Original Article

Foraging guild influences dependence on heterospecific alarm calls in Amazonian bird flocks

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Interspecific eavesdropping on alarm calling has been considered evidence that species participating in mixed-species groups benefit from reduced risk of predation. Few studies, however, have examined interspecific variation in dependence on and ability to evaluate alarm signals in mixed-species groups. We conducted a playback experiment to evaluate how species in different foraging guilds varied in their response to alarm calls of birds that lead Amazonian mixed-species flocks in both upland and inundated forests. We predicted that species that search nearby substrates myopically would react more strongly to alarm calls (i.e., take longer to resume foraging) than flycatching species that search for insects at a greater distance from a perch. We used likelihood functions to model the latency response to resume foraging for both upland and inundated forests samples, and we were able to detect significant differences among different foraging guilds. Our results indicate that flycatching birds respond weakest in both forest types, but contrary to our predictions, live-leaf gleaners showed a stronger response to alarms than dead-leaf–gleaning insectivores in inundated forest and no difference in upland forest. These results suggest that foraging guild may underlie different levels of dependence on public versus private information and, thus, the dependence of different species on heterospecific informants. These different levels of dependence on alarm calls provide a potential mechanistic basis for understanding assembly rules of flocks. *Key words:* alarm calls, communities, foraging ecology, mixed-species flocks, public information, threat evaluation. *[Behav Ecol]*

INTRODUCTION

Information use by animals reduces uncertainty and minimizes risks. A growing body of literature stresses the pervasiveness of information use and its consequences for animals and its potential as a unifying concept in ecology and evolution (Schmidt et al. 2010). Information can be broadly defined as being either private where it is possessed by an organism and inaccessible to others or public which can be obtained through interactions with other organisms (Wagner and Danchin 2010). Although all animals use private information to reduce uncertainty, the use of social information both through cues and signals has received particular attention because of its consequences for conspecifics and heterospecifics from both an evolutionary and ecological perspective (Dall et al. 2005; Seppanen et al. 2007; Schmidt et al. 2010). Much less is known, however, about the implications of social information use by heterospecifics in influencing the organization of animal communities (Goodale et al. 2011).

Assessing the types of information transfer that occur among organisms has been a primary approach for attempting to understand the mechanisms underlying multispecies animal group formation. Eavesdropping on alarm calls of other species is a primary example of the use of public information

in multispecies groups and has been the focus of numerous studies across a range of taxa (Boinski and Garber 2000; Kirchoff and Hammershmidt 2006; Sridhar et al. 2009; Sharpe 2010). There have been many approaches to studying the consequences of alarm calling and how it reduces predation risk. From an evolutionary perspective, alarm calls have been shown to have adaptive value by including a large amount of information, encoding both the types and the degree of threats (Templeton 2005; Courter and Ritchison 2010; Sieving et al. 2010). On the other hand, the use of false alarms has demonstrated an evolved role of providing false information to deceive eavesdropping individuals and thus to manipulate eavesdropping heterospecifics for the benefit of conspecifics that provide the alarms (Munn 1986; Ridley and Child 2009). Other studies have shown the interspecific dependence of species on each other's alarms and have inferred that mutualistic interactions underlie heterospecific group formation (Magrath et al. 2007; Goodale and Kotagama 2008). Thus, it seems reasonably clear that information transfer is an underlying advantage of forming groups.

In birds, minimizing predation risk through eavesdropping has been hypothesized to be a primary advantage of mixed-species flock formation (Sridhar et al. 2009). To date, attention has focused on variation in information provided by the alarms of the signaler. Flocks, however, contain species with different foraging ecologies, which might make them more or less vulnerable to predators. We know little, however, about whether species with different foraging behaviors respond differently to alarm calls.

High species diversity within Neotropical bird flocks is thought to be made possible by the diverse array of foraging

specializations among flocking birds: insectivorous birds specialize on live leaves, dead leaves, twigs, branches, and tree trunks and some catch insects in the air (Munn 1985). These different foraging ecologies, by influencing the field of vision experienced by a bird, may play a role in determining the extent to which different species depend on heterospecific information as a resource in mixed-species flocks. Understanding species' variation in responses to threat information therefore may, in part, dictate the rules that determine the assembly of species within flocks and determine the nature of interspecific interactions within flocks.

