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EXPERIMENTAL EVIDENCE OF ALARM EAVESDROPPING ON AMAZONIAN MIXED-FLOCK FOLLOWERS BY TWO SOCIAL SENTINEL SPECIES: THE DUSKY-THROATED ANTSHRIKE (*THAMNOMANES ARDESIACUS*) AND THE CINEREOUS ANTSHRIKE (*T. SCHISTOGYNUS*)

Chelsey Hunts[1] **· Meredith Heather**[2] **· Ari E. Martínez**[3] **· Eliseo Parra**[4]*****

[1]Gili EcoTrust, Jalan Ikan Hiu, Gili Trawangan, Lombok, NTB, Indonesia 80111

[2]Department of Marine and Ecological Sciences, Florida Gulf Coast University, 10501 FGCU Blvd, Fort Myers, Florida 33965, U.S.A.

[3]Department of Biological Sciences, California State University Long Beach, Long Beach, California, 94268, U.S.A.

[4]Department of Biology, San Francisco State University, San Francisco, California, 94132, U.S.A.

E-mail: Eliseo Parra · parra@mail.sfsu.edu

Abstract · Mixed-species flocks of birds represent an ecological phenomenon resulting from a diversity of complex interactions and evolutionary pressures. Tropical and temperate forests include many examples of passerine birds that interact by forming mixed-species flocks and by eavesdropping on the alarm calls produced by heterospecifics. In the mixed-flock systems of the Amazonia, species of antshrikes (*Thamnomanes* sp.) have been shown to provide other flock members valuable information regarding threats from predation through their frequent alarm calls. Several species of flock attendees respond to the alarms of antshrikes with predator-avoidance behaviors, but no study has yet shown a reciprocal relationship between flock members and flock-leading antshrikes. Apparently distinct from mixed-flock systems of other forests, there has been little evidence to support that flock-leading species of antshrikes benefit from the alarm signals of other flock members. Using alarm signals recorded during *in situ* exposures of mixed-flock species to trained raptors, we conducted a playback experiment on 16 different mixed flocks to see to what degree antshrikes may be eavesdropping on the alarms of *Myrmotherula* antwrens. Eight Dusky-throated Antshrikes (*Thamnomanes ardesiacus*) and eight Cinereous Antshrikes (*T. schistogynus*) were presented with i) conspecific alarms, ii) White-flanked Antwren (*Myrmotherula axillaris*) alarms, iii) Grey Antwren (*M. menetriesii* alarms), and iv) a control. The results of our experiment support that the alarms of the two species of antwrens elicit a significant response from both species of antshrikes. Our model also shows that the responses of antshrikes to antwrens' alarms are indistinguishable from their response to conspecific alarms, yet different from a control (Marginal $R^2 = 0.36$, Conditional $R^2 = 0.37$). This suggests that highly social flock-leading species such as *Thamnomanes* antshrikes may benefit from the information provided by flock mates regarding predators. Furthermore, these patterns are consistent with eavesdropping interactions observed within mixed-flocks in ecologically similar but geographically distant forests.

