



## ALARM CALLING IN SRI LANKAN MIXED-SPECIES BIRD FLOCKS

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**ABSTRACT.**—Vocal alarm calls are important to the vigilance and likely the organization of mixed-species flocks, but community-wide studies of alarm calling in flocks are lacking. We investigated which species alarm-call, and the characteristics of their calls, in a large flock system of a Sri Lankan rainforest. We recorded naturally elicited alarm calls during several attacks by *Accipiter* hawks and while following flocks for 10 h. We then artificially elicited alarms by throwing a stick to the side of the flock, in a total of 70 trials at 30 flock sites. The Orange-billed Babbler (*Turdoides rufescens*) was the most frequent caller to both the artificial and natural stimuli, followed by the Greater Racket-tailed Drongo (*Dicrurus paradiseus*). Several other species also called, and multiple species often called to the same stimulus (in 23 trials, and in all of the hawk attacks). The species differed in their rapidity of response and in their sensitivity to different natural stimuli. Calls of the gregarious babbler usually provided a first, unreliable warning of an incoming threat, whereas later calls of other species emphasized the seriousness of the threat. We suggest that birds in mixed-species flocks may be particularly aware of aerial predators for two reasons: (1) a “numbers effect,” whereby nongregarious species are more aware of predators when surrounded by large numbers of other species; and (2) an “information effect,” whereby species differ in the information available in their alarm calls, leading to an accumulation of information in a mixed-species flock. Received 2 May 2003, accepted 25 August 2004.

**Key words:** *Accipiter* hawks, alarm calls, community ecology, *Dicrurus paradiseus*, mixed-species flocks, Orange-billed Babbler, predator vigilance, Greater Racket-tailed Drongo, Sri Lanka, *Turdoides rufescens*.

### Llamadas de Alarma en Bandadas Mixtas de Aves en Sri Lanka

**RESUMEN.**—Las llamadas de alarma son importantes en la vigilancia y probablemente en la organización de las bandadas mixtas, pero existen pocos estudios sobre llamadas de alarma en bandadas a nivel de comunidad. Investigamos cuáles especies presentan llamadas de alarma y las características de sus llamadas en un amplio sistema de bandadas en una selva lluviosa de Sri Lanka. Registramos llamadas de alarma emitidas naturalmente durante varios ataques llevados a cabo por rapaces del género *Accipiter* y mientras seguíamos bandadas por un período de 10 h. Luego inducimos artificialmente llamadas de alarma arrojando una vara sobre el costado de la bandada, en un total de 70 pruebas en 30 sitios. *Turdoides rufescens* fue la especie que llamó con más frecuencia en relación con los estímulos artificiales y naturales, seguida por *Dicrurus paradiseus*. Otras varias especies también llamaron, y múltiples especies comúnmente reaccionaron con el mismo estímulo (en 23 pruebas y todos los ataques de *Accipiter*). Las especies difirieron en su velocidad de respuesta y en su sensibilidad a diferentes estímulos naturales. Las llamadas de

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*T. rufescens* usualmente brindaron una primera señal de alerta no confiable sobre la aparición de una amenaza, mientras que las llamadas posteriores de otras especies enfatizaron la seriedad de la amenaza. Sugerimos que las aves en bandadas mixtas podrían estar particularmente atentas a depredadores aéreos por dos razones: (1) un "efecto del número," en el cual especies no gregarias están más atentas a los depredadores cuando están acompañadas por una gran cantidad de individuos de otras especies; y (2) un "efecto de información," en el cual las especies difieren en la información disponible en sus llamadas de alarma, generando la acumulación de información en una bandada mixta.

VOCAL ALARM CALLS are an important component of vigilance in mixed-species bird flocks. The evidence continues to mount that mixed-species flocks are in large part an adaptation to reduce predation (Powell 1985, Thiollay 1999), and that increased vigilance is an important component of the benefit (Pulliam 1973, Elgar 1989). Although birds can use the movements of other species as alarm cues (e.g. Lima 1995), vocal alarm calls are crucial in low-light environments such as rainforests (Terborgh 1990). Alarm calls, and responses to them, have been observed in many mixed-species flock systems (e.g. Morse 1970, MacDonald and Henderson 1977, Munn 1986, Ficken 1990), though only a few studies have set out to document the alarm-calling behavior of most or all species in a flock system (Gaddis 1980, Wiley 1980, Sullivan 1985).

It has also been hypothesized that alarm calls are an important factor in the organization of flocks, with calling species surrounded by noncalling ones (Gaddis 1980, Greig-Smith 1981). Two systems of such asymmetrical alarm-calling have been described. In the first system, alarm calls are made by the most gregarious species in the flock. Gregarious species may produce vocalizations like alarm calls that are costly to the caller but beneficial to the caller's kin (Maynard Smith 1965, Gaston 1977, Sherman 1977) or the caller's mate in a flock (Witkin and Ficken 1979, Hogstad 1995). Other species in flocks eavesdrop on the gregarious species, as has been shown for the Downy Woodpecker (*Picoides pubescens*), which lowers its vigilance when associating with flocks led by Black-capped Chickadees (*Poecile atricapillus*) and Tufted Titmice (*Baeolophus bicolor*) (Sullivan 1984, 1985). Such eavesdropping on alarm calls may be widespread (Gaddis 1980) and may account for the fact that gregarious species often play an important role in flocks (Moynihan 1962, Hutto 1994). In the second

system, a sallying (fly-catching) species is the primary alarm caller (Bell 1983, Munn 1986, Diamond 1987, Terborgh 1990); sallying species are highly vigilant, because they are constantly scanning for prey while perched (Munn 1984). In both systems, many noncalling species take advantage of one or two calling species. A more mutualistic system, in which several species alarm-call, has not previously been described.