Species that forage by myopically searching substrates should depend on alarm calls more than species that search for prey at a distance and would therefore be more likely to detect predators on their own. These latter species may have more opportunities to evaluate heterospecific signals because they have private information on predation risk based on their own monitoring of the environment. Because the multispecies flocks of the Amazon contain species with a wide array of foraging tactics, they provide an opportunity to evaluate how species ecologies influence reliance on heterospecific threat information. We ask: how does variation in foraging guild influence species responses to heterospecific threat information? Because species that forage in dead leaves myopically probe their head into dead leaf clusters, we predicted they would be at the greatest risk of predation and most dependent on public information in the form of alarm calls. Species that are live-leaf insectivores search leaves myopically but appear less vulnerable to predators than dead-leaf insectivores because their vision is less obstructed by their foraging behavior. We predicted that these species would show a lower level of response to simulated alarm calls; in other words, they would resume foraging sooner than dead leaf counterparts. Species that catch prey in the air (flycatching) search for prey at greater distances because they scan beyond the immediate vegetation close to the perch and therefore have a greater opportunity to use private information about the true level of threat posed during alarm calls. By using playbacks of alarm calls when there are no real predators attacking, we are measuring the dependence on alarm callers and the potential dependence of different species on heterospecific alarm calls.

METHODS

Study site

This project was conducted in the vicinity of the Madre Selva Biological Station, along the Rio Orosa, a blackwater tributary of the Amazon east of Iquitos, in the region of Loreto, Peru (lat 3°37′2′′S, long 72°14′8′′W). Playback experiments were conducted within tierra firme forests adjacent to the station and seasonally inundated forest approximately 4 km upriver. Within each forest, mixed-species flocks are abundant, and although only a few species are shared between them, both forest types contain species with similar foraging ecologies. Each flock type consists of one species that is responsible for the majority of alarm calls. In the upland tierra firme forests, the alarm-calling species is *Thamnomanes saturninus*, the Saturnine Antshrike. Conversely, the main alarm-calling species in the inundated forests is its congener, *Thamnomanes schistogynus*, the Bluish-slate Antshrike (see Figure 1a,b for alarm calls of *T. saturninus* and *T. schistogynus*, respectively). In many areas, 2 species of *Thamnomanes* occur in the same flocks (Munn and Terborgh 1979; Jullien and Thiollay 1998), but in the Madre Selva area, they rarely occur together; instead, each species forms the nucleus of its own flock (Martínez AE, unpublished data).

From each forest type, we selected a flocking species representing each of 3 distinct foraging guilds: a live-leaf gleaner,
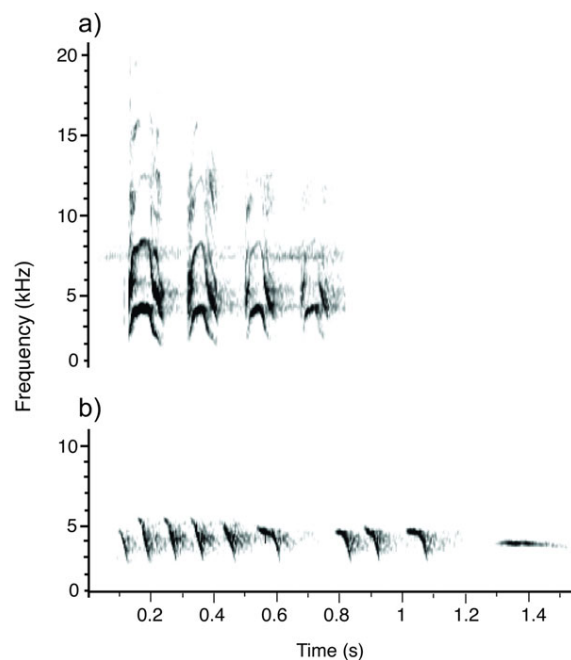
Figure 1
Sonogram of alarm call of (a) *Thamnomanes saturninus* and (b) *Thamnomanes schistogynus*.

a dead-leaf gleaner, and a flycatching species. In the inundated forest type, we selected the gray antwren, *Myrmotherula menetriesii* (a live-leaf gleaner), the moustached wren *Thryothorus genibarbis* (a dead-leaf gleaner), and gray-headed tanager *Eucometis penicillata* (a flycatching tanager). In the tierra firme forest, we selected the white-flanked antwren, *Myrmotherula axillaris* (a live-leaf gleaner), the stipple-throated antwren *Epinecrophylla haemotonota* (a dead-leaf gleaner), and the Cinnamon-rumped flycatcher *Terenotriccus erythrura* (a flycatcher).

