species found in 48% of flocks. The barbet song is a series of simple notes, sometimes starting in a rapid trill, which is similar in amplitude to the alarm calls of babbler and drongos.

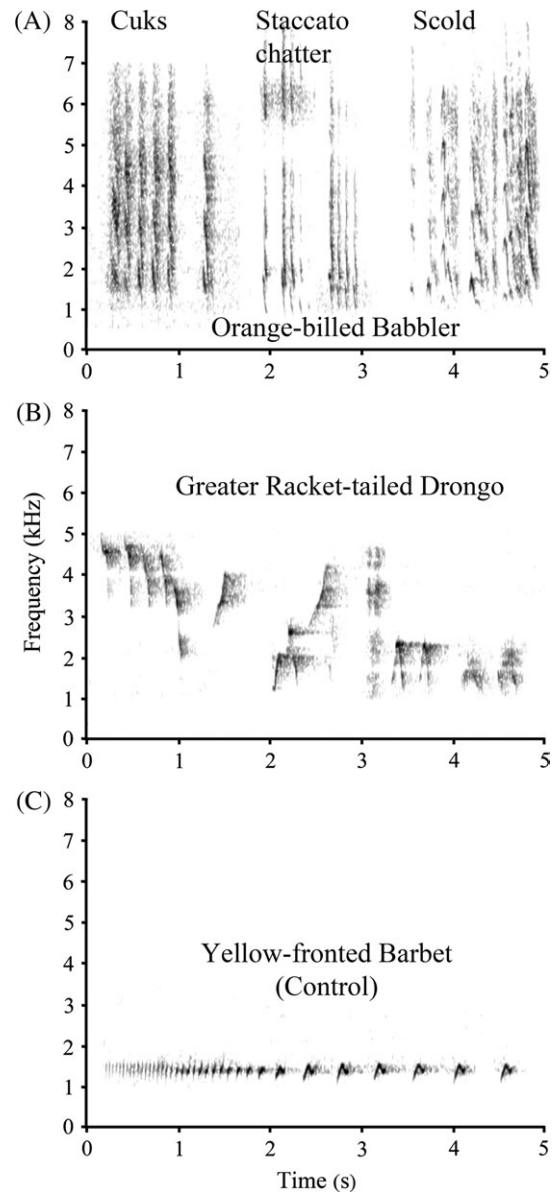


Figure 1

Sample spectrograms of call types that were included in the playback tapes. (A) The alarm calls of the Orange-billed Babbler; (B) the alarm calls of the Greater Racket-tailed Drongo; and (C) the nonalarm calls of the Yellow-fronted Barbet (control).

The alarm calls always started with a call type specific to encounters with aerial predators: a short “cuk” note for the babbler or a high-pitched (>4 kHz) note for the drongo. Some notes toward the end of the alarm calls have some acoustic qualities more similar to mobbing calls than aerial alarm calls (Marler 1955): later drongo notes are often of wide frequency bandwidth and the end of 5 exemplars of babbler calls included “staccato chatter” or “scold” notes usually used in mobbing ground predators (Goodale E, unpublished data). We have suggested previously (Goodale and Kotagama 2005a) that this change over time in the alarm calls of these species is correlated with a change over time in the risk of a hawk attack: risk is high when the hawk is first detected but is lower once the hawk has flown through the flock. Because hawks often return to make another sortie, it is important for birds to signal the predator's presence, and thus, the calls at

Table 1

Although the amplitude and the duration of the different treatment types were controlled to be similar, they varied in other acoustic characteristics

Treatment type	Peak frequency (Hz)	Frequency bandwidth (Hz)	Frequency modulation ^a (Hz)
Babbler alarms	2898 ± 1342	4516 ± 757	363 ± 211
Drongo alarms	3790 ± 970	1572 ± 832	638 ± 416
Barbet control	1462 ± 243	412 ± 251	119 ± 68

Means are shown ± standard deviations.

^aFrequency modulation was defined independently of time as the difference in frequency of the beginning and ending of a note.

the ends of these alarms are designed to draw attention in the same way as mobbing calls. In the case of the elicited calls, later calls may also draw attention to the presence of the observers.