Here, we present a study of alarm calls in a large and complex mixed-species system of a Sri Lankan rainforest. The flock system includes both kinds of potential alarm-callers: highly gregarious species, such as the Orange-billed Babbler (hereafter "babbler"; scientific names of species are given in Table 1), and sallying species, including the Greater Racket-tailed Drongo (hereafter "drongo") (Kotagama and Goodale 2004). We hypothesized that other species would eavesdrop on babblers and not call if the information available in babbler calls was sufficient for them and if alarm-calling was costly. We observed, however, that babblers, drongos, and several other species alarm-called during attacks by raptors. To determine the quality of the information available in these species' calls, we recorded natural alarm calls and artificially elicited alarm calls by throwing a stick to the side of the flock. We then measured how reliable the calls were (i.e. what percentage of natural alarms were made to raptors), and how often and quickly they called. We also measured the acoustic structure of the calls, and we use the connection between the form and function of predator-related calls (Marler 1955, Klump and Shalter 1984) to suggest how costly the calls were and what benefits the birds gained by calling.

#### METHODS

*Study site and species.*—The Sinharaja World Heritage Reserve (6°21'N, 80°21'E) is located in

the humid southwestern lowland of Sri Lanka. Vegetation within the reserve is broadly classified as evergreen dipterocarp rainforest (Gunatilleke and Gunatilleke 1981). Our study area, near the Sinharaja Research Center in the northwestern sector of the forest (between 450 and 600 m above sea level), was logged in the 1970s.

Mixed-species flocks on the study area have been studied since 1981; they average 11 species and >40 individuals (Kotagama and Goodale 2004). The babblers and drongos are by far the most frequent species, present in ~90% of flocks. The babbler and another member of the family Timaliidae, the Ashy-headed Laughingthrush (hereafter "laughingthrush"), are highly gregarious, averaging 16 and 7 individuals per flock, respectively; most other species average between 1 and 3 individuals per flock. These bird flocks also involve squirrel species, a phenomenon common on the Indian subcontinent (Henry 1971, Ali and Ripley 1987).

*Recordings of naturally elicited alarm calls.*—Over several years, we opportunistically recorded occasions when an avian predator flew directly into the flock. The primary avian predators we encountered were three species of *Accipiter* hawks: the Shikra (*A. badius*), the Crested Goshawk (*A. trivirgatus*), and the Besra Sparrowhawk (*A. virgatus*).

To systematically study alarm calls, we recorded 10 h of flock vocalizations from 12 separate flocks throughout the northwestern sector of the reserve, in August 2001 and February 2002. We noted when an alarm call was made as a response to a stimulus (a raptor or a large or fast-moving nonraptorial bird) or was followed by alarm behavior (a scattering of birds or a sudden silence). On listening to the tapes, we scored alarm calls by the more precise definitions given below.

*Sampling design for artificially elicited calls.*—Between June and August 2001, we artificially elicited alarm calls from birds. To encounter flocks, we walked a circuit of ~15 km composed of the main road to the forest as well as footpaths, completing a full circuit every two days. To avoid overestimating sample size, we divided the circuit into sites where flocks were repeatedly encountered and used flock sites as the unit of replication. Sites were defined to be  $\geq 250$  m from other sites (with 150 m allowed in two exceptional areas, where neighboring flocks were often seen <250 m apart). During previous work in the

reserve, we documented that flocks have stable home ranges and that flocks seen  $\geq 250$  m apart are highly likely to include different birds. The total number of flocks thus defined was consistent with our previous estimates of flock density. For example, in our fieldwork between 1996 and 1998, we regularly encountered nine flocks on a 3.5-km stretch of road (Kotagama and Goodale 2004), and that same stretch included 10 sites in the present study. Overall, we performed 70 trials at 30 flock sites.

*Experimental procedure.*—Because we noticed that any fast aerial movement elicited alarm calls from birds, we artificially elicited alarm calls by throwing sticks to the side of flocks. Sticks were thrown ~10 m high and ~10 m distant, so that they passed ~3 m from the closest bird. We used a Marantz PMD 222 cassette recorder and a Sennheiser ME62 microphone with a Telinga parabola to record the birds' baseline activity for 30 s before throwing the stick, and for a further 30 s after a throw. Because a stick sometimes failed to elicit a response, we threw three sticks consecutively, with 30 s to 1 min between throws; in analyses, we used the response to the first stick that elicited an alarm call. We also took notes on how many individuals of each species were present in the 10-m<sup>2</sup> area located between the place from which the stick was thrown and where it hit the vegetation.

*Definition of an alarm call.*—We defined an alarm call as a change in a bird's vocalizations in the 10 s after the natural or artificial stimulus as compared with the 30-s period before (note that this operational definition may differ from traditional definitions of alarm calls based on function or acoustic structure, e.g. Klump and Shalter 1984; see below). Some species were always silent during the 30-s baseline period, and an alarm call was simply the beginning of a vocalization. However, several species were often vocal during the baseline period. For those species, we defined an alarm call as a change in note type (descriptions of note types are included in the results).

*Analysis of characteristics of alarm calls.*—Recordings were analyzed using the sound-analysis program AVISOFT, version 3.9e (R. Specht, Berlin, Germany). Recordings were digitized at 22.05 kHz, 16-bit sample rate, and sonograms were constructed with a fast Fourier transform (FFT) size of 1,024 points. For both the naturally and artificially elicited

calls, we measured which species called first. For artificially elicited calls, we also measured duration of alarm calls (including calls of all individuals of a species) and rapidity of response (measured as the time elapsed after the stick was thrown).

We made acoustic measurements on the first note of artificially elicited calls, where a note was defined as an uninterrupted vocalization. We constructed a power spectrum of that note and measured the frequency with strongest amplitude ("peak frequency"), and the frequency bandwidth, defined as the difference between the minimum and maximum frequencies that had amplitudes within  $-15$  dB of the peak frequency (Podos 2001). For 41 of 91 calls thus analyzed, a constant band of cricket noise between 4.5 and 6 kHz interfered with the measurements. For those calls, we determined the extent of the cricket peak in the amplitude spectra before the note and subtracted that from the spectra of the note, using the following relationship (measurements in volts; R. Specht pers. comm.): square root (signal) = square root (signal + cricket) - square root (cricket).

*Statistical analysis.*—To characterize the units of replication for artificially elicited calls, we scored the species on their responsiveness in each trial, and determined their scores for each flock site. A species scored "1" if some individuals called, and "0" if individuals were present near the stick and did not call, even though a bird of another species called (we refer to such behavior as "keeping silent"). If there were no individuals of that species near the stick, or if no bird called during a trial, the species was given no score and not included in the mean for the flock site. Similarly, we determined note-types used in alarms within sites; a species scored "1" if it used the note-type being counted and "0" if it used a different note-type. These methods of averaging within sites resulted in fractional values (e.g. Table 1, column 5). We also determined the characteristics of the alarm calls of a species within flock sites.