Recordings

We recorded alarm calls using a Sennheiser ME-66 directional shotgun microphone and a TASCAM DR-07 Portable Digital recorder during the dry season (mid-June to mid-July) 2009 and 2010. All recordings were made under 44.1 kHz and 24-bit waveform file format. Alarm calls were recorded under 2 types of conditions: 1) after throwing artificial hawk models at alarm-calling birds and 2) under natural conditions by following flocks and recording alarm calls generated by birds responding to perceived threats. In the former case, a hawk was made out of balsa wood and covered with pheasant feathers and thrown from approximately 10–20 m away from alarm-calling birds. A second person would record any vocalizations generated while simultaneously holding a sound meter to record the decibel level of the recording. In the latter case, flocks were followed within 15–20 m with a microphone constantly recording between approximately 2 and 5 h. Alarms were prompted in response to actual predators such as hawks and also to larger birds such as woodpeckers and pigeons that fly into or through the flock. We used length of each alarm and peak frequency to determine whether alarm calls generated under the 2 protocols shared the same characteristics (Table 1). In the case of *T. schistogynus*, the only alarm that was generated using a model hawk fell within the range of values observed for natural calls (Table 1). We found no significant differences between calls generated by the 2 protocols in any of the characteristics measured (call length: t-test = 0.273, degrees of

Table 1

Characteristics of alarm calls for both natural and model prompted alarm calls

Species	Model prompted	Sample size	Alarm length mean	Alarm length SD	Peak frequency mean	Peak frequency SD
T. saturninus	Y	3	0.74	0.09	4019.53	99.48
T. saturninus	N	5	0.71	0.09	3962.10	507.16
T. schistogynus	Y	1	1.371	—	3273	—
T. schistogynus	N	7	1.84	0.72	3420.69	321.19

Alarm length is in seconds and peak frequency is in kilohertz. Mean, mean length of alarm calls; SD, ±1 standard deviation; *n*, sample size; Y, alarm was prompted through model presentation; N, alarm was recorded without model presentation.

freedom [df] = 3.686, P = 0.7995; peak frequency: t-test = 0.281, df = 4.645, P = 0.791), which allowed us to use all playbacks for subsequent experiments. Alarm calls were filtered to remove background signals attributed to other bird calls. Previous work has only described short and long alarm calls by *T. schistogynus* (Munn 1986). However, there is likely to be referential information (type of threat) provided by alarm calls of both species as well. For *T. saturninus*, the alarm calls naturally vary from 2 to 6 repetitions of the same note. *T. schistogynus* calls vary both in length and in the types of notes they use. Because short-term calls were much more frequently generated, both under natural and induced conditions, we selected them for use in the experiment during which we maintained a sample rate of 44.1 kHz and 24-bit waveform file format.

The volume of recordings can vary greatly depending on the conditions under which the recording was made. Using a sound meter, playback volume of alarms was established at 55 dB at 15 m based on measurements made using a sound meter to measure the loudness of natural alarms (in decibels) by birds when a hawk model was used to generate alarms. Control stimuli were made using digital white noise recordings using Raven software to filter the controls to the frequency range and length of alarm calls of the respective species used in each forest flock.

Playback trials

Alarm calls were used to test the response of individuals of each of the target species using alarm calls of sentinels from their respective flock type. We used alarm calls from each of 8 individuals only once per species. We intended to test 8 individual responses per species (based on variances in preliminary data) to playbacks of alarms and controls. Thus, in each forest type, we conducted 48 trials: 8 controls and 8 alarms for each of 3 species from 15 July to 29 of August 2010. Because species in mixed-species flocks often share the territory, we tested individuals of different species that were approximately 300 m apart, to assure that tests of individual birds were from different territories based on territory sizes of flocks from past studies (Munn and Terborgh 1979; Jullien and Thiollay 1998). We revisited the same areas on different days to test different species. Two-observer teams alternated between forest types in order to complete enough trials. In each area, we conducted just one trial per day. We measured the response by having a primary observer locate an individual of the target species and observing foraging activity for approximately 20-s prestimulus. A second person would playback the assigned stimuli by placing on the ground a pignose amplifier in the direction of the target species at a distance of approximately 15 m from the bird. Sentinel birds range widely in their perch heights in the un-