Resumen · **Evidencia experimental de respuesta de dos especies centinelas a las alarmas de dos especies seguidoras en bandadas mixtas Amazónicas: el batará gorjioscuro (*Thamnomanes ardesiacus*) y el batará azulino (*T. schistogynus*)**
Las bandadas mixtas de aves representan un fenómeno ecológico fruto de una diversidad de interacciones complejas y presiones evolutivas. Se ha demostrado que muchas especies de aves Passeriformes interactúan en bandadas mixtas para aprovecharse de las alarmas producidas por otras especies en bosques tropicales y templados. En los sistemas de bandadas mixtas de la Amazonía, las especies de batará (*Thamnomanes* sp.) proveen a otros miembros de la bandada información valiosa sobre las amenazas de depredación a través de la emisión de alarmas frecuentes. Varias especies de la bandada responden a las alarmas de los batarás con comportamientos anti-depredadores, pero hasta el momento, ningún estudio ha mostrado una relación recíproca entre miembros de la bandada y las especies de batará. Este sistema de bandadas mixtas ha sido considerado distinto de otros, ya que no existe evidencia de que las especies líderes de batará se pueden beneficiar de las señales de alarma de los otros miembros de la bandada. Usando señales de alarma grabadas *in situ* de bandadas mixtas expuestas a aves rapaces entrenadas, realizamos un experimento de *playback* en 16 bandadas mixtas distintas para evaluar el nivel de respuesta de los batarás al escuchar señales de alarma de especies del género *Myrmotherula*. Presentamos ocho *T. schistogynus* y ocho *T. ardesiacus* con alarmas i) conespecíficas, ii) alarmas de *Myrmotherula axillaris*, iii) alarmas de *M. menetriesii* y iv) un control. Los resultados de nuestro experimento demuestran que las alarmas de las dos especies de *Myrmotherula* provocan una respuesta significativa en ambas especies centinela del género *Thamnomanes*. Nuestro análisis también muestra que las respuestas de los batarás a las alarmas de *Myrmotherula* sp. son similares a la respuesta ocasionada por las señales de alarma de conespecíficos, pero diferentes en comparación con un control (R^2 marginal = 0,36, R^2 condicional = 0,37). Esto sugiere que especies altamente sociales, como los líderes *Thamnomanes* sp., pueden beneficiarse de la información sobre amenazas de depredadores proporcionada por los otros miembros de la bandada. Además, estos patrones son consistentes con interacciones del uso de información heteroespecífica observadas en bandadas mixtas en áreas ecológicamente similares en otras regiones del mundo.

Key words: Eavesdropping · Fear landscape · Heterospecific · Mixed-species · Network · Playback

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INTRODUCTION

Many social animals produce signals intended for communicating information to conspecifics and family groups regarding the threat of predation (Kirchhof & Hammerschmidt 2006, Faust 2015, Gil et al. 2016). These valuable cues may also strongly influence the assembly, structuring, and maintenance of mixed-species groups (Goodale & Kotagama 2005, Martínez & Zenil 2012, Mokross et al. 2013). Closely associated species, which dedicate energy to predator avoidance, often supplement their own vigilance by "eavesdropping" on the alarms produced by heterospecifics (Rainey et al. 2004, Magrath et al. 2009, Martínez & Zenil 2012, Ridley et al. 2014). Associating with alarm-providing species has been shown to correspond with reductions in vigilance-related behaviors and increases in the time an individual spends foraging (Dolby & Grubb 1998, Sridhar et al. 2009, Ridley et al. 2014, Schmitt et al. 2016). In many rainforest systems, alarm eavesdropping and communication between individuals within mixed-species flocks (MSFs) of understory birds is studied as a driving feature of complex signal-based associations, where multiple species share information regarding predators (Munn & Terborgh 1979, Thiollay 1999, Goodale & Kotagama 2005, Terborgh et al. 2013). Within Sri Lankan tropical forests, Goodale & Kotagama (2008) provided strong evidence that Greater Racket-tailed Drongo (*Dicrurus paradiseus*), the Orange-billed Babblers (*Turdoides rufescens*), and several other species respond with predator-avoidance behaviors to the alarms of one another; this suggests that in these Paleotropical systems, more gregarious species, such as drongos, can benefit from participating in mixed-species flocks by gaining information from less social species. In temperate systems, mixed parid flocks containing titmice (*Baeolophus* sp.), chickadees (*Poecile* sp.), and tits (*Parus* sp.) are described as alarm generators within flocks often containing several species of parid birds (Sullivan 1984, Morse 1973, Dolby & Grubb 1998).