We analyzed only those species that were present near the stick in at least five flock sites. To compare the characteristics of alarm calls among species, we used a general linear model in SAS, release 8.00 (SAS Institute, Cary, North Carolina). Variables that did not conform to assumptions of homoscedasticity (as measured by a modified Levene test; Neter et al. 1996)

or normality (as measured visually by normal probability plots) were transformed. We used a log transformation or, if the variable included only integers, a square-root transformation (Sokal and Rohlf 1995). Multiple comparisons were made using the Tukey HSD method. We used a G-test for independence with Williams's correction when analyzing proportions (Sokal and Rohlf 1995).

## RESULTS

### NOTE-TYPE CATEGORIZATION AND ALARM-CALL DEFINITIONS

Alarm calls were unambiguous, and all species used predominantly a distinct note-type as an alarm, responding similarly to natural and artificial stimuli. We describe here the note types we identified for each species (illustrated in Fig. 1) and document which ones were used as alarm calls.

*Ashy-headed Laughingthrush.*—This species was constantly vocal in the baseline period, producing "ping" notes, which had strongest amplitudes  $\sim 4$  kHz with a suppressed fundamental at  $\sim 2$  kHz, and "laugh" notes, which were of broad frequency spectrum and of duration  $>0.20$  s. All alarm calls ( $n = 5$  naturally elicited calls,  $n = 5$  artificially elicited calls) consisted of a switch from those note-types to a series of "cak" notes, each of which had a broad frequency spectrum and duration of  $\sim 0.10$  s. "Cak" notes were followed by periods of silence.

*Black-naped Monarch.*—This species (hereafter "monarch") was usually silent during the baseline period. Alarm calls usually (5 of 7 naturally elicited calls, 6.5 of 8 artificially elicited calls) consisted of "zee" notes, which had frequencies sweeping from 2 kHz up to 7 or 8 kHz. Occasionally, when the monarch was producing "zee" notes in the baseline period, it switched after the stimulus to a "trill" call, which consisted of a series of notes sweeping from 2 to 4 kHz.

*Greater Racket-tailed Drongo.*—The drongo's calls, and the notes within them, were highly varied. We distinguished only between calls that started with notes that had strong amplitude between 4 and 6 kHz ("high-pitched notes") and calls that did not. Drongos were usually silent during the baseline period and usually (16 of 16 naturally elicited calls, 13.5 of 15 artificially elicited calls) started alarm

TABLE 1. Alarm-call responses, to natural and artificial stimuli, of several species in the flocks of the Sinharaja World Heritage Reserve, Sri Lanka. Although Orange-billed Babblers called most frequently, that was a consequence of their abundance in flocks; babblers were not reliable in the natural observations, nor did they have a high propensity to call to artificial stimuli. Scientific names of species are consistent with Grimmett et al. (1999).

Species	Natural stimuli			Artificial stimuli			
	Total <sup>a</sup>	Raptor (r)	Nonraptor (nr)	Reliability ratio (r/(r + nr))	Alarm calls (ac) <sup>b</sup>	Kept silent (ks) <sup>c</sup>	Propensity ratio (ac/(ac + ks))
Orange-billed Babbler ( <i>Turdoides rufescens</i> )	32	7	19	0.27	14.4	9.5	0.60
Greater Racket-tailed Drongo ( <i>Dicrurus paradiseus</i> )	19	9	5	0.64	12.4	4.6	0.73
Black-naped Monarch ( <i>Hypothymis azurea</i> )	8	4	2	0.67	5.5	1.5	0.79
Yellow-browed Bulbul ( <i>Iole indica</i> )	6	3	1	0.75	6.0	1.0	0.86
Ashy-headed Laughingthrush ( <i>Garrulax cinereifrons</i> )	5	1	1	0.50	3.5	2.5	0.58
Squirrel species ( <i>Funambulus</i> spp.)	0	0	0	NA	7.0	1.0	0.88
Red-faced Malkoha ( <i>Phaenicophaeus pyrrhocephalus</i> )	0	0	0	NA	0	7.0	NA
Malabar Trogon ( <i>Harpactes fasciatus</i> )	0	0	0	NA	0	5.0	NA

<sup>a</sup> Number of times birds alarm-called during five opportunistic recordings of predator attacks and 10 h of following 12 separate flocks, including calls elicited by raptors, large or fast-flying birds that were not raptors, and unknown events.

<sup>b</sup> Number of times birds alarm-called to artificial stimuli ( $n = 30$  flock sites, including information from 70 trials, resulting in fractional values).

<sup>c</sup> Number of times birds were present near artificial stimuli and did not alarm-call, even though an individual of another species called.

