## Original Article

# Asymmetric eavesdropping between common mynas and red-vented bulbuls

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Heterospecific eavesdropping on alarm calls is well documented, but less is known about the factors influencing asymmetry in the reliability of heterospecific alarm calls. Partial overlap of predators between heterospecifics has been hypothesized as 1 possible mechanism driving asymmetric eavesdropping. We tested the responses of common mynas (*Acridotheres tristis*) and red-vented bulbuls (*Pycnonotus cafer*) to reciprocal playbacks of alarm and social calls by measuring changes from baseline in the rates of fly-bys near the speaker and in rates of singing. We found an asymmetric communication network between bulbuls and mynas: bulbuls only responded to conspecific alarm calls, whereas mynas responded to both bulbul and conspecific alarm calls. This communication asymmetry may be due to a partial overlap in predators between species. Mynas were observed to spend time in both trees and on the ground and may be susceptible to both aerial and ground predators. We observed bulbuls primarily in trees and therefore may be susceptible primarily to aerial predators. If this is the case, then the alarm calls of mynas are less reliable to bulbuls compared with the reliability of alarm calls of bulbuls to mynas. However, further studies into the predators of each species are necessary before drawing a definitive conclusion. Our study demonstrates a differential responsiveness of 1 species on the alarm calls from another species for predator information and underscores the importance in considering heterospecific communication networks in the removal of species from a community.

*Key words*: acoustic communication, alarm call, asymmetric eavesdropping, common myna, communication network, heterospecific eavesdropping, information transfer, interspecific communication, red-vented bulbul.

## INTRODUCTION

Eavesdropping is where an individual other than the intended receiver gains information from a signaling interaction between 2 or more individuals, and can occur between or within species (McGregor and Peake 2000; Magrath et al. 2014; Ridley et al. 2014). Heterospecific eavesdropping of alarm calls has been well documented (e.g., Marler 1955 1957; Shriner 1998; Fichtel 2004; Magrath et al. 2007, 2009; Lea et al. 2008; Fallow and Magrath 2010; Goodale et al. 2010; Ridley et al. 2014). Any system of 2, or more, sympatric species that have predators in common has the potential for eavesdropping. Alarm calls typically communicate an immediate threat to conspecifics, so by being sensitive to the alarm calls of other species that have predators in common, individuals may have a higher chance of avoiding predation (Forsman and Mönkkönen 2001; Rainey et al. 2004).

A 2-species eavesdropping system may not be symmetrical, meaning that 1 species obtains more information from heterospecific alarm calls than the other species (Magrath et al. 2009;

Randler and Vollmer 2013; Ridley et al. 2014). Magrath et al. (2009) developed a framework for predicting asymmetric eavesdropping networks. This framework defines the utility of interspecific calls in terms of stimulus "reliability." Reliability is a function of the relevance of the alarm call to the receiving species, the degree to which the alarm calling species discriminates between threats and nonthreats, and the extent to which the signaling species uses signals for deception. More useful heterospecific alarm calls have greater relevance, greater discriminability and/or are used less for deception. Consequently, asymmetric eavesdropping is predicted in systems described by between-species differences in any of these 3 characteristics. We refer readers to Magrath et al. (2009) for a formal development of this framework and examples of each of the 3 characteristics of information reliability.

Despite predictions of the characteristics of systems with asymmetric eavesdropping (Magrath et al. 2009), to date, these predictions have rarely been explicitly tested. Many documented heterospecific eavesdropping systems are symmetric (Shriner 1998; Fichtel 2004; Magrath et al. 2007 2009). By comparing the level of response to the signals of conspecifics and heterospecifics, one can ascertain the degree to which eavesdropping is symmetric. In symmetric eavesdropping, a heterospecific alarm call should evoke

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the same response as a conspecific alarm call. In asymmetric eavesdropping, the species receiving a heterospecific alarm call with less relevance should exhibit a less intense response compared with that evoked from a conspecific alarm call.