The general reciprocity of information-sharing within MSFs has been explored in flocks in many geographic locations, including the Paleotropics and temperate forests, but literature focused on South American MSFs remains missing (Magrath et al. 2007, Goodale & Kotagama 2008, Magrath et al. 2009). Amazonian MSFs share many characteristics with mixed-flocks in other parts of the world, including a social sentinel species and several associate flock "members" (Munn & Terborgh 1979, Thiollay 1999, Sridhar et al. 2009). The mixed-flocks occurring in Amazonian forests are remarkably stable communities that consistently include species of antshrikes from the genus *Thamnomanes* (Munn 1985, Martínez & Gomez 2013). The unidirectional effects of antshrike alarms on other MSFs members has been the focus of research for fear landscapes, eavesdropping networks, and the rules of community assembly (Martínez & Zenil 2012, Martínez et al. 2016, 2017, 2018). With the exception of antshrikes, the alarm signals of other species within South American MSFs are poorly studied or absent from literature. Through *in situ* experimental playback of multiple Amazonian MSFs species' alarm calls, we have explored the hypothesis that the social "leader" species (antshrikes) in Neotropical MSFs eavesdrops on the alarm signals of other core member species. Furthermore, by comparing the antshrikes' response to both conspecific and heterospecific alarm signals, we evaluated the relative symmetry of the alarm signals' effects on antshrikes. In doing so, we provide evidence that the interchange of information between MSFs members is common to flocks in multiple tropical locations, including the forests of the Amazonia.

METHODS

Study Species and Site. We conducted experimental playback trials on 16 different MSFs located in the vicinity of the Pantiacolla Lodge. Pantiacolla is located along the west bank of the Rio Alto Madre De Dios (12°39'2.0"S, 71°13'48"W), in the department of Madre de Dios, Peru. It is characterized as moist, tropical forest. Playback trials were completed over a one-week period from 25 July through 1 August 2015. The flocks located at Pantiacolla Lodge have been the focus of research beginning in 2013, and many territories include color banded individuals whose territories have been repeatedly observed over multiple years.

The MSFs at the Pantiacolla field site are always composed by a pair of antshrikes from the genus *Thamnomanes,* either the Dusky-throated Antshrike (*T. ardesiacus*), or the Cinereous Antshrike (*T. schistogynus*). The two species are generally separated by habitat, with the latter preferring locations with denser vegetation and tracts of bamboo. While flocks at Pantiacolla can be occasionally found with both antshrike species, we chose to use flocks where only one species of *Thamnomanes* was present. Regardless of the species of antshrike present, all of the flocks used in playback trials also included several species of antwrens from the genus *Myrmotherula*, including the White-flanked Antwren (*M. axillaris*) and the Gray Antwren (*M. menetriesii*). While MSFs in the Amazonia often contain several other species (e.g. *Automolus* sp., *Philydor* sp., *Tangara* sp.), these species often range between several different flock territories or are inconsistent in their flocking attendance. The antwren species chosen for our study represent core mixed flock species occupying a single flock territory and are found most consistently within MSFs (Munn & Terborgh 1979, Munn 1985).

Recordings. The examples of alarms used in the playback trials were recorded during previous research into alarm behavior of MSFs members at Pantiacolla. These alarms were produced in response to live, trained raptors. In depth information regarding the production and collection of those sounds is available in the methods of Martínez et al. (2017).

Alarm signals were trimmed and prepared from larger recordings using the sound editing applications Reaper (V. 5.03, Cuckos 2016) and Raven (V. 1.5, Cornell Lab of Ornithology 2014). We digitally removed other bird calls or unwanted noise from the samples and shortened each sample to the length of one alarm. The overall recording amplitude was adjusted so that each one would play at its maximum volume without any digital loss of quality (clipping). The final sample was then verified not to exceed 50 decibels when played at a distance of 15 m with a medium volume setting on the playback device (Tascam DR-05 digital audio recorder; Martínez & Zenil 2012). Any minor adjustments made to the Tascam volume to accomplish this was noted and replicated during the experimental trials. The final number of unique recordings used in the playback experiment included signals