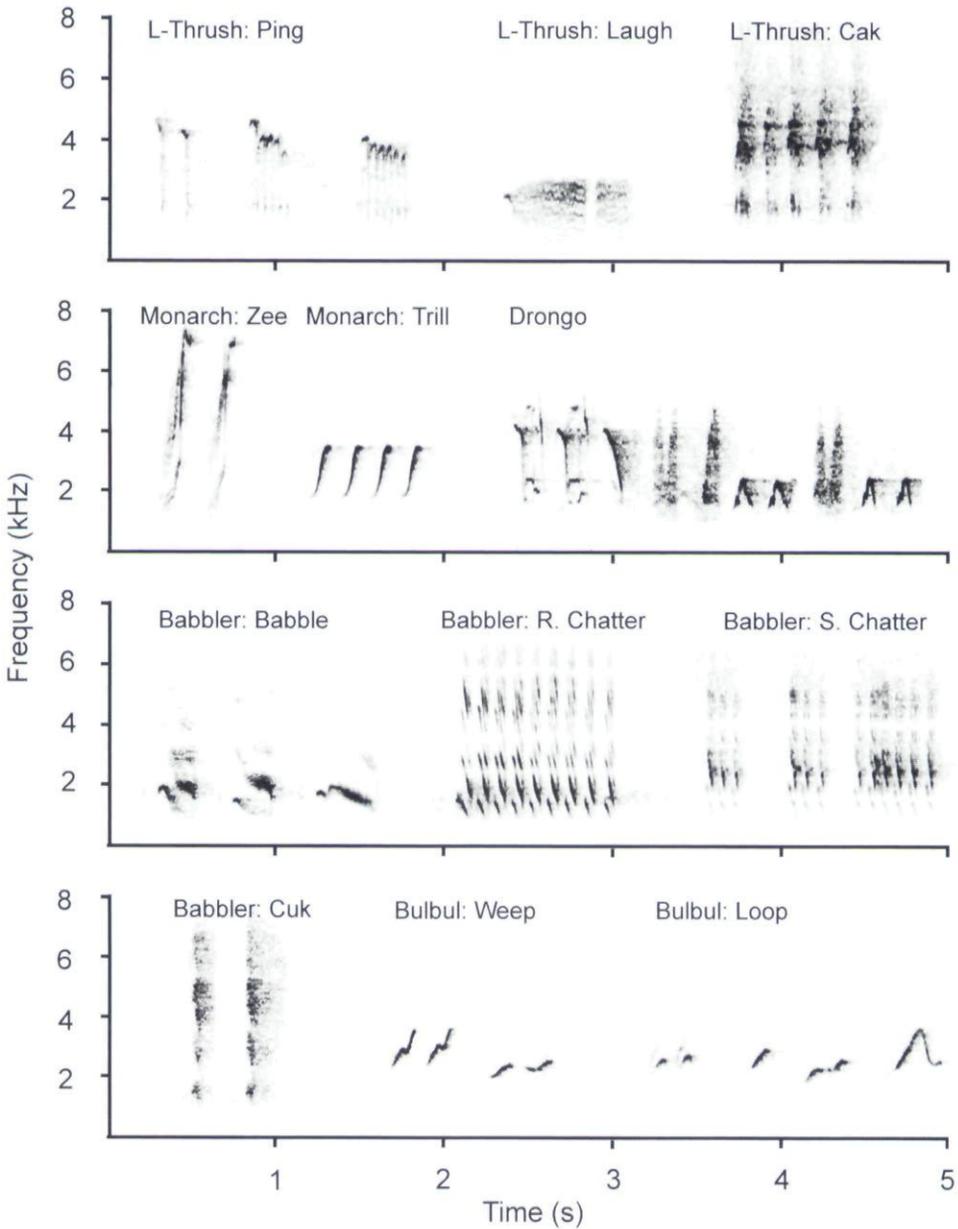


FIG. 1. Note-types of vocal flock participants. Alarm calls were defined as a change in note-type following the stimulus, and all species predominantly used a distinct note-type as an alarm (the “cak” note of the Ashy-headed Laughingthrush, the “zee” note of the Black-naped Monarch, phrases of the Greater Racket-tailed Drongo starting with a high-pitched note, the “cuk” note of the Orange-billed Babbler, and the “weep” note of the Yellow-browed Bulbul).

calls with their high-pitched notes, followed by phrases (defined as a series of notes with no interval  $>0.50$  s) that were repeated several times. We measured the end of the drongo call as the last note of a phrase or series of identical phrases introduced by a high-pitched note (in Fig. 1, the call lasts for 2.5 s).

It should be noted that drongos are capable of mimicry, and we have found, in fieldwork subsequent to the present study, that drongos mimic the alarm calls of other species when they themselves appear to be alarmed. We do not believe that such mimicry poses a serious problem for the identification of alarm calls, because it is rare in comparison with drongos' use of their own alarm notes (E. Goodale and S. W. Kotagama unpubl. data) and because our aural scoring of alarm calls was consistent with our field notes on the direction from which the alarm call came and the spatial position of the birds. Drongo mimicry is often identifiable, because mimicked notes are typically repeated and included in sequence with regular drongo notes, and can have harmonic patterns or other features unusual for the species that was mimicked (we documented three occasions when the drongo used mimicry in the present study).

*Orange-billed Babbler.*—This species was constantly vocal in the baseline period, producing mostly "babble" notes distinguished by a short chevron-shaped beginning to the note and an ending of falling frequency. Less common call-types included "regular chatter," a machine-gun-like series of evenly spaced notes with a short interval between notes (0.09–0.12 s) and "staccato chatter," a similarly fast-paced series of notes that were unevenly spaced. Alarm calls usually (28 of 31 naturally elicited calls, 21 of 21 artificially elicited calls) consisted of a switch from those call types to "cuk" notes, unevenly spaced notes with a relatively long interval between notes (0.20–0.40 s). "Cuk" notes were then followed by a period of silence.

*Yellow-browed Bulbul.*—This species (hereafter "bulbul") was usually silent during the baseline period. Alarm calls usually (five of six naturally elicited calls, seven of nine artificially elicited calls) consisted of "weep" notes, which rose in frequency and were produced in an unpredictable order. We distinguished "weep" notes from the "loop" call, which was a series of notes always presented in a predictable order and repeated regularly, much like a song.

#### NATURALLY ELICITED ALARM CALLS

*Stimuli that elicited alarms.*—*Accipiter* hawks were involved in five of the six attacks we recorded (the sixth attack was by a Crested Serpent Eagle [*Spilornis cheela*], though these eagles are not known to prey on birds; Henry 1971). In their attacks, the hawks flew low (5–10 m above ground) directly through the flock (see similar observations by Morse [1973]). In one of the *Accipiter* attacks, however, we did not record the first several seconds of the alarm; we do not include that attack in the analysis. In three of the *Accipiter* attacks, the hawks were seen making repeated flights through the flock, several minutes apart, which resulted in several bursts of alarm-calling per attack (though we analyze only the first burst of an attack).

In the 10 h of systematic recording, there were 36 alarm-call episodes in which at least one species called. Of the 27 episodes in which we observed the stimulus that elicited the call, 21 included a large or fast-flying nonraptorial bird, and 6 a raptor (though no direct attacks were observed during that period).

*Commonness of alarm calls.*—The species differed considerably in their responsiveness to the natural stimuli. Babblers called the most, drongos were next, and birds of the other species mentioned above called less commonly (Table 1, column 1). Birds of six additional species called just one time each and are not analyzed. Commonness of calling may have been a function of the number of individuals of each species (see Table 1; for artificially elicited alarms, the number of individuals near the stick was known).