Asymmetric eavesdropping systems may arise due to partially overlapping predators. In these cases, the alarm calls of a heterospecific are less relevant to the other species because heterospecific alarm calls do not consistently correspond to a threatening predator. Randler and Vollmer (2013) found that blue tits (*Cyanistes caeruleus*) responded more strongly to heterospecific mobbing calls than did chaffinches (*Fringilla coelebs*), possibly because chaffinches are relatively larger and thus are less vulnerable to particular predators. Asymmetric eavesdropping due to partially overlapping predators between intraspecific age classes has been documented within bonnet macaques (*Macaca radiate*). Adult alarm calls elicited a more intense response from juveniles compared with adults, possibly because juveniles are more vulnerable to the predators of adults (Ramakrishnan and Coss 2000).

Here, we tested for asymmetric eavesdropping between common mynas (*Acridotheres tristis*) and red-vented bulbuls (*Pycnonotus cafer*), which are sympatric on the island of Mo'orea, French Polynesia. Mo'orea is part of an isolated island chain that is home to relatively few species of birds (Pratt et al. 1987; Spotswood et al. 2013). Mynas and bulbuls are mid-sized passerines that are native to India where they have historically been sympatric (Ali and Ripley 2002). Mynas and bulbuls were first documented on the island in the early 1900s (Thibault et al. 2002) and the 1980s (Spotswood et al. 2013), respectively. On Mo'orea, mynas and bulbuls share overlapping habitats (Thibault et al. 2002; Spotswood et al. 2013). Mynas are gregarious, forming predominately conspecific communal roosts in trees, are very vocal and forage in conspecific flocks (Counsilman 1974b; Tindall et al. 1996). Mynas primarily eat ground-dwelling invertebrates and small vertebrates, but occasionally eat fruits and seeds (Counsilman 1974b; Pell and Tidemann 1997). Conspecific disputes over non-nesting sites are rare (Pell and Tidemann 1997). However, mynas are commonly aggressors of and often harass other avian species to gain access to nesting sites, food, and territory (Counsilman 1974a; Byrd et al. 1983; Rowe and Empson 1996; Tindall et al. 1996; Pell and Tidemann 1997; Thibault et al. 2002; Blanvillain et al. 2003; Dhami 2009).

Bulbuls are arboreal and primarily forage on fruit, leaves, and nectar, but have been known to occasionally eat flying and ground-dwelling insects (Bhatt and Kumar 2001). Bulbuls are nonterritorial (Bhatt and Kumar 2001), but have been known to be aggressive with other avian species on islands outside Mo'orea (Thibault et al. 2002), and sing throughout the year (Kumar 2004).

Given that mynas and bulbuls were sympatric in our study sites, we expected that mynas and bulbuls should have an established communication network on Mo'orea. In terms of Magrath et al.'s (2009) framework for asymmetric eavesdropping, bulbuls and mynas are of similar size so we expected both to have common predators (Dalesman et al. 2007). Thus, we expected that heterospecific alarm calls should be relevant to both species. The ability of mynas and bulbuls to discriminate between threats and nonthreats is relatively unknown. Between species, foraging competition should be relatively low given the different diets, making the use of alarm calls for heterospecific deception likely low. However, we expected that Mynas, being more social, may be more likely to use alarm calls for intraspecific deception compared with bulbuls.

We also tested for eavesdropping to heterospecific nonalarm songs. Singing often indicates that an area is void of predators

(Møller 1992). Also, heterospecifics that share similar resources and/or habitat may eavesdrop on song in order to ascertain the location of quality habitat or resources (Sridhar et al. 2009; Goodale et al. 2010). Given that mynas eat everything that bulbuls eat and bulbuls only partially overlap with the diet of mynas, we predicted that eavesdropping to nonalarm vocalizations would be asymmetrical because not everything that mynas eat is relevant to bulbuls. However, in our system, as mynas are generally aggressive to heterospecifics, social vocalizations from mynas may indicate the presence of an aggressive threat from the perspective of bulbuls. Therefore, we predicted that bulbuls would leave the area of the playback of myna songs. In terms of responses to conspecific social calls, we predicted that mynas would be more drawn to myna social calls, observed as an increase in flights near the playback speaker, as they tend to be more gregarious than bulbuls. Meanwhile, we expected that bulbul social calls would evoke minimal response in terms of flights near the playback speaker as they are less territorial and less social.