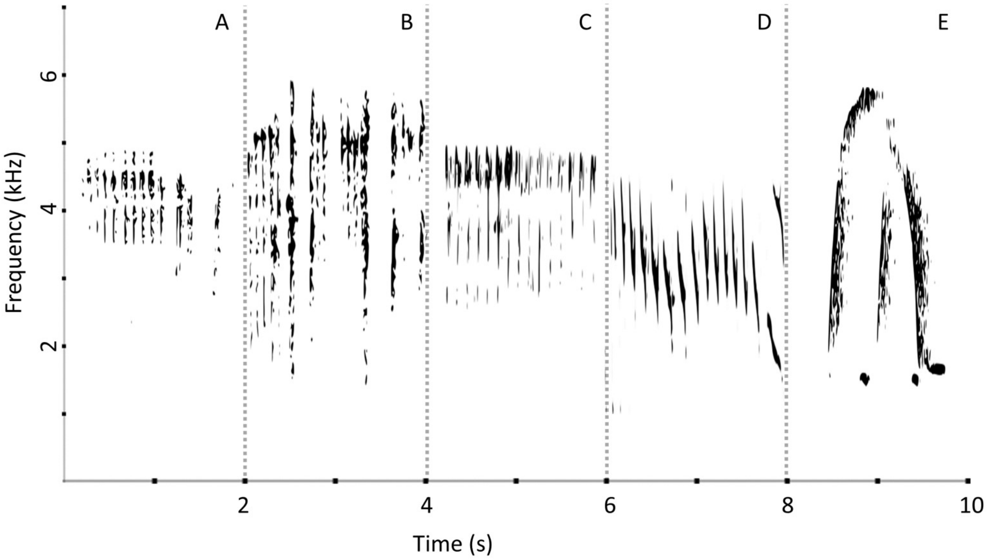

Figure 1. Spectrograms of alarm and control examples used during playback experiments. A) Alarm: Dusky-throated Antshrike (*T. ardesiacus*). B) Alarm: Bluish-slate Antshrike (*T. schistogynus*). C) Alarm: Gray Antwren (*M. menetriesii*). C) Alarm: White-flanked Antwren (*M. axillaris*). D) Song (control): Screaming Piha (*Lipaugus vociferans*).