*Order of alarm calls.*—Both babblers and drongos tended to call first. Babblers called first in 21 of the 31 times they called, and drongos called first in 12 of the 17 times they called. Other species called later: monarchs were never first in the seven times they called, and bulbuls were first in only two of the six times they called. Those last two species called first significantly less often than did babblers and drongos ( $G_{adj} = 11.94$ , two-tailed  $P < 0.002$ ).

*Comparison of calls elicited by raptors and by nonraptorial birds.*—Babblers made many more alarms to birds that were not raptors than did the other species (Table 1, column 3). Babblers were thus less reliable than birds of the other species considered together ( $G_{adj} = 7.73$ ,

two-tailed  $P < 0.012$ ) or drongos in particular ( $G_{adj} = 5.16$ , two-tailed  $P < 0.044$ ).

Significantly more species responded if the stimulus was a raptor (average = 2.4 species calling;  $n = 11$ ) than if the stimulus was a non-raptorial bird (average = 1.5;  $n = 21$ ; two-sample  $t$ -test for means,  $t = 2.71$ ,  $df = 30$ , two-tailed  $P < 0.013$ ). The most species responded in the four attacks by *Accipiters* (average = 3.0 species calling).

Duration of alarm calls was also much longer when the stimulus was a raptor than when the stimulus was a nonraptorial bird. Alarms lasted an average of 48.0 s in response to raptors ( $n = 10$ ), and an average of 5.3 s in response to other birds ( $n = 16$ ; two-sample  $t$ -test for means,  $t = 5.23$ ,  $df = 24$ , two-tailed  $P < 0.0001$ ). Response during the four *Accipiter* attacks was very long (average = 88.7 s). Much of the duration of alarms in response to raptors was attributable to drongos, which were the last birds to stop calling in 7 of 10 responses to raptors (including 3 of the 4 responses to *Accipiter* attacks).

ARTIFICIALLY ELICITED CALLS

*Commonness of alarm calls.*—The species differed in the number of alarm calls they made to

artificial stimuli, and the pattern was similar to that seen in response to natural stimuli. Babblers called the most frequently; drongos were next; and bulbuls, monarchs, and laughingthrushes called at a lower rate (Table 1, column 5). Squirrels (including two *Funambulus* spp. that we did not distinguish in our observations) also called to the artificial stimulus, switching from silence to a high-pitched series of notes in all ( $n = 7$ ) of their calls. As in the natural observations, birds of several species sometimes (23 of 70 trials) called to the same presentation of the predator model (see Fig. 2 for an example). Birds of two species, the Red-faced Malkoha and the Malabar Trogon, never called (Table 1, column 6), despite their frequent presence in the flocks.

The number of calls a species produced was in part a consequence of the abundance of the species within flocks. To produce a measure of a species' propensity to call, we divided the number of times a species called by the number of times it kept silent. By that measure, the babbler had a lower propensity to call than several other species (Table 1, column 7; more exact measures of the number of alarm calls per individual cannot be made, because we were unable to determine how many individuals of a species called).

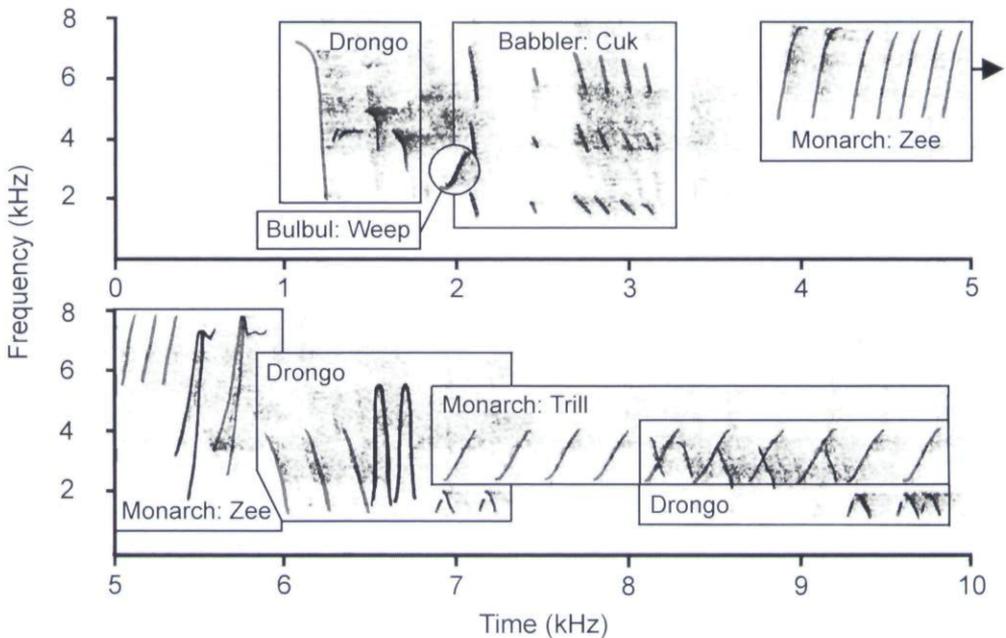


FIG. 2. An example of a multispecies alarm in response to a stick throw. Calls of four species are evident in the sequence; the stick was thrown at 0 s. Elements of the original sonogram are traced manually for emphasis.

*Order and rapidity of alarm calls.*—Babblers and drongos tended to call first, as in the natural observations, though babblers were more often (18.4 of 21 calls) and drongos less often (8.3 of 15 calls) first. Monarchs called first in only 2.6 of the 8 times they called, and bulbuls in 2.5 of the 9 times they called, significantly less often than babblers and drongos ( $G_{adj} = 9.11$ , two-tailed  $P < 0.006$ ).

The order of the calls was a consequence of the rapidity of response, which differed significantly among the species ( $F = 6.51$ ,  $df = 5$  and  $59$ ,  $P < 0.0001$ ). Specifically, babblers responded significantly more rapidly than monarchs (Tukey HSD multiple comparisons,  $P < 0.01$ ), drongos ( $P < 0.025$ ), and bulbuls ( $P < 0.05$ ). Rapidity of response was correlated with the numbers of individuals of each species that were near the stick: the more individuals nearby, the quicker the response (Fig. 3A). The same trend can be seen within babblers, the species with the largest sample size: the more babblers present, the shorter the response time (Fig. 3B).