## METHODS

### Site

Experiments were conducted within the UC Berkeley Gump Station (−17°29.428′, −149°49.586′) and 6 surrounding sites in Mo'orea, French Polynesia, from 28 January to 5 February 2014. We chose these sites because both of our study species, mynas and bulbuls, were found at these locations. A mix of forest and anthropogenic forest clearing occurred within each location. Each site contained multiple trial locations at least 50 m apart. We performed multiple trials within a sampling site on a given day. We revisited sites by >1 day and did not resample trial locations. These sampling methods helped to ensure that the groups of birds in each trial were naive to playbacks.

### Exemplar selection

We recorded myna and bulbul vocalizations at our experimental sites. These recordings contained considerable background noise from traffic, running water, and other calling birds. As this noise will likely evoke behavior (e.g., startle response) unrelated to response to the experimental social or alarm calls, we elected to use vocalizations obtained on the Internet for playback. None of these vocalizations were recorded in Mo'orea.

We obtained all high-quality recordings made off the island from Michigan State University's Avian Vocalization Center (AVoCet Database, 2008–2014), NZ Biosecurity (Ministry for Primary Industries, New Zealand), and Xeno-Canto online databases (Xeno-Canto Foundation, 2005–2014; Figure 1). In total, we found 4 exemplars of myna songs, 6 exemplars of bulbul songs, 3 exemplars of myna alarm vocalizations, and 2 exemplars of bulbul alarm vocalizations (Figure 1; Appendix 1). Background noise was reduced using Audacity 2.0.5's "Noise Removal" Effect (Audacity Team 2012). Spectrograms were created using Raven Lite 1.0 (Charif et al. 2006).

The spectrograms of nonalarm vocalizations from bulbuls, which we recorded from 6 different individuals on Mo'orea, corresponded in terms of spectral frequency and vocalization rate of the contact calls of red-vented bulbuls studied in India (Kumar 2004). Thus, we feel confident that they were indeed bulbul contact calls.

Mynas have a complex vocal repertoire and likely have some individual variation in their song, but future studies are required
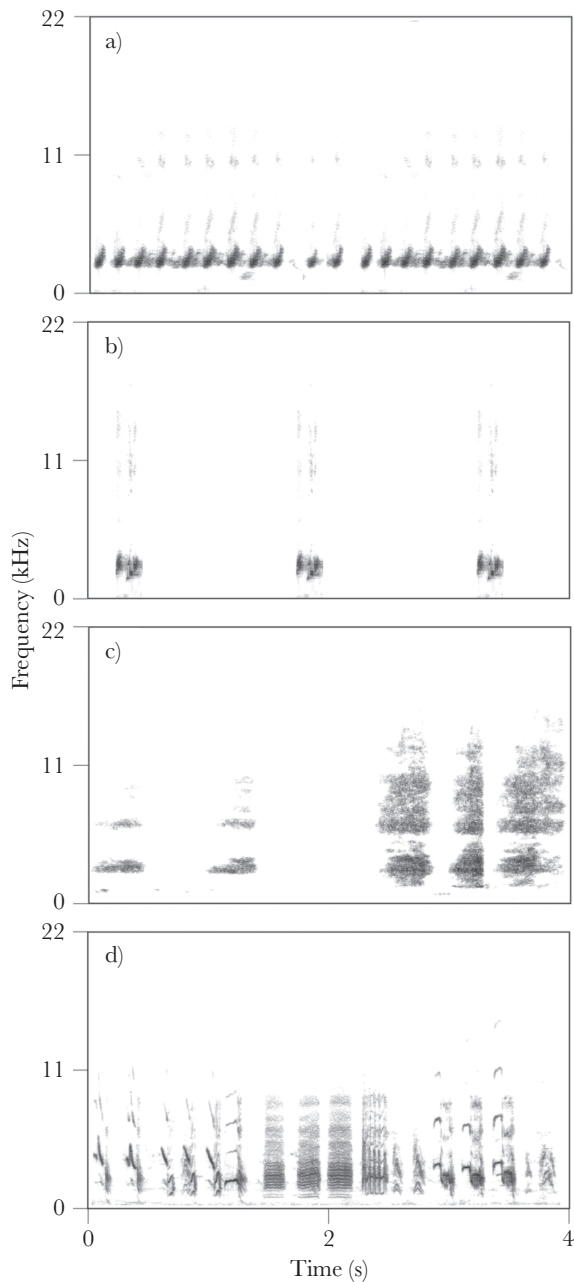
**Figure 1**