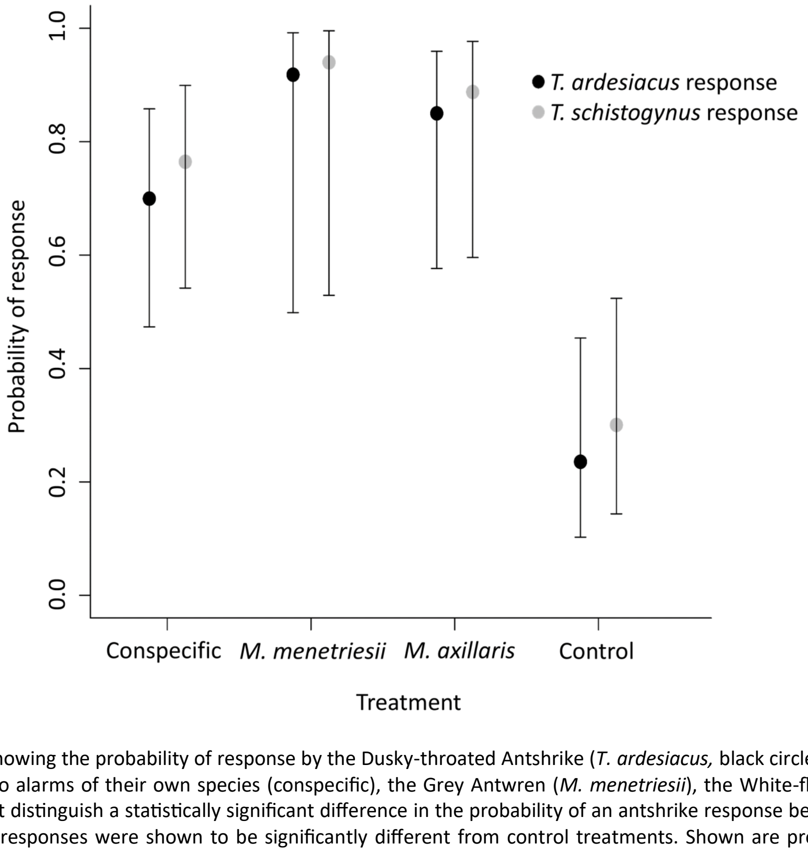

Figure 2. Summary graph showing the probability of response by the Dusky-throated Antshrike (*T. ardesiacus,* black circles) and the Bluish-slate Antshrike (*T. schistogynus,* grey circles) to alarms of their own species (conspecific), the Grey Antwren (*M. menetriesii*), the White-flanked Antwren (*M. axillaris*), and a control. Our model does not distinguish a statistically significant difference in the probability of an antshrike response between any of the alarm treatments. All of the alarm treatment responses were shown to be significantly different from control treatments. Shown are predicted means and 95% confidence intervals derived from model results.

from eight *T. ardesiacus,* eight *T. schistogynus*, three *M. axillaris*, three *M. menetriesii*, and five control calls from *Lipaugus vociferans*. The call of *L. vociferans* was chosen due to its nearly ubiquitous presence in Amazonian daytime soundscapes, its paucity of heterospecific flock interactions (Munn & Terborgh 1979), and the fact that its call shares similar temporal and frequency characteristics with all of the treatment alarm signals (Figure 1).

Playback Experiment. To test our hypothesis, we performed a series of *in situ* playback trials to flocks including either *T. ardesiacus* (N = 8) or *T. schistogynus* (N = 8). One antshrike was selected at each flock as the focal bird. Each antshrike was presented with four different sound stimuli in random

Table 1. Summary table of statistical model results from playback experiments showing the response of the flock sentinel (antshrike) to conspecific alarms, heterospecific alarms and a control. The flock sentinels response to conspecific alarms (flock sentinel) is not significantly different from their response to heterospecific alarms (*M. axillaris* and *M. menetriesii*). All responses were significantly different from the flock sentinels response to a control sound, presented at the same amplitude and overlapping in frequency and temporal characteristics with alarm signals.

Model Terms	Estimate	95% confidence interval	df	P-value
Intercept[†]	0.85	(-0.52, 2.21)	1,53	0.22
Species			4,53	
M. axillaris	1.57	(-0.78, 3.92)		0.19
M. menetriesii	0.89	(-1.01, 2.79)		0.36
Control	-2.02	(-3.78, -0.27)		0.02*
Sentinel Species	0.33	(-1.04, 1.70)	1,53	0.63

[†] The level of species corresponding to conspecific (*Thamnomanes sp.*) was used as the intercept in combination with *Thamnomanes ardesiacus* for the level when comparing among Sentinel Species. *Statistical significance.

order on a single day, which were i) conspecific alarm ii) *M. axillaris* alarm iii) *M. menetriesii* alarm, and iv) *L. vociferans* control. Flocks were located close to a frequently used trail system and are habituated to the presence of observers. The order of flocks used in playback trials was chosen at random. Playback trials were performed between 06:00 and 15:00 h, with a minimum of 15 minutes of rest in between treatments.

Two observers were used to perform playback trials. When a treatment flock was located, both observers positioned themselves and remained at a distance of 15 m from the focal antshrike and 15 m from each other. Observer A recorded behavioral data, while observer B played the stimulus audio from a playback speaker. Prior to each treatment, observer A recorded 30 seconds of flock vocal activity. This period was used to gather vocal behavior before the stimulus. After this time, observer A would signal observer B to play the recorded alarm or control. After the stimulus alarm was played, observer A made behavioral observations directly into a hand-held digital voice recorder, noting whether the focal bird responded with predator-avoidance behaviors (fleeing, freezing), or produced vocal responses immediately following the alarm, following methods used in other systems (Goodale & Kotagama 2005). Observer A also recorded the vocal activity of the focal bird for 30 seconds after the stimulus using a Tascam DR-05 digital recorder, and registered the species present in the flock. Playback treatments were postponed if the focal bird appeared agitated in response to other stimuli including: naturally occurring alarms, the presence of predators (i.e. Raptors), disruptive activity of wildlife (i.e. Peccaries), and territorial disputes with neighboring flocks.