derstory and occasionally can be found on the ground. Although it is unlikely that alarm calls are generated frequently from the ground, the most important feature is where the receiver is in relation to the alarm signal. As listening birds can be located and do respond in virtually any direction (above, below, and to the side) from alarm-calling birds, we feel that placing the speaker on the ground should not greatly influence responses of individual birds. Playbacks were conducted using an Edirol R-07 waveform recorder. The first observer would continue to observe the response of the individual poststimulus until the bird was lost from view. Birds typically respond to alarms by scanning up and either freezing or diving into thicker cover. We measured the length of the response from the start of evasive action (either freezing or diving) until the bird resumed foraging activity. In several cases, when birds dived into thicker cover, they were lost from view in which case we were unable to use the trial because we could not see when they resumed foraging. We retested these birds 2 or more days later.

Data analysis

We compared the responses of species among foraging guilds for each forest type. In order to detect differences among foraging guilds, we chose to model the latency to resume foraging after an alarm stimulus. We considered that this random variable could be modeled through an exponential distribution because it is well-known in the literature its ability to represent waiting times until the occurrence of some event (Karlin and Taylor 1975; Williams et al. 2002). This assumption was tested using a Kolmogorov–Smirnov test (Corder and Foreman 2009) for each foraging guild in each forest type. Kolmogorov–Smirnov tests for each group did not reject the hypothesis of an exponential distribution, except for the flycatching guild in the inundated forest. We proceeded using this model for resumption of foraging because it assigns high probability to short-latency responses and low probability to long-latency responses, which can be observed in our samples. The parameter of an exponential distribution θ is understood as mean time that a bird waits until resuming foraging activity. We were interested in making inferences about the time to resume foraging so we calculated the likelihood function of the parameter θ using the sample of the latency responses per foraging group and per forest. In order to detect differences in latency response according to foraging group, we performed a likelihood ratio test (LRT). The null hypothesis of this type of test states that the latency response of all foraging guilds is the same. Our main goal was to reject the latter hypothesis because this represents significant evidence of differences in latency response by foraging group. Subsequently, for each of the 2 forest types, we estimated the mean latency responses for 3 different groups (θ) and calculated the confidence intervals for each mean assuming the exponential distribution for latency responses. Maximum-likelihood estimation (MLE) for the mean latency response and confidence intervals around the MLE allowed us to detect relevant differences of response to alarm calls among species within different foraging guilds for both upland and inundated forests. All data analyses was done with R package 2.12.1.

RESULTS

We combined trials among observers but analyze forest types separately in order to generalize how birds with different foraging ecologies responded to alarm calls. Differences were statistically significant for lengths of response to alarm calls by foraging guild for each forest and showed little or no effect of controls on influencing bird responses (Figure 2). The exponential
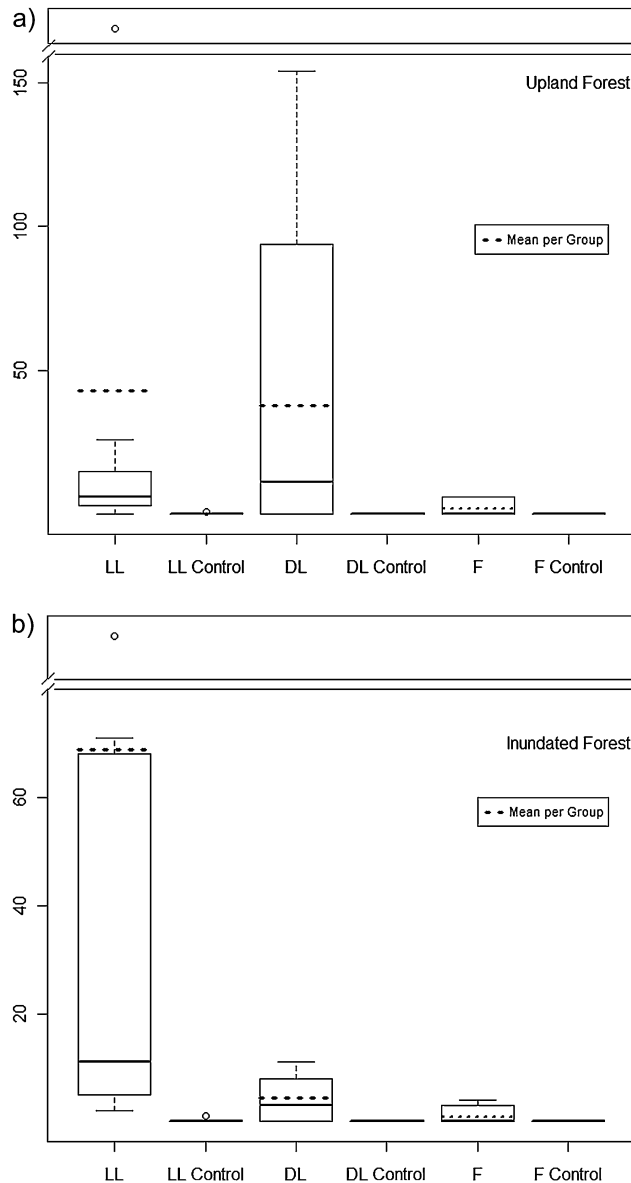
Figure 2