Another factor that may have influenced the rapidity of response was the noise created by the stick when it hit the vegetation. Babblers tended to alarm-call before the noise (16.0 of 21 calls), but the other species mostly called after it (32.8 of 44 calls for the species combined; comparison with babblers,  $G_{adj} = 14.93$ , two-tailed  $P < 0.0003$ ). Indeed, both squirrels (0 of 7 calls) and monarchs (0 of 8 calls) never called before the stick noise. That audio component made the artificial disturbance quite different from that of any actual threat, and we discuss its significance below.

*Acoustic characteristics of alarm calls.*—Duration, peak frequency, and bandwidth of calls varied significantly among species. Of those variables, duration varied least, though significantly ( $F = 2.45$ ,  $df = 5$  and  $59$ ,  $P < 0.044$ ), with a tendency for alarm calls of drongos to be longer than those of babblers or laughingthrushes (Fig. 4A).

The species differed more strongly in the acoustic characteristics of their calls. Peak frequency was significantly different among species ( $F = 15.31$ ,  $df = 5$  and  $58$ ,  $P < 0.0001$ ), and several of the multiple comparisons were significant, particularly those involving the high-pitched calls of monarchs or the low-pitched calls of bulbuls (Fig. 4B). Frequency bandwidth also differed significantly among

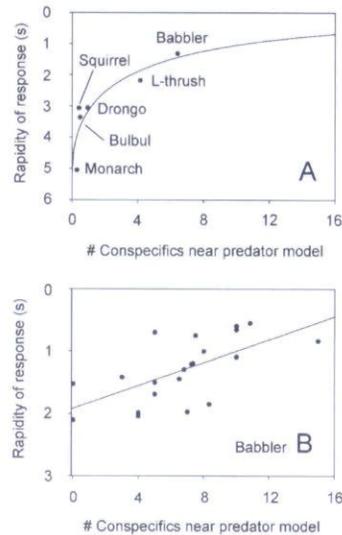


FIG. 3. Rapidity of response was related to the number of individuals present near the artificial stimulus. (A) Species with many individuals near where the stick fell responded more rapidly ( $F = 24.32$ ,  $df = 1$  and  $4$ ,  $P < 0.008$ ,  $r^2 = 0.86$ ). (B) A similar trend is shown by the most numerous species, the Orange-billed Babbler, including the data from all sites in which the babbler called ( $F = 13.15$ ,  $df = 1$  and  $19$ ,  $P < 0.002$ ,  $r^2 = 0.41$ ).

species ( $F = 11.83$ ,  $df = 5$  and  $50$ ,  $P < 0.0001$ ), and several comparisons were significant, particularly between the richly harmonic calls of babblers and laughingthrushes and the more tonal calls of bulbuls (Fig. 4C).

## DISCUSSION

More species make alarm calls in these Sri Lankan flocks than in any other reported flock system. We hypothesized that the gregarious babblers would be the primary alarm-callers in the system, because of their numerical dominance and the high probability that many of the babblers in a flock are closely related, which makes them more likely to produce costly signals that benefit their kin (Maynard Smith 1965; see Gaston [1977] and Zahavi [1990] for studies of congeneric species). Although that species did call most frequently and rapidly, other species also called, and often several species called at once. To understand why the other species called, we first look at the cost of alarm-calling by examining the acoustical structure of the

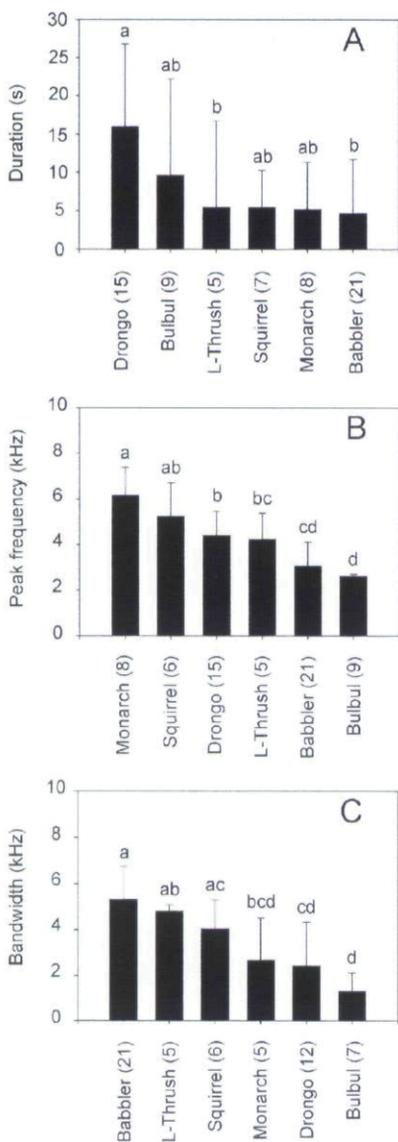


FIG. 4. Alarm-call characteristics differed among species. Species with the same letter were not significantly different, as determined by Tukey HSD multiple comparisons. Number of flock sites at which calls were recorded is indicated in parentheses. Calls varied among species in (A) duration (comparisons significant at  $\alpha = 0.10$ ), (B) peak frequency (comparisons significant at  $\alpha = 0.01$ , except that between Monarch and L-Thrush, significant at  $\alpha = 0.05$ , and that between L-Thrush and Bulbul, significant at  $\alpha = 0.10$ ), and (C) bandwidth (comparisons significant at  $\alpha = 0.01$ , except those between

calls. We then discuss the differences among species in their alarm-calling behavior, focusing on the unreliability of the babbler as one reason why other species needed to call.

It should first be noted that our definition of an alarm call, as simply a change in vocalization pattern following a stimulus, is operational; the question arises whether the changes are specific to the predator context. We believe that our definition is appropriate for an initial survey of birds in mixed-species flocks. Because birds responded with the same changes in vocalization repeatedly in many trials, those changes appear to be context-specific.