Statistical Analysis. We fitted the responses to alarm calls using a generalized linear model with a binomial distribution. We modeled responses using species-specific alarm calls (including *Thamnomanes sp*. as conspecifics, and *M. axillaris*, *M. menetriesii* and *L. vociferans* as a control) and among sentinel species (represented by *T. ardesiacus* and *T. schistogynus*) as a fixed effect, and individual flocks as a random effect. We analyzed the goodness of fit of our model by analyzing the behavior of the residuals with respect to the predictor by using data simulations to scale the residuals to obtain values between 0 and 1 under the assumptions of each probability distribution (Hartig 2016). Subsequently, we derived R^2 values for fixed effects (Marginal R^2) and the full model (including the random effects, i.e. Conditional R^2). Our analyses were run using the lme4 and DHARMA packages (Bates et al. 2015, Hartig 2019) with the statistical application R version 3.3.2 (Bates, R Core Team 2015).

RESULTS

Our model revealed that both *T. ardesiacus* and *T. schistogynus* responded equally strongly to their own alarm calls and to the alarm calls of *M. axillaris* and *M. menetriesii*, but significantly less strongly to the alarm calls of *L. vociferans* (Table 1, Marginal $R^2 = 0.36$, Conditional $R^2 = 0.37$, Figure 2). Responses did not vary by antshrike species (Table 1).

DISCUSSION

Our results provide evidence that leading species of antshrikes in Amazonian MSFs participate in an eavesdropping relationship between heterospecific flocking members of *Myrmotherula* antwrens. As measured, there was no significant difference in the magnitude of response by antshrikes to the alarms of conspecifics or heterospecifics. This suggests that the alarms of heterospecific antwrens and conspecifics may impart a similar amount of threat information to antshrikes.

Previous research has shown a significant response of *M. menetriesii* and *M. axillaris* to the alarms of *Thamnomanes* antshrikes, as well as the response of several other flock associate species (Martínez et al. 2012). To our knowledge, no studies have demonstrated the reciprocal response in antshrikes, likely due to the rarity of available antwren alarm recordings and lack of first-hand observation regarding predation attempts within Amazonian MSFs. Our study addresses these limitations by sourcing audio from repeated exposures to live predators. This resource was unavailable to earlier researchers.

Several limitations may affect our studies' ability to draw significant conclusions regarding the relative importance of heterospecific alarm signals to antshrikes: our measure of response was generalized and summarily collected in a way that limits the measured effect to either including predator-avoidance behavior, or not. A more detailed collection of specific predator-avoidance behaviors (such as the direction of a focal animals' attention following the alarm stimulus) may be necessary to fully understand the comparison between antshrike responses to conspecific and heterospecific signals. It is also likely that several flocking species outside of the genus *Myrmotherula* produce alarms, such as the Red-crowned Ant Tanager (*Habia rubica*), the Plain-throated Antwren (*Isleria hauxwelli*), and other flock associates. These species were not addressed in this study. Further research should look for relationships between other flocking species. Special care should be taken to analyze soundscapes surrounding predation events, such as raptor fly-throughs, with attention given to the immediate community-wide vocal response.

Mixed-species groupings offer a substantial opportunity to better understand and test the rules that shape communities and ecological structures. Fear-based communication networks may have broad and far-reaching implications, from driving diversity in heterospecific groups, to cascading effects that result in the restructuring of entire ecosystems (Laundre 1978, Laundré et al. 2010, Gil et al. 2016, Martínez et al. 2018). We demonstrated that eavesdropping relationships in Amazonian mixed-flocks may share information more symmetrically than previous literature would suggest. Furthermore, we support a broader hypothesis that fear-driven communication relationships between highly social "sentinel" species and associate species may be a feature common to mixed-species groups sharing similar conditions and evolutionary pressures.

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REFERENCES

Brown, JS, JW Laundré & M Gurung (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal *of Mammalogy* 80: 385–399.

Dolby, AS & TC Grubb (1998) Benefits to satellite members in mixed -species foraging groups: an experimental analysis. Animal *Behaviour* 56: 501–509.