We constructed 15 playback exemplars for each of the 3 treatments using the sound analysis program Avisoft (Version 3.9, Avisoft Bioacoustics, Berlin, Germany). Each exemplar started with 15 s of baseline flock activity, composed of contact calls. Then the alarm call, and the natural vocalizations that followed the alarm call (usually subdued contact calls), was played for 30 s (e.g., if the alarm call was 5 s long, it would be followed by 25 s by the vocalizations of the flock after the alarm call). Although the species differed in the duration of their alarm calls (Goodale and Kotagama 2005a), we chose all the long babbler calls so that duration of the babbler calls (range 0.1–30 s, mean 11.3 s) was not that different from the duration of drongo calls (range 0.2–30 s, mean 15.2 s). We artificially shortened the calls of the barbet so that they included calls ranging from 1 to 30 s (mean 13.1 s), comparable to the durations of the other treatments (the 3 treatments did not vary significantly in the duration of the alarm calls; $F_{2,42} = 0.47$, $P > 0.60$). After exemplars were transferred to tape, playback volume was controlled so that the average notes were ~80 dB and the maximum volume ~84 dB, as measured by a Realistic Sound Level Meter 5 m away from a directional speaker (Mineroff Electronics, Elmont, NY). Such a playback volume was judged by ear to be similar to the natural production of these calls.

Experimental protocol

We focused on the responses of 4 species: the babbler, the drongo, the trogon, and the Ashy-headed Laughingthrush (*Garrulax cinereifrons*). We selected these last 2 species in part because of their foraging techniques are similar to drongos and babblers, respectively, and foraging technique is likely to influence the escape behavior of birds (Lima 1993). Laughingthrushes are gregarious (7 individuals per flock) members of the babbler family *Timaliidae*; they forage by leaf gleaning, similar to Orange-billed Babblers, although they forage in the understory and on the ground, whereas babblers forage in the upper storey and subcanopy. Trogons sally for prey from perches, similar to drongos, and are likewise not gregarious (2 individuals per flock).

To conduct a playback trial, we first found a flock by walking through a 15-km circuit of old logging roads and footpaths. When we encountered a flock, 2 observers followed the flock off road, spreading approximately 10 m apart. We followed flocks for at least 15 min before starting a trial so that the birds habituated to our presence. When we were in position

close to the birds, we stopped moving and waited to be sure that the flock was foraging normally without making any alarm vocalizations.

We then selected a focal bird of one of the 4 species that was foraging approximately 10 m away from us and that was clearly visible with binoculars. Focal birds were in exposed positions on branches or on the ground. One of us watched the bird with binoculars while the other began to tape record the bird's baseline vocalizations using a Marantz PMD 222 audiocassette recorder and a Seinhesier ME 62 omnidirectional microphone in a Telinga parabolic dish. We recorded 15 s of background activity at which time the playback speaker (assembled by Mineroff Electronics, Elmont, NY) held in one observer's hand was turned on and the exemplar played. After the exemplar was finished, we continued to record for 15 s. We then wrote in a notebook the response of the bird—any jumping or flying movements, head turns greater than 90°, or alarm calls—paying particular attention to when the response was made relative to the start of the playback stimulus. We also noted whether movements were away from, or toward, the speaker. Due to the poor visibility in the thick vegetation and the relatively large area over which a flock is spread, a predator is likely to be close to where an alarm call is made, and thus, we expected birds to move away from the source of an alarm call.

Alarm behavior subsided quickly after a playback, rarely lasting more than a minute. We would then move again with the flock and would repeat the process after 15 min (in a study of natural alarms, we detected 3.6 alarms per hour, Goodale and Kotagama 2005a). We ensured that only one trial of a treatment–subject pair could be made per flock (hence a maximum of 12 playback experiments—3 treatments × 4 subjects—per flock). We were usually unable to conduct all 12 playback experiments on a single flock because of difficulties following the birds through thick vegetation, so we completed any remaining trials on a separate flock (we used 24 flocks in all). We used a different exemplar tape for each trial of a treatment–subject pair (Kroodma et al. 2001). We picked which subject to use opportunistically based on when birds were foraging undisturbed nearby, but we randomized the order of the treatments to the subjects. To ensure that trials were independent, we followed separate flocks in different areas of the 15-km circuit, so we believe it is highly unlikely that we recorded the response of an individual bird more than once. A bird would, however, have the opportunity to hear each treatment as many as 4 times, and for this reason, we investigated in the statistical analysis the effect of the order of the trial on the birds' response.