Audio spectrograms of an example of (a) bulbul alarm call, (b) bulbul nonalarm vocalization, (c) myna alarm vocalization, and (d) myna nonalarm vocalization used in playback. These units were repeated at a natural rate to generate our playback exemplars. Spectrograms were produced in Raven Pro 1.0 and set to a Hamming window function, 1024 points Fast Fourier Transform size, 80 dB from peak clipping level, temporal grid resolution of 0.726 ms with 96.88% overlap, and a frequency grid resolution of 43.07 Hz. Frequency axis is shown 0–22 kHz. Time axis is shown 0–4 s.

to properly document this. We recorded the nonalarm vocalizations of 10 mynas that were either foraging in a group on the ground ($N = 4$) or vocalizing on a perch ($N = 6$). From these recordings, we identified 8 unique syllables. Ground-foraging mynas used 6 unique syllables. Perched mynas used all 8 unique syllables. Song structure of both socializing and lone mynas was

highly variable with no obvious repeated pattern of syllables. Given a lack of any vocalization feature(s) that clearly distinguish mynas foraging in groups from perched mynas, we believe the nonalarm vocalizations that we recorded from perched mynas can also function as contact calls. We use the term "social vocalization" interchangeably with nonalarm vocalization throughout the article.

We compared off-island exemplars with the recordings that we made on Mo'orea. By examining spectrograms, we saw that vocalization types, except for myna social vocalizations, were similar between calls recorded on Mo'orea and the off-island exemplars (the bandwidths slightly differed mostly likely because the exemplars we used in our playbacks were particularly high quality and did not have substantial frequency-dependent attenuation). In addition, we identified 11 unique syllables among the myna social vocalizations from the off-island exemplars. Four of these syllables were not found in our recordings made on Mo'orea. One syllable from recordings made on Mo'orea was not found in the off-island exemplars. We interpreted these differences as slight, and as the off-island recordings were of substantially higher quality, we elected to only use the off-island exemplars.

We measured average rates of vocalizations from our recordings of bulbuls and mynas on Mo'orea. We looped a single social call or a single alarm call (1 call from a different recording source per playback exemplar) by inserting intervals of silence between vocalizations such that playbacks were at the natural rate (interbout intervals: 3.5 s for the myna alarm calls, 1.6 s for the myna songs, 0.1 s for the bulbul alarm calls, and 2.6 s for the bulbul songs).

The sounds were uploaded in AIFF format onto an iPod Touch and an iPhone 4S (Apple Inc., Cupertino, CA). Using Sound Studio 4.5 (Felt Tip Inc., New York City, NY) and a Sper Scientific Digital Sound Meter 840029 (weighting level A, peak amplitude; Sper Scientific, Scottsdale, AZ), the audio files were calibrated with a Tivoli Audio, PAL speaker to be broadcast at $85 \pm 1$ dB SPL, measured at 1 m. This amplitude was chosen because calls sounded natural.