The calls recorded in the present study are, however, not typical of alarm calls made to aerial predators. Alarm calls to aerial predators are usually of high pitch and narrow bandwidth, which makes it difficult for avian predators to detect or localize them (Marler 1955, Klump and Shalter 1984, Klump et al. 1986, Jurisevic and Sanderson 1998). Calls like those recorded here (no species had peak frequencies >6 kHz, and several species had frequency bandwidths >3 kHz) are more often associated with calls made to terrestrial predators or during distress or mobbing situations, when signals advertise the location of the predator to recruit other birds to mob or attack it (Marler 1955, Curio 1978, Jurisevic and Sanderson 1994). Yet the calls in our observations were all made to moving aerial stimuli, and the call notes evoked by the artificial disturbance were also elicited by real *Accipiter* attacks.

One explanation of the acoustical properties of alarm calls in this system is that they are made during a stage in a predator attack when the cost of alarm-calling is low. We noticed that *Accipiter* hawks sometimes flew straight through flocks several times. Thus, a bird that observed a hawk moving out of the flock after the initial attack may have had a low cost of calling but a high benefit in attracting the attention of conspecifics to the danger in the area. Such a change in costs is consistent with a distinction between the very first calls during an attack—which were closer to theoretical expectations for

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L-Thrush and Drongo, and Squirrel and Bulbul, which were significant at  $\alpha = 0.05$ ).

alarm calls—and the later, more conspicuous calls that followed. The first calls included the short calls of the babbler species, followed by silence, and the high-pitched beginning of drongo calls; whereas the later calls consisted of longer and repeated phrases by drongos and birds of several other species (see Fig. 2). Two other studies have also noted that hawk attacks can be followed by prolonged volleys of calling (Morse 1970, Jurisevic and Sanderson 1998), which could either confuse the hawk or serve notice that it has been seen (Caro 1995). Given that calls made in such situations seem intermediate in function between alarm calls and mobbing calls, it is not surprising that the acoustical structure may be intermediate as well.

Species differed significantly in their rapidity of response to the artificial disturbance and their sensitivity to different natural stimuli. As expected, the babbler was the most frequent and rapid alarm-caller in the system. That is largely an effect of its abundance in flocks: a threat was detected more quickly when there were more babblers present (see Fig. 3). The observation that awareness rises with the number of individuals in a group is consistent with many studies on group vigilance (reviewed by Elgar 1989). Babblers were not reliable, however, because they made twice as many calls to non-predators as they did to predators in our natural observations (see Haftorn 2000 for a description of similar unreliable calling by the Willow Tit [*Parus montanus*]). Indeed, babblers appear to be simple "motion detectors," stimulated by any fast movement—a conclusion supported by the artificially elicited alarms when the babblers usually called before the stick made contact with the vegetation. On an individual level, babblers also are not highly sensitive to aerial threats, given that they kept silent in response to sticks more than any other species. Overall, then, the information available in babbler calls is far from perfect.

Monarchs and bulbuls were usually preceded in calling by babblers but continued calling, probably to emphasize a serious threat. The lateness of those species' calls may be a direct consequence of their small numbers of individuals in flocks; both species called first at least once to either natural or artificial stimuli, so it is unlikely they were waiting for other species to call. Rather, they may have been responding to some stimulus other than the initial movement. In the

artificially elicited trials, the sound of the stick hitting the vegetation may have been unusual enough to stimulate those species into calling (that may explain the behavior of the squirrels also). Similar movement by nonpredaceous birds would not have that audio component and were mostly disregarded by the monarchs and bulbuls. In the naturally elicited alarms, those species' contribution resulted in the higher number and length of the calls made to real predators, thus reinforcing the initial information given by the babblers about the threat.

It also appears that, beyond merely amplifying babbler calls, drongos may be more sensitive to initially perceiving true threats. Like the calls of monarchs and bulbuls, drongos' long, drawn-out phrases after the initial alarm emphasized the encounters with raptors. In contrast to those species, however, drongos called more to real predator stimuli than did babblers, despite having far fewer individuals per flock, and drongos tended to call as rapidly as babblers to the natural stimuli. The drongo's sensitivity may be attributable to its need to scan before sallying (e.g. Munn 1984), though the connection between sallying and alarm-calling is not causative: Malabar Trogons mostly sally for prey and do not call at all. The sensitivity of drongos to real threats, and the conspicuousness of their calls (qualitatively, drongos are louder than the other species), make drongo vocalizations a good source of information about aerial threats for other species. That drongos also occasionally mimic the alarm calls of other birds (see description of their vocalizations above) may further extend the influence of their calls on other species.

The different information available in the different species' calls is one reason why birds in mixed-species flocks may be more aware of predators than birds in single-species groups. Morse (1977) first hypothesized that predator vigilance might be a benefit of mixed-species associations, arguing that species used different parts of the vegetation and thus were aware of threats coming from different locations. Two other reasons why birds in mixed-species flocks may be more aware of predators are suggested here. First, there is a "numbers effect": predators are detected more rapidly when there are more individuals, and some nongregarious species will be more aware of predators when associating with large

numbers of heterospecifics than they could be in their small, single-species groups. Second, there is an "information effect": species differ in the characteristics of their calls and thus in the information provided in them; therefore, associating with more species may increase a bird's total source of information. Both of these hypotheses assume that species are responding to heterospecific calls, an assumption that must be tested with playback experiments (e.g. Munn 1986).

#### ACKNOWLEDGMENTS

We thank B. E. Byers and D. E. Kroodsmas for their assistance in all phases of this study. E.G. thanks P. S. Ashton, C. V. S. and I. A. U. N. Gunatilleke, N. E. Pierce, and the late D. R. Griffin for their help in getting him to Sri Lanka and living in the country. The Sri Lanka Forest Department provided permission and facilities at the Sinharaja Research Station. K. T. Jayarathna and P. A. Jayarathna were excellent field assistants, and U. M. Goodale and B. W. M. Wijesinghe provided invaluable help in the field. We thank J. Podos and R. Specht for advice on measuring the frequencies of calls. Earlier drafts of this manuscript were improved by the suggestions of B. E. Byers, U. M. Goodale, R. L. Hutto, S. Johnson, D. I. King, P. B. McIntyre, S. M. Smith, K. A. Sullivan, and two anonymous reviewers. The study was made possible by financial assistance to E.G. from a National Science Foundation predoctoral fellowship, a Sigma-Xi grant-in-aid, and a Woods Hole scholarship for field research.