The playback experiment proved more difficult to carryout with some species than with others. Trogons in particular were difficult because they tended to move during the baseline period. Thus, sample sizes are different for the 4 species: 15 trials per treatment for babblers and drongos, 10–12 trials per treatment for laughingthrushes, 5–6 trials per treatment for trogons. In total, there were 140 trials.

Follow-up experiments

As some response was obtained to the control and responses of some species to the alarm calls were not clear, we performed a follow-up experiment, measuring response to silence and to what we expected would be an especially strong stimulus: the alarm calls of multiple species calling after actual hawk attacks. Playback numbers were limited by the number of hawk attack playback tapes, which were made from 5 good recordings. Each of the playback tapes of the hawk attacks included both babbler and drongo alarms; in addition, the alarms of Yellow-browed Bulbuls (*Iole indica*), Black-naped Monarchs (*Hypothymis azurea*), and Jungle Squirrels (*Funambulus* sp.) were included

on 2 exemplars each. To compare with the earlier experiment, the length of the multiple alarms was shortened to 30 s. For each of the 4 responding species, there were 5 trials of silence (no playback) and 5 trials of multiple alarms, for a total of 40 trials. In a final experiment, we repeated the same experiment comparing silence and multiple alarms, this time using 120-s sections of the same recordings of hawk attacks (the natural response to hawks was this long or longer). In presenting results of these later experiments, we average the results for the trials of 30-s alarm and the 120-s alarm that used the same recording to avoid pseudoreplication (Kroodsma et al. 2001).

Analysis of response

We analyzed 3 nonmutually exclusive categories of responses:

- 1) Immediate responses—head turns, jumps, or flights, usually away from the speaker, within 5 s of the start of the played-back alarm call or control. Because nonalarmed foraging birds would make some movements and head turns in any prolonged observation, we ignored such movements after 5 s (other cutoff points such as 2 s gave similar results; we chose 5 s because the first phrase of a drongo alarm can last this long).
- 2) Delayed movements toward the speaker, between 5 and 45 s after start of the alarm. Movements away from the speaker during this time were common due to the flocks' slow but continuous movement while foraging. Delayed movements toward the speaker were often associated with mobbing activity such as wing quivering, directed gaze, and the clumping of individuals of gregarious species; such movements invariably took at least 5 s to develop.
- 3) Aerial alarm calls, made within 45 s of the start of the alarm (for criteria by which vocalizations were classified as alarm calls, see Goodale and Kotagama 2005a). Alarm calls were exclusive to the alarm context, so we counted them at any time; some alarm calls may have been undetected because they were masked by the playback sounds.

Our statistical analyses focused on immediate responses because they were far more common than the other responses. We used binary logistic regression (0 = no response and 1 = response) to determine the factors that best predicted immediate response. Analyses were done separately for the different experiments. The overall model that was tested included the effects of the treatment, the species identity of the subject, and the order of the trial to a particular flock (first, second, third etc.). For experiments in which species responded differently to playback, we did analyses for each species' response separately; because order was not found to be a significant contributor to the overall model, it was not included in these further analyses. For analyses in which we made multiple tests to compare responses of the 4 different species to the 3 different treatments, we adjusted the *P* value by the Dunn-Šidák method (Sokal and Rohlf 1995).