## Experimental setup

Trials were divided into a 2-min baseline of silence followed by 5 min of playback. By playing the calls in loops for 5 min, we expected that the time over which calls were broadcast would overshadow the effect of each call's length on the likelihood of being heard. During the baseline period, we counted the number of mynas and bulbuls flying within 20 m of the speaker ("fly-bys") and the number of social and alarm vocalizations of mynas and bulbuls heard. During the playback, we recorded the above behaviors in addition to latency to approach within 10 and 5 m of the speaker. We also recorded factors that may influence bird behavior and response to playback, such as habitat type, maximum number of mynas and bulbuls observed at a given time during the trial, wind velocity using the Beaufort scale (Grubb 1975; Finney et al. 1999; Shamoun-Baranes et al. 2006), percent cloud cover (Finney et al. 1999), presence of rain (Elkins 2004), speaker's distance to cover, and type of cover (Horn et al. 2003). Based on the dominant landscape characteristics, the habitat for each trial was categorized as quiet road, busy road, forest, or an open clearing of grass to account for differential behavior between environments (Glennon 2005).

We walked along roads and public areas and placed the speaker at a location where at least 1 myna was located by sight or sound.

Bulbuls were less visible and vocalized less frequently than mynas at our study sites. Thus, as both mynas and bulbuls were sympatric, by placing the speaker at a confirmed location of a myna we assumed both mynas and bulbuls would hear the playback.

The trial began 30 s after placing the speaker, during which time observers moved ca. 20 m from the speaker. A trial consisted of 2 min of baseline silence followed by 5 min of looped vocalizations. Vocalizations were looped in such a way as to reflect natural rates of vocalizations established by personal observation of recordings from the island. Exemplars and treatments were systematically varied according to a predetermined schedule to avoid potential carry-over effects. Groups of 2 observers collected data simultaneously in different study sites. Groups were made up of the same people each day to account for observer variability and we subsequently tested for observer effects.

## Statistical analysis

We analyzed the change in rate of behavior from baseline (the 2 min of silence preceding playback) to the change in rate after playback. Post-playback rate was measured between mins 2 and 3 after playback. We chose this time period because most responses did not take place within min 1 and most birds had left the area by min 4. Behaviors analyzed were fly-bys and vocalizations of mynas and bulbuls. We analyzed changes in rates of bulbul behaviors only for those trials where bulbuls sang or were seen in the baseline period (i.e., instances where we knew bulbuls were nearby). We fitted generalized linear models with change in rate of behavior as the dependent variable, and playback treatment (4 levels: bulbul alarm, bulbul social, myna alarm, and myna social) as independent variables. We used a Gaussian identity link function because responses were heterogeneous across treatments and could not be normalized through transformation. If a model was statistically significant, indicating that bulbuls or mynas could discriminate among treatments, then we performed planned pairwise comparisons using Tukey's method and no correction for multiple comparisons.

In order to identify whether or not birds responded to a playback treatment compared changes in rates of behaviors to 0 using Wilcoxon signed-rank tests (Wilcoxon 1945).

We used contingency table analyses to evaluate the homogeneity of exemplars, observers, habitats, and locations across treatments in order to eliminate the possibility that these were confounding factors for avian response to treatment. To determine whether other covariates (the initial and maximum number of conspecifics) explained variation in changes in rates of vocalizations or fly-bys, we fitted generalized linear models with these covariates as independent variables.

We checked for exemplar effects independently by fitting generalized linear models of response to a given playback as dependent variable onto the exemplar of that given playback. For example, to test for the effect of myna exemplars on bulbul fly-bys, we modeled bulbul fly-bys on myna alarm exemplars. Similarly, we created separate models of bulbul fly-bys onto myna social exemplars, bulbul alarm exemplars and bulbul social exemplars. We tested separate models because it does not make sense to test for an effect of bulbul alarm exemplars on responses to myna alarm playback. We then repeated this process for the other response variables: bulbul vocalizations, myna fly-bys, and myna vocalizations.

We tested for the possibility that a given response (fly-bys or vocalizations of either species) during a trial influenced any other responses (i.e., correlations among observations) by fitting generalized linear models with Gaussian identity link functions. For

example, with bulbul fly-bys as the dependent, we fitted 3 models with bulbul vocalizations, myna fly-bys, or myna vocalizations as the independent variable. Similarly, we repeated this process with bulbul vocalizations, myna fly-bys, or myna vocalizations as the dependent variable.