Box and whisker plots of latency to resume foraging after hearing alarm stimulus (in seconds) grouped by foraging guild. Dashed lines show mean response in seconds by averaging all trials by foraging guild. A "response" indicates that birds take some sort of evasive action on hearing an alarm stimulus. LL, live-leaf foraging guild; DL, dead-leaf foraging guild; F, flycatching guild. Upland forest: live leaf ($n = 8$), dead leaf ($n = 8$), and flycatching ($n = 3$); inundated forest: live-leaf ($n = 8$), dead-leaf ($n = 8$), and flycatching ($n = 8$).

Table 2

Results of Kolmogorov–Smirnov tests to determine whether the distribution of data from each guild × forest type is derived from the exponential distribution

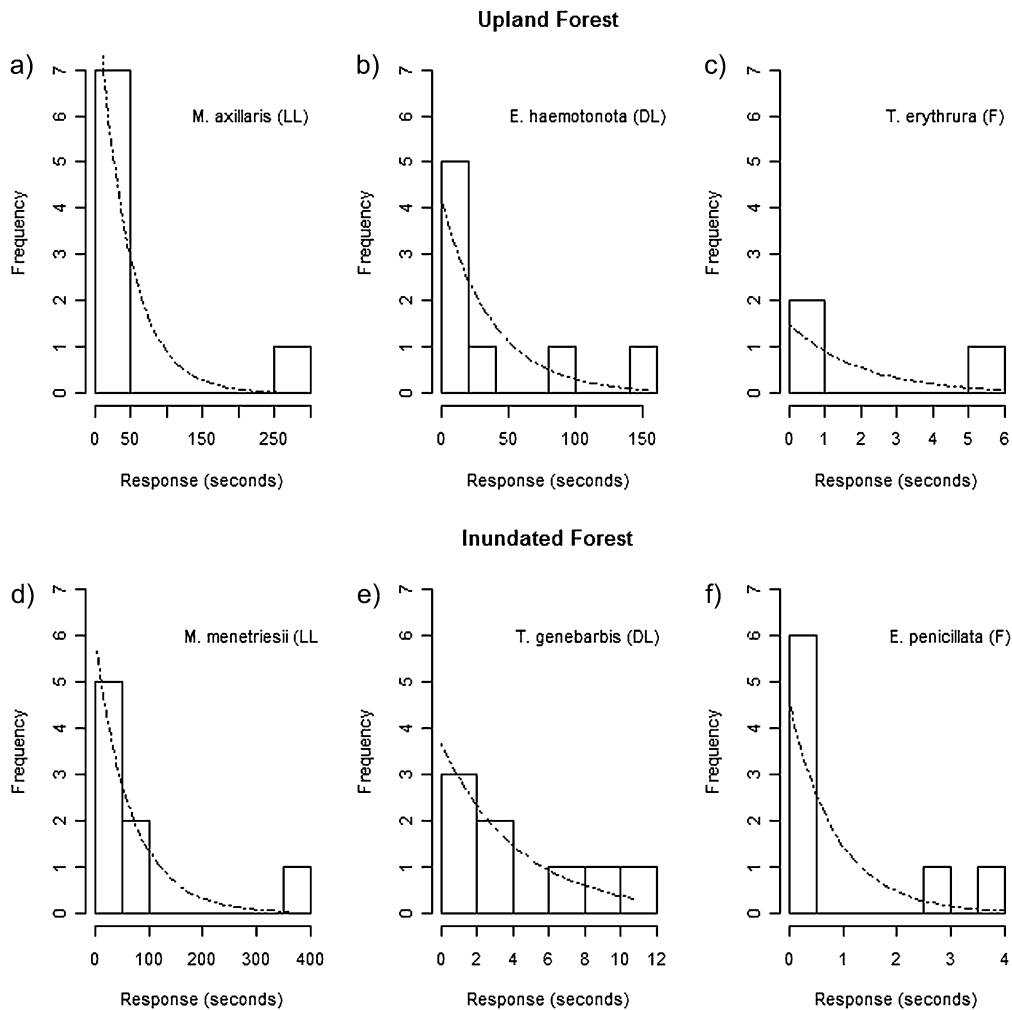| Forest type	Guild	D	P value
U	LL	0.4548	0.04957
I	LL	0.3524	0.2151
U	DL	0.375	0.2106
I	DL	0.25	0.6994
U	F	0.6667	0.1389
I	F	0.75	0.002468