Acoustical analysis

To determine how the acoustical characteristics of the playback tapes affected response, we made several acoustic measurements of each playback tape using Avisoft. Because we were most interested in what produced the common immediate responses, we randomly selected 3 notes within the first 5 s of the alarm. We measured the peak frequency (frequency of the highest amplitude) and the low and high frequencies (frequencies at which the amplitude is within 15 dB relative to the peak frequency, following an approach similar to Podos 2001) for the first and last 0.025 s of each note (a duration

that represents ~20% of the average note). From this information, we calculated: peak frequency (averaged over 6 measurements), frequency bandwidth (high – low frequency, averaged over 6 measurements), and frequency modulation (the absolute value of the peak frequency of the start of a note minus the peak frequency of the end of the note, averaged over 3 measurements).

We then investigated how these acoustic variables affected immediate response. Because each species was subjected to the same playback tapes, we conducted the analysis for each responding species separately. The analyses were conducted for all the trials that involved a responding species (e.g., laughingthrush responses) and then repeated for only those trials within a treatment type (e.g., laughingthrush responses to drongo alarms) to investigate whether acoustic variables explained variation within responses to a treatment. Again, when making multiple tests, we adjusted the *P* value by the Dunn-Šidák method.

RESULTS

Analysis of response

For the original 140-trial experiment, immediate response was significantly affected by both the playback treatment and the species identity of the subject but not by the order of the trial (Table 2). After adjusting for all other effects, drongo calls were more than 12 times more likely to elicit a response than the control sound; babbler calls were nearly 7 times more likely to elicit a response. There was no detectable difference when comparing the response to babbler versus drongo alarms. In the subsequent experiments, response to multiple alarms was clearly higher than response to silence (30-s trials, Wald $\chi^2_1 = 0.02$, $P < 0.005$, odds ratio 48.20; 120-s trials, Wald $\chi^2_1 = 10.01$, $P < 0.002$, odds ratio 32.49). Yet, the overall percentage of trials in which birds responded was no higher for multiple alarms than for babbler or drongo alarms alone (Figure 2).

The species that responded the most reliably to playback were the Orange-billed Babbler and the Ashy-headed Laughingthrush (see Figure 2). Individuals of these species occasionally made some flights or jumps within 5 s even during the silent treatments, and such movements increased slightly

Table 2

Results analyzed by a binomial logistic regression model that included the effects of playback treatment, the species identity of the subject, and the order of the trial

Factor	Comparison	χ^2_{a}	df	<i>P</i>	Odds ratio
Overall model		41.91	6	<0.001	
Playback treatment		23.92	2	<0.001	
	Drongo > control	19.72	1	<0.001	12.24
	Babbler > control	14.59	1	<0.001	6.95
	Drongo > babbler	1.00	1	0.317	1.76
Subject species		12.60	3	0.006	
	Drongo > trogon	10.63	1	0.001	12.03
	Drongo > ashy	7.19	1	0.007	5.20
	Drongo > babbler	7.04	1	0.008	4.80
	Babbler > trogon	1.78	1	0.183	2.51
	Babbler > ashy	0.02	1	0.880	1.08
	Ashy > trogon	1.40	1	0.237	2.31
Order of trial		0.90	1	0.343	

df, degrees of freedom.

^a The value for the overall model is a log-likelihood χ^2 ; all other values are Wald χ^2 .