Faust, K (2015) *Animal Social Networks*. 1st ed. Oxford University Press, Oxford, United Kingdom.

Gil, MA, Z Emberts, H Jones & CMS Mary (2016) Social information on fear and food drives animal grouping and fitness. *American Naturalist* 189: 227–241.

Goodale, E & SW Kotagama (2005) Alarm Calling in Sri Lankan Mixed-Species Bird Flocks. *Auk* 122: 108–120.

Goodale, E & SW Kotagama (2008) Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behavioral Ecology* 19: 887–894.

Kirchhof, J & K Hammerschmidt (2006) Functionally Referential Alarm Calls in Tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) – Evidence from Playback Experiments. *Ethology* 112: 346–354.

Laundré, JW, L Hernandez & WJ Ripple (2010) The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal* 3: 1–7.

Magrath, RD, BJ Pitcher & JL Gardner (2007) A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behavioral Ecology* 18: 944–951.

Magrath, RD, BJ Pitcher & JL Gardner (2009) An avian eavesdropping network: Alarm signal reliability and heterospecific response. Behavioral Ecology 20: 745–752.

Martínez, AE, & JP Gomez (2013) Are mixed-species bird flocks stable through two decades? *American Naturalist* 181: E53–E59.

Martínez, AE, JP Gomez, JM Ponciano & SK Robinson (2016) Functional traits, flocking propensity, and perceived predation risk in an amazonian understory bird community. *American Naturalist* 187: 607–619.

Martínez, AE, E Parra, LF Collado & VT Vredenburg (2017) Deconstructing the landscape of fear in stable multi-species societies. Ecology 98: 2447-2455

Martínez, AE, E Parra, O Muellerklein & VT Vredenburd (2018) Fear-based niche shifts in neotropical birds. *Ecology* 99: 1338–1346.

Martínez, AE, & RT Zenil (2012) Foraging guild influences dependence on heterospecific alarm calls in Amazonian bird flocks. Behavioral Ecology 23: 544–550.

Mokross, K, TB Ryder, MC Côrtes, JD Wolfe & PC Stouffer (2013) Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. *Proceedings of the Royal Society B*: Biological Sciences 281.

Morse, DH (1973) Interactions between tit flocks and Sparrowhawks *Accipiter Nisus*. *Ibis International Journal of Avian Science* 115: 591–593.

Munn, CA (1985) Permanent canopy and understory flocks in Amazonia: species composition and population density. *Ornithological Monographs* 36: 683–712.

Munn, CA & JW Terborgh (1979) Multi-species territoriality in Neotropical foraging flocks. *Condor* 81: 338–347.

Rainey, HJ, K Zuberbu, PJB Slater, S Andrews & SA Ky (2004) Hornbills can distinguish between primate alarm calls. *Proceedings of the Royal Society B*: Biological Sciences 271: 755–759.

Research, B (2014) Raven Pro: Interactive Sound Analysis Software. Cornell Lab of Ornithology. Ithica, New York, USA. Available at http://www.birds.cornell.edu/raven.

Ridley, AR, EM Wiley & AM Thompson (2014) The ecological benefits of interceptive eavesdropping. *Functional Ecology* 28: 197–205.

Schmitt, MH, K Stears & AM Shrader (2016) Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe. *Behavioral Ecology* 27: 1073–1077.

Sridhar, H, G Beauchamp & K Shanker (2009) Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behavior* 78: 337–347.

Sullivan, KA (1984) Information exploitation by Downy Woodpeckers in mixed-species flocks. Behaviour 91: 294–311.

Team, RD (2016) Reaper Digital Audio Workstation. Cockos. New York, NY, USA. Available at http://www.reaper.fm/index.php.

Team, RDC (2015) R: A Language and Environment for Statistical Computing. Available at http://www.r-project.org.

Terborgh, J, SK Robinson, TA Parker III & CA Munn (2013) Structure and organization of an Amazonian forest bird community. *Ecological Society of America* 60: 213–238.

Thiollay, JM (1999) Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: an intertropical comparison. *Journal of Avian Biology* 30: 282.