For forest type: U, upland forest and I, inundated forest. For guild: LL, live-leaf–gleaning species; DD, dead-leaf–gleaning species; and F, flycatching species. D, test statistic providing the ratio difference between the data and exponential function.

being a poor fit, it would nonetheless approximate the data relatively better than other distributions. The LRTs indicated differential effects of foraging guild depending on forest type (Table 3). In the case of the upland forest, both the live-leaf and dead-leaf species showed similar latency responses (Table 3, $\chi^2 = 0.605$, $P = 0.799$, Figure 4a), and when combined these 2 groups, they show significantly different behavior compared with the latency response of the flycatching species, *T. erythrurus* (Table 3, $\chi^2 = 0.605$, $P = 0.0006$, Figure 4a). In the analysis of species from the inundated forest, the LRTs for each of the groups showed significant differences in their latency responses (Table 3, live-leaf gleaner vs. dead-leaf gleaner, $\chi^2 = 23.9$, $P = 1.0 \times 10^{-06}$, and for distributions of all 3 groups, $\chi^2 = 68.45$, $P = 1.0 \times 10^{-15}$, Figure 4b,c). The relative likelihoods showed that for the inundated forest, each group responded differently to alarms with flycatching species responding the least and live-leafers showing the strongest response (Table 4, Figures 2 and 4b,c).

DISCUSSION

Our results suggest that foraging guild influences both the dependence of different species on heterospecific alarm calls and the ability of species to evaluate threat information (Tables 3 and 4, Figures 2 and 4). As we predicted, species that search for prey at a distance from a perch responded weakest and recovered fastest from alarm calls suggesting that their foraging strategy makes them less dependent on heterospecific alarm calls. In this system, species that searched myopically were more dependent on the alarm calls; they usually stopped foraging. Thus, although flycatching species have the lowest response in both forest types, consistent with our prediction, there is no difference in the response of live-leaf– and dead-leaf–gleaning species in the upland forest and a stronger response of live-leaf–gleaning species compared with dead-leaf–gleaning species in the inundated forest, contrary to our prediction. Therefore, these species may depend more completely on public threat information of the sort that is available in flocks where vigilant species frequently give alarm calls of the kind used in the experiment. We nonetheless recognize that a limitation of our study is the use of only 2 species per foraging guild and that future studies will need to incorporate more species per foraging guild.

Nonetheless, there were differences in responses of dead-leaf searching species by forest type: dead-leafers responded less strongly to alarm calls than those that searched in live leaves in the inundated forest, which suggests that other factors may determine their dependence on heterospecific alarm calls. Dead leaves sometimes occur in dense clusters in vine

assumption was analyzed using the Kolmogorov–Smirnov tests, and results are shown in Table 2. In all cases but one, we are not able to reject the assumption of an exponential distribution for latency responses (Table 2, Figure 3a–f). In the only case (flycatching species in inundated forests) where we rejected this assumption, we were able to detect that a significant departure from the exponential is given by the large number of zeros in the data (no response) and the sample size, which could indicate a zero-inflated exponential distribution (Figure 3f). However, in order to compare with other foraging guilds, it is reasonable to maintain the exponential assumption: in spite of

Upland Forest

Inundated Forest

Figure 3
Histograms of latency response by species with superimposed estimated exponential distribution. LL, live-leaf guild; DL, dead-leaf guild; and F, flycatching guild. Upland forest: (a) *Myrmotherula axillaris*, (b) *Epinecrophylla haemotonota*, and (c) *Terenotriccus erythrurus*; inundated forest: (d) *Myrmotherula menetriesii*, (e) *Thryothorus genibarbis*, and (f) *Eucometis penicillata*.