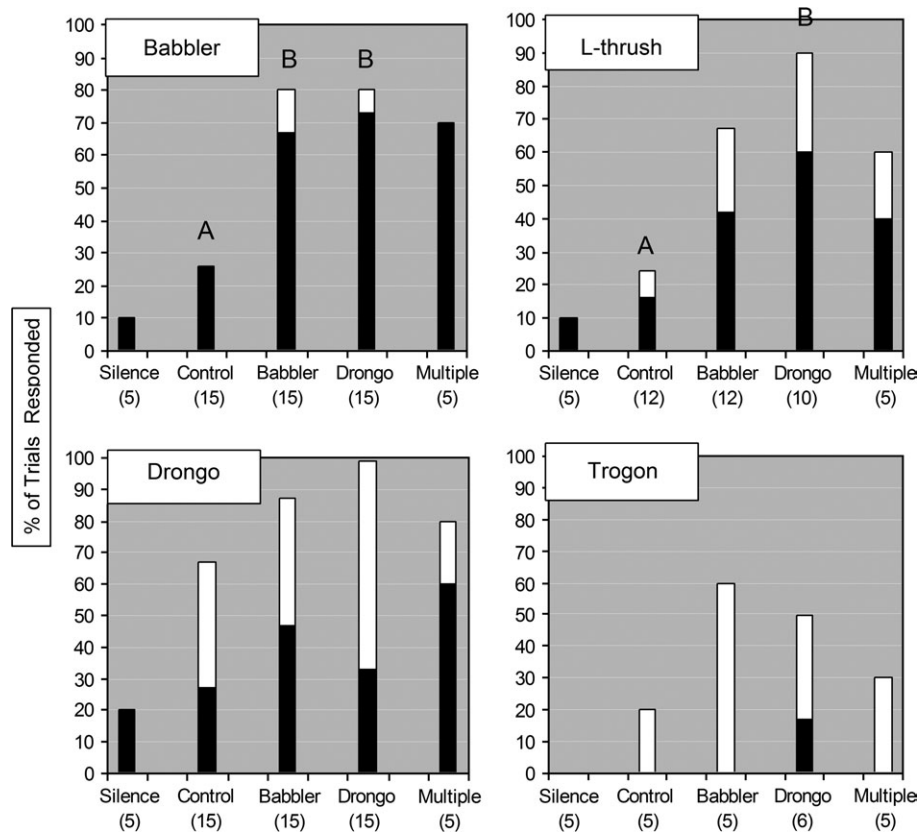


Figure 2 Response of 4 species to alarm calls and control sounds. Black bars represent flying or jumping movements by the focal bird within 5 s of the start of the alarm, and white bars represent head turns during this time without other movement. Bars with letters are statistically different from bars with different letters; statistics are based on total response (movement and head turns). Babblers responded to babbling and drongo alarm calls more than to control sounds, and laughingthrushes similarly responded to drongos more than to the control sound. Drongos and trogons, however, showed no difference between their response to alarm calls and to the control sounds. The control, babbling, and drongo treatments were part of the original 140-trial experiment. The silence and multiple (several species alarm calling simultaneously) treatments were conducted in subsequent experiments; results are averaged between the 2 experiments. Numbers of trials in parentheses.

and were combined with head movements when we broadcast the barbet control calls. Reaction to alarm calls, however, was clearly higher than that to the control calls: babblers jumped or flew after the majority of babbling and drongo alarms (comparison to control sounds, log-likelihood $\chi^2_1 = 9.05$, Dunn-Šidák adjusted $P < 0.04$, odds ratio 11.00). Laughingthrush response was greater to drongo alarms compared with the control sound (log-likelihood $\chi^2_1 = 10.31$, Dunn-Šidák adjusted $P < 0.02$, odds ratio 27.00). Most of these immediate movements by these species were away from the speaker: of 49 quick movements by these species in all experiments, 55% were away and only 8% were toward the speaker (the rest could not be clearly described as away or toward).

The immediate response by the Greater Racket-tailed Drongo and the Malabar Trogon was less consistent. Neither species moved significantly more to the alarm calls than to the control sounds (for drongos, log-likelihood χ^2_2 for effect of treatment = 8.02, Dunn-Šidák adjusted $P = 0.07$; for trogons, log-likelihood $\chi^2_2 = 1.88$, Dunn-Šidák adjusted $P = 0.39$). Trogons appear not to move when alarmed, except for head turns, which they also make continually while scanning for insects. Indeed, in the follow-up experiments, trogons stayed significantly longer on their perch during multiple alarms (average = 71 s) than during silence (average = 34 s; Wilcoxon signed-rank test, $W^+ = 28$, $W^- = 0$, $P < 0.02$). The immediate response of drongos is more complicated, as they were the

most responsive species in terms of movement (see Table 2), often flying before 5 s regardless of the treatment.