#### LITERATURE CITED

- ALI, S., AND S. D. RIPLEY. 1987. Compact Handbook of the Birds of India and Pakistan, Together with Those of Bangladesh, Nepal, Bhutan and Sri Lanka, 2nd ed. Oxford University Press, New Delhi.
- BELL, H. L. 1983. A bird community of lowland rainforest in New Guinea. 5. Mixed-species feeding flocks. *Emu* 82:256–275.
- CARO, T. M. 1995. Pursuit-deterrence revisited. *Trends in Ecology and Evolution* 10: 500–503.
- CURIO, E. 1978. The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Zeitschrift für Tierpsychologie* 48:175–183.
- DIAMOND, J. 1987. Flocks of brown and black New Guinea birds: A bicoloured mixed-species foraging association. *Emu* 87:201–211.
- ELGAR, M. A. 1989. Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews of the Cambridge Philosophical Society* 64:13–33.
- FICKEN, M. S. 1990. Acoustic characteristics of alarm calls associated with predation risk in chickadees. *Animal Behaviour* 39:400–401.
- GADDIS, P. 1980. Mixed flocks, accipiters, and antipredator behavior. *Condor* 82:348–349.
- GASTON, A. J. 1977. Social behaviour within groups of Jungle Babblers (*Turdoides striatus*). *Animal Behaviour* 25:828–848.
- 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., C. INSKIPP, AND T. INSKIPP. 1999. *A Guide to the Birds of India, Pakistan, Bangladesh, Bhutan, Sri Lanka and the Maldives*. Princeton University Press, Princeton, New Jersey.
- GUNATILLEKE, C. V. S., AND I. A. U. N. GUNATILLEKE. 1981. The floristic composition of Sinharaja—A rain forest in Sri Lanka with special reference to endemics and dipterocarps. *Malayasian Forester* 44:386–396.
- HAFTORN, S. 2000. Contexts and possible functions of alarm calling in the Willow Tit, *Parus montanus*: The principle of 'better safe than sorry'. *Behaviour* 137:437–449.
- HENRY, G. M. 1971. *A Guide to the Birds of Ceylon*, 2nd ed. Oxford University Press, Oxford.
- HOGSTAD, O. 1995. Alarm calling by Willow Tits, *Parus montanus*, as mate investment. *Animal Behaviour* 49:221–225.
- 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.
- JURISEVIC, M. A., AND K. J. SANDERSON. 1994. Alarm vocalizations in Australian birds—Convergent characteristics and phylogenetic differences. *Emu* 94:67–77.
- JURISEVIC, M. A., AND K. J. SANDERSON. 1998. Acoustic discrimination of passerine anti-predator signals by Australian raptors. *Australian Journal of Zoology* 46:369–379.
- KLUMP, G. M., E. KRETZSCHMAR, AND E. CURIO.

1986. The hearing of an avian predator and its avian prey. *Behavioral Ecology and Sociobiology* 18:317–323.
- KLUMP, G. M., AND M. D. SHALTER. 1984. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm calls. II. The functional significance and evolution of alarm calls. *Zeitschrift für Tierpsychologie* 66:189–226.
- KOTAGAMA, S. W., AND E. GOODALE. 2004. The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. *Forktail* 20:63–70.
- LIMA, S. L. 1995. Collective detection of predatory attack by social foragers: Fraught with ambiguity? *Animal Behaviour* 50:1097–1108.
- MACDONALD, D. W., AND D. G. HENDERSON. 1977. Aspects of the behaviour and ecology of mixed-species bird flocks in Kashmir. *Ibis* 119:481–491.
- MARLER, P. 1955. Characteristics of some animal calls. *Nature* 176:6–8.
- MAYNARD SMITH, J. 1965. The evolution of alarm calls. *American Naturalist* 99:59–63.
- MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecological Monographs* 40:119–168.
- MORSE, D. H. 1973. Interactions between tit flocks and sparrowhawks *Accipiter nisus*. *Ibis* 115:591–593.
- MORSE, D. H. 1977. Feeding behavior and predator avoidance in heterospecific groups. *BioScience* 27:332–339.
- MOYNIHAN, M. 1962. The organization and probable evolution of some mixed-species flocks of Neotropical birds. *Smithsonian Miscellaneous Collections* vol. 143, no. 7.
- MUNN, C. A. 1984. The behavioral ecology of mixed-species bird flocks in Amazonian Peru. Ph.D. dissertation, Princeton University, Princeton, New Jersey.
- MUNN, C. A. 1986. Birds that 'cry wolf'. *Nature* 391:143–145.
- NETER, J., M. H. KUTNER, C. J. NACHTSCHEIM, AND W. WASSERMAN. 1996. *Applied Linear Statistical Models*. WCB/McGraw-Hill, Boston.
- PODOS, J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* 409:185–188.
- POWELL, G. V. N. 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. Pages 713–732 in *Neotropical Ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, and R. S. Ridgely, Eds.) *Ornithological Monographs*, no. 36.
- PULLIAM, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38:419–422.
- SHERMAN, P. W. 1977. Nepotism and the evolution of alarm calls. *Science* 197:1246–1253.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*, 3rd ed. W. H. Freeman, New York.
- SULLIVAN, K. A. 1985. Selective alarm calling by Downy Woodpeckers in mixed-species flocks. *Auk* 102:184–187.
- SULLIVAN, K. A. 1984. The advantages of social foraging in Downy Woodpeckers. *Animal Behaviour* 32:16–22.
- 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. 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.
- WILEY, R. H. 1980. Multispecies antbird societies in lowland forests of Surinam and Ecuador: Stable membership and foraging differences. *Journal of Zoology* (London) 191:127–145.
- WITKIN, S. R., AND M. S. FICKEN. 1979. Chickadee alarm calls: Does mate investment pay dividends? *Animal Behaviour* 27:1275–1276.
- ZAHAVI, A. 1990. Arabian Babblers: The quest for social status in a cooperative breeder. Pages 105–130 in *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behaviour* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.

Associate Editor: R. L. Holberton

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