tangles or in fallen branches, areas where *T. genibarbis* often forages, and thus may provide abundant cover from predators. Dense clusters of vine tangles with dead leaves in fact are more common in the inundated forest than the upland forest (Martínez AE, personal observation). When foraging in

Table 3
Results of likelihood ratio test with null hypothesis that foraging guild does not influence latency responses

Foraging guild comparisons	Forest type	Chi-square test	Degrees of freedom	P value
LL versus DL	U	0.065	1	0.799
LL and DL versus F	U	0.065	1	0.0006
LL versus DL	I	23.9	2	1.01×10^{-06}
LL and DL versus F	I	68.45	2	1.36×10^{-15}

For forest type: U, upland forest and I, inundated forest. For guild: LL, live-leaf–gleaning species; DD, dead-leaf–gleaning species; F, flycatching species. All null hypotheses are rejected indicating significant different behavior of each foraging group. The only exception occurs in U where we were not able to detect differences in responses between LL and DL species.

these contexts, dead-leafers may not need to rely as much on heterospecific alarms calls. Of the trials in these species that resulted in no response in each forest type, 4 of the 5 occurred when the species was in dense vegetation and therefore safe from attack (Martínez AE, personal observation). Vegetation density has often been proposed as a primary determinant of vulnerability (Suhonen 1993) and to affect which species do and do not join flocks (Jullien and Thiollay 1998; Thiollay 1999). Our results suggest that foraging guild may further influence the degree to which species are found in vegetation of varying density and therefore exposed to aerial predators.

Flycatching birds may be the least likely to join flocks because of antipredator benefits but may benefit from enhanced foraging opportunities. Indeed, one of the alarm-calling species, *T. schistogynus*, which seems to form the core of the floodplain flocks, appears to benefit primarily from the prey flushed by the other members of the flock (Munn 1986). Srinivasan et al. (2010) suggested that flycatching birds should be highly associated with flocks because they are often group leaders that maintain cohesion and or play the role of vigilant species. Although flycatching antshrikes in the genus *Thamnomanes* are thought to be the flock leaders in Amazonian forests, those species represent only a small percentage of the flycatching
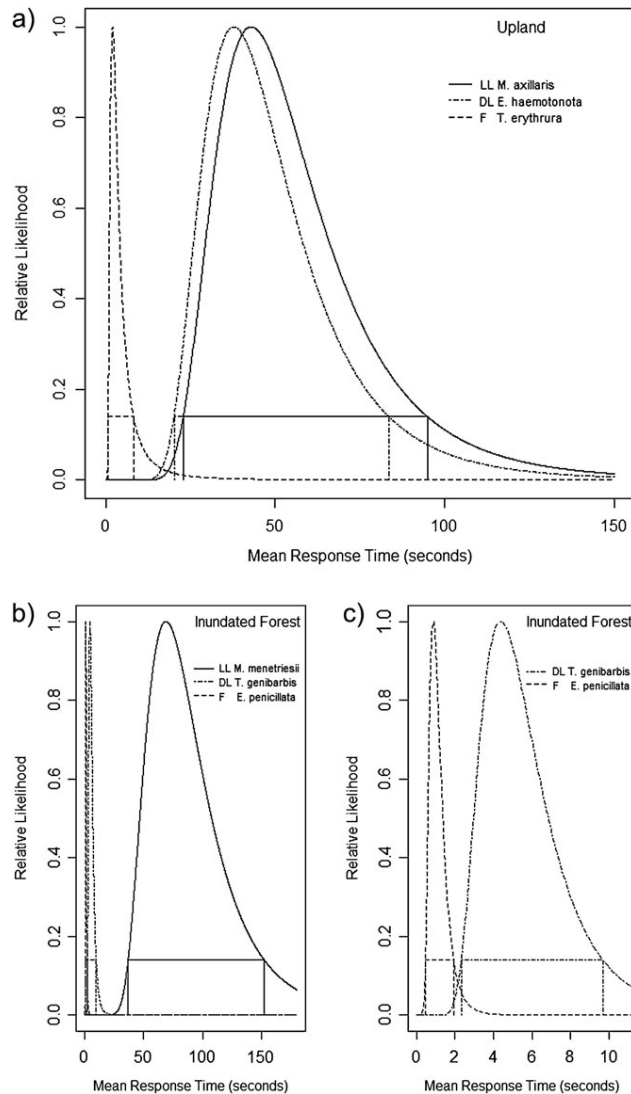
Figure 4