Delayed responses, in which birds slowly moved toward the speaker, were rarer than the immediate responses described above and were made mostly in response to drongo alarms. The most dramatic responses were by groups of laughingthrushes, which clustered together and performed mobbing activity within a meter of the speaker, twice after drongo alarms and twice after 30-s multiple alarms. Orange-billed Babblers also showed clustering and approaching behavior but responded to a wider range of stimuli: 3 responses to drongo alarms, 2 to babbling alarms, 1 to a 120-s multiple alarm, and 1 to a barbet call. Drongos approached the speaker too, 7 times during trials with their own alarm calls, 3 times to 30-s multiple alarms, and 2 times to 120-s multiple alarms. Drongos never approached after babbling alarms or control sounds (comparison to response to their own alarm calls; $\chi^2_1 = 6.71$, $P < 0.01$). But in contrast to laughingthrushes and babblers, drongos did not show clear mobbing behavior; rather they inspected closely the speaker, looking either for a predator or for an unknown conspecific.

Alarm calls by focal birds were rare and made almost entirely in response to drongo alarm calls. There were 9 trials in which focal birds made alarm calls: 3 drongo alarm calls responded to by babblers, 3 drongo calls responded to by laughingthrushes, 2 drongo calls responded to by drongos, and 1 barbet call

responded to by a babbler. We did not measure how many birds alarm called in response to the hawk attack stimuli because the sounds of the birds on the tape made it difficult for the observers to hear any response.

Acoustic analysis

The treatment types (babbler alarm, drongo alarm, and barbet control) were adjusted to be similar in amplitude and total duration, as described in Materials and methods, but differed in their acoustic characteristics (see Table 1). The 3 treatment types differed from one another significantly in peak frequency ($F_{2,42} = 22.42$, $P < 0.001$; all Tukey Honest Significant Difference (HSD) comparisons $P < 0.05$), frequency bandwidth ($F_{2,42} = 151.62$, $P < 0.001$; all Tukey HSD comparisons $P < 0.05$), and frequency modulation ($F_{2,42} = 13.65$, $P < 0.001$; all Tukey HSD comparisons $P < 0.05$). The alarm calls were of higher peak frequency, bandwidth, and modulation than the control calls. Babblers and drongo alarm calls also differed significantly between themselves in their acoustic characteristics: babbler calls were broadband calls, whereas drongo calls were more tonal with a greater degree of frequency modulation.

Because of these differences between the alarm calls and the control and because of higher response by some species to the alarm calls, response was related to the acoustic variables. Babblers responded more to exemplars with higher peak frequencies (log-likelihood $\chi^2_1 = 11.63$, Dunn-Šidák adjusted $P < 0.003$, odds ratio = 2.67—i.e., an increase of 1 kHz increased the odds of a response 2.67 times) and with greater bandwidth (log-likelihood $\chi^2_1 = 6.79$, Dunn-Šidák adjusted $P < 0.04$, odds ratio = 1.63); laughingthrushes responded more to exemplars with higher frequencies (log-likelihood $\chi^2_1 = 6.46$, Dunn-Šidák adjusted $P < 0.04$, odds ratio = 2.26); and drongos responded more to exemplars with greater frequency modulation (log-likelihood $\chi^2_1 = 7.71$, Dunn-Šidák adjusted $P < 0.02$, odds ratio = 2.32—an increase of 100 Hz increases the odds of a response 2.32 times; this later result is explained by drongos responding heavily to their own calls). We then asked whether such acoustic characteristics explained variation in response within a treatment type. We found only one such relationship: Orange-billed Babblers responded more strongly to drongo alarm calls that had high peak frequencies (log-likelihood $\chi^2_1 = 7.68$, Dunn-Šidák adjusted $P < 0.03$, odds ratio = 15.14).

DISCUSSION

This experiment provides evidence that birds in mixed-species flocks use the information encoded in the alarm signals of other species. Orange-billed Babblers and Ashy-headed Laughingthrushes were far more likely to move away from the speaker after playback of heterospecific (drongo) alarm calls than after playback of barbet calls or silence. It is possible that these birds were not responding to the playback directly but to the responses of other nonfocal birds. However, even if this occurred, the results still provide evidence for heterospecific information transfer because drongos did not respond to their own calls and thus could not have served as the cues for the babblers and laughingthrushes to respond. Babblers and laughingthrushes also responded to heterospecific calls by performing mobbing behavior and making alarm calls themselves. The responses of the Greater Racket-tailed Drongo and the Malabar Trogon were less clear, although trogons stayed on their perch longer during the playback of multiple heterospecific alarms than during silence. This response of trogons could simply have been a response to any noise as opposed to silence, although their response to the barbet control also showed the same trend to stay perched longer during an alarm

(3/5 birds flew before 30 s in trials with the barbet control, whereas only 3/11 birds flew before 30 s in trials with alarm calls; trogons' normal flightiness limited experiments with them to small sample sizes, as they often flew before the playback started).

An interesting comparison can be made between these results and those of Magrath et al. (2007), who showed recently that 2 passerine birds respond to each other's alarm calls. One difference is that there was greater variability in response in this experiment—birds in the experiments of Magrath et al. (2007) responded to both conspecific and heterospecific calls in nearly every trial. Another difference is in the characteristics of the alarm calls: the 2 species studied by Magrath et al. (2007) had similar calls, whereas the calls of the babbler and the drongo in this study are acoustically quite different. Below, we discuss these 2 issues in turn and then focus on the larger implications of the study as to whether species respond to each other's alarms and what such response means for the organization of mixed-species flocks.

Factors leading to variability in response

Some of the variability in response in this study may be due to the design of the experiments. In particular, the positioning of the speaker near the ground in the hands of the observers may have lessened the response to alarms and increased the response to the control sound because both these sounds usually come from higher in the canopy. In current fieldwork, also measuring alarm responses, we have altered the protocol by decreasing the volume slightly and attempting playback when steep slopes allow the observers to be closer to the height of the birds, and we are getting a clearer distinction between multiple alarms and barbet control sounds.

The variation in response, however, was also likely due to biological factors, in particular differences among species in their ecology and their escape behavior. The 2 species that responded most to alarms, babblers and laughingthrushes, are leaf-gleaning species that are constantly foraging near leaf clusters and thus have very limited visibility. They would be expected to rely heavily on audio alarms, and their response is in line with observations of the alarm responses of other gleaning birds in dense vegetation (Lima 1993). Drongos and trogons, on the other hand, are sallying species that are constantly looking around to scan for prey and hence may rely more on their own visual acuity than on vocal alarm calls (Munn 1984). Also, observational studies on alarm responses by sallying birds show that such species can have a variety of responses, including rapid aerial maneuvers (Lima 1993). Drongos are aggressive birds which we have observed to chase and attack *Accipiter* hawks in flocks, and this may explain their lack of immediate response and their delayed movement toward the speaker (in addition, we think it is likely that drongos did respond to the alarms in ways that we did not measure, e.g., in the number of head turns per minute). Trogons are brilliantly plumaged birds that may bring attention to themselves by any sort of movement. These differences in the ecology, behavior, and morphology of species will likely complicate the mapping of the flow of information in flocks until the escape behavior of forest birds is better understood. We hope that playback experiments will play a role in investigating such escape behaviors further.

The influence of acoustic variables on response

The alarm calls used in this study are typical of aerial alarm calls in being of generally higher frequency than other call types of similar amplitude (Klump and Shalter 1984). In particular, drongo alarm notes fit the general pattern of aerial alarms

in starting out with high frequency (always >4 kHz and sometimes >5 kHz). It is possible that the frequency of the drongo alarms is related to the urgency of the situation, as has been shown in other species (Leavesley and Magrath 2005). Given that babblers responded more to drongo alarms of greater frequency, it is likely that this feature of an alarm call is one that is salient to the birds. At the same time, babblers also responded to their own calls, which are strikingly different from the drongos' calls and show deviations from typical alarms. Whereas most aerial alarms are tonal, babbler alarm calls have a wide frequency bandwidth (this is perhaps due to some physical constraint of the species, as all its vocalizations have wide bandwidths).