Relative likelihood functions for the mean response time to resume foraging by foraging strategy. The horizontal lines show the 95% confidence intervals for each likelihood. LL, live-leaf; DL, dead-leaf; and F, flycatching. Upland forest: LL ($n = 8$), DL ($n = 8$), and F ($n = 3$); inundated forest: LL ($n = 8$), DL ($n = 8$), and F ($n = 8$). (a) Compares all 3 groups in upland forest. (b) Compares all 3 groups in inundated forest and (c) magnifies the estimates in (b) between the dead-leafing species and flycatching species.

species present in these forests (Terborgh et al. 1990). The vast majority of flycatching species do not participate regularly in mixed-species flocks, suggesting that they derive few benefits (Munn and Terborgh 1979; Martínez AE, unpublished data). Thus, the only flycatching species that may benefit consistently from flock formation may be those that regularly catch prey flushed by other flock members.

In our study, we standardized the experiments by using short alarm calls and thus do not address potential variation in threat information. There is considerable evidence from previous studies that both degree and types of threat significantly influence the behavior of species receiving the information (Rainey et al. 2004; Templeton 2005; Soard and Ritchison 2009; Sieving et al. 2010). Determining how graded and referential information interact with foraging guild would help us understand the

Table 4

MLE for the mean time of latency responses per foraging guild in each forest type and 95% confidence intervals

Species	Foraging guild	Forest type	MLE for mean response time	95% Confidence intervals
Myrmotherula axillaris	LL	U	42.87	22.9–94.9
Epinecrophylla haemotonota	DL	U	37.7	20.1–83.4
Terenotriccus erythrurus	F	U	2.0	0.764–8.19
Myrmotherula menetriesii	LL	I	68.9	36.7–152
Thryothorus genibarbis	DL	I	4.37	2.33–9.6
Eucometis penicillata	F	I	0.875	0.467–1.93

For forest type: U, upland forest and I, inundated forest. For guild: LL, live-leaf–gleaning species; DD, dead-leaf–gleaning species; and F, flycatching species.

mechanisms that promote the evolution of dependence on heterospecific signals. The short alarm calls used in our experiments are urgent signals that do not always accurately reflect threat (distant raptors or large, but harmless species such as woodpeckers that may have been mistaken for threatening species). Indeed, alarm calls that provide a higher sense of urgency have generated responses in flycatching species (Martínez AE, unpublished data) and are generated when raptors or raptor-sized birds fly directly through the flock. In both flock types, however, short alarm calls are far more frequent suggesting that responding to these calls is potentially costly in terms of lost foraging opportunity when alarm callers mistakenly perceive threats (woodpeckers or nonraptors flying through flocks). Our results suggest that the degree of dependence on heterospecific information should make some species more easily manipulated than others and therefore might have led to the evolution of kleptoparasitism, which has previously been documented in this system (Munn 1986).

Much attention has recently focused on the linkage between information transfer and its implications for animal communities (Goodale et al. 2011). Schmidt et al. (2010) suggested that information use may play a role as an axis in evaluating ecological niches. We suggest that variation in species' dependence on heterospecific information could be incorporated as a trait to assess assembly rules in mixed-species flocks. Species joining mixed-species flocks are known to vary greatly in their flocking propensities, and this has often been correlated with vegetation density (Jullien and Thiollay 1998) or with home range size (Munn and Terborgh 1979; Munn 1985; Jullien and Thiollay 1998). However, if species within flocks have foraging ecologies that influence their response to alarms and thus reliance on heterospecific threat information, then this may also explain variation in flocking propensity among species. Magrath et al. (2009) demonstrated that ecologically distinct species (flocking vs. a nonflocking species) showed variation in response to heterospecific alarms as a function of perceptions of signal reliability. Species-specific variation in antipredator vigilance has been linked to other traits such as body height and size in African grazers (Fitzgibbon 1990; Illius and Fitzgibbon 1994) and auditory bullae and bipedal development in rodents (Brown et al. 1988). These traits potentially provide a mechanism to interpret interspecific dependence and a partial basis for understanding the formation of mixed-species groups in the context of predation risk. Additional experiments testing whether variation in different traits influences whether species use heterospecific information as a resource would be a useful step in incorporating information use in community ecology and evolution.

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