The difference between the drongo and the babbler alarm calls is an interesting distinction between this study and that of Magrath et al. (2007). The alarm calls of the 2 species in the study of Magrath et al. (2007) were statistically distinguishable but similar to each other in their frequency, tonality, and cadence. From the results of their study, one can wonder whether the birds are responding to heterospecific calls in part because those calls are so similar to their own. The results of our study are important to answer this question: not only did birds respond to alarms that were quite different from their own but also babblers responded as much to the acoustically distinct heterospecific calls as they did to conspecific ones.

The question of the degree to which species are responding to the acoustic characteristics of the alarm calls may seem like an esoteric chicken-or-the-egg question: if they respond, what does it matter which feature they are responding to? But underlying this question is the deeper issue of what percentage of response to heterospecific calls is learned. If there are general rules that dictate what an aerial alarm is, such as high frequency/high-amplitude sounds, then response does not require learning. An interesting follow-up experiment to this one would be to see if a novel, computer-generated alarm call of high frequency would evoke response. Yet, from the number of recent studies that demonstrate that birds respond to variation in the calls of heterospecifics (Rainey et al. 2004; Templeton and Greene 2007) or even produce heterospecific calls in the appropriate context (Goodale and Kotagama 2006), the weight of the evidence would suggest that birds are recognizing the context of other species' vocalizations through associative learning. The degree of learning determines how flexibly animals can use the information available to them. For example, if birds can learn various species' calls, rather than responding to an acoustic cue, they could selectively respond to those species that are more reliable alarm callers, for example, drongos, in a manner analogous to how some social mammals can discriminate among individually distinctive alarm callers (Blumstein et al. 2004).

Mutualism in information use in mixed-species flocks

Due to the variability in responses to alarms, particularly the variability among species, it is difficult to make hard conclusions about the original hypotheses of the study. As to the mutuality of the interaction, babblers responded to drongos, but it is unclear whether drongos responded to babblers because drongos did not respond strongly to their own calls. We were able to show that other species in this flock system, the Ashy-headed Laughingthrush (which makes alarm calls of its own) and the Malabar Trogon (which does not), responded to the calls of babblers and drongos. As to the hypothesis that response to drongo calls would be greater than to babblers, because of the greater reliability of the information available in drongo calls, the trend was in the suggested direction, with laughingthrushes responding more to drongos than babblers

and more focal birds responding to drongo alarms with subsequent mobbing or alarm calls than to babbler alarms. However, the drongo–babbler difference was not statistically significant in any test.

The results of this experiment can, however, answer related questions about the organization of flocks and the roles of the different species. First, a novel conclusion from this study is that the gregarious, leading species of the flocks, the Orange-billed Babbler, responds to another species' alarm calls and thus would seem to benefit from participating in flocks. Gregarious species such as babblers are often considered nuclear species for flocks, that is, they form the center of flocks (Moynihan 1962; Hutto 1994). For example, members of the *Paridae* family such as chickadees and tits play an analogous role to babblers in wintering flocks of North America and Europe (Morse 1970; Dolby and Grubb 1998). But it has been unclear from previous studies whether these species benefit at all from the flock that follows them. For example, Hino (1998) provided data that suggested a gregarious nuclear species in Madagascar does not increase its foraging in flocks. Because babblers are responding to drongo calls, it might be expected that they would forage more and perform less vigilance in the presence of drongos (e.g., Sullivan 1985), a hypothesis that could be tested observationally.

The present study also demonstrates the important role in flocks that can be played by sentinel, alarm-calling species such as drongos (Terborgh 1990). Because the original definition of a nuclear species suggested by Moynihan (1962) was broad (i.e., species important to flock formation and/or maintenance), species with very different ecologies have been classified as nuclear species. Given the extensive work on sentinel antshrike/shrike-tanager species in the Peruvian system (Munn and Terborgh 1979; Munn 1986) and drongos in the Sri Lankan system (Goodale and Kotagama 2005b), it would seem now appropriate to divide nuclear species into 2 categories: gregarious species and sentinel species. We suspect that most species would fall into one of these 2 categories, although some species could potentially play both roles at once.

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