Analyses were performed using R 3.0.2 (R Core Team 2013). We interpreted $P$ values $\leq 0.05$ as significant.

## RESULTS

### Response to playback type

We conducted 84 playback experiments in areas where mynas were heard or seen before setup. In 61 of these trials, bulbuls were seen or heard during the baseline (2 min of silence before playback). Bulbuls increased the rate of fly-bys from baseline in response to the playback of bulbul alarm calls ($W = 26$, $P = 0.041$, $\mathcal{N} = 14$; Figure 2, Table 1). Bulbuls decreased the rate of vocalizing in response to bulbul social ($W = 5$, $P = 0.038$, $\mathcal{N} = 11$) and myna social ($W = 28$, $P = 0.038$, $\mathcal{N} = 18$) playbacks. Bulbuls did not significantly change their rate of fly-bys to bulbul social vocalizations (change in fly-by rate was nearly uniformly 0, so a test statistic could not be computed; $\mathcal{N} = 11$), myna alarm calls ($W = 3$, $P = 0.053$, $\mathcal{N} = 18$), or myna social vocalizations ($W = 16$, $P = 0.42$, $\mathcal{N} = 18$). Bulbuls did not significantly change their rate of vocalizing in response to bulbul alarm calls ($W = 48.5$, $P = 0.83$, $\mathcal{N} = 14$) or myna alarm calls ($W = 54.5$, $P = 0.48$, $\mathcal{N} = 18$).

Mynas increased their rate of fly-bys in response to bulbul alarm calls ($W = 79$, $P = 0.017$, $\mathcal{N} = 21$), bulbul social vocalizations ($W = 81$, $P = 0.01$, $\mathcal{N} = 19$), and myna alarm calls ($W = 148$, $P = 0.027$, $\mathcal{N} = 22$). Mynas did not significantly change their rate of fly-bys in response to myna social vocalizations ($W = 72.5$, $P = 0.056$, $\mathcal{N} = 18$). Mynas did not change their rate of vocalizations in response to any type of playback: bulbul alarm calls ($W = 32$, $P = 0.11$, $\mathcal{N} = 21$), bulbul social vocalizations ($W = 38.5$, $P = 0.13$, $\mathcal{N} = 19$), myna alarm calls ($W = 70$, $P = 0.19$, $\mathcal{N} = 18$), or myna social vocalizations ($W = 66.5$, $P = 0.15$, $\mathcal{N} = 18$; Figure 2, Table 1).

### Discrimination among playback types

Playback treatment influenced the change in rate of bulbul fly-bys ($F_{3,57} = 4.62$, $P = 0.006$, $\mathcal{N} = 61$; Figure 2a, Table 2). Bulbuls flew by the playback speaker more often after hearing a bulbul alarm playback compared with myna alarm calls ($\mathcal{Z} = -3.46$, $P < 0.001$) and compared with myna social vocalizations ($\mathcal{Z} = -3.07$, $P = 0.002$). These results indicate that bulbuls discriminated between bulbul alarm calls and myna social vocalizations, and between bulbul alarm calls and myna alarm calls.

Although bulbuls decreased their rates of vocalizing to bulbul social and myna social playbacks, they did so in a similar way such that playback type did not differentially affect the change in rate of bulbul vocalizations ($F_{3,57} = 0.98$, $P = 0.41$, $\mathcal{N} = 84$; Figure 2b). Similarly, mynas increased their rates of vocalizing to bulbul social and bulbul alarm playback to the same extent such that playback type did not differentially affect the change in rate of myna fly-bys ($F_{3,80} = 0.017$, $P = 1.00$, $\mathcal{N} = 84$; Figure 2c). Playback type did not significantly change the rate at which mynas vocalized ($F_{3,80} = 0.27$, $P = 0.84$; Figure 2d).

Treatments were not significantly uneven in distribution among observers ($\chi^2 = 1.18$, $P = 0.76$), habitat ($\chi^2 = 3.63$, $P = 0.93$), or location ($\chi^2 = 10.1$, $P = 0.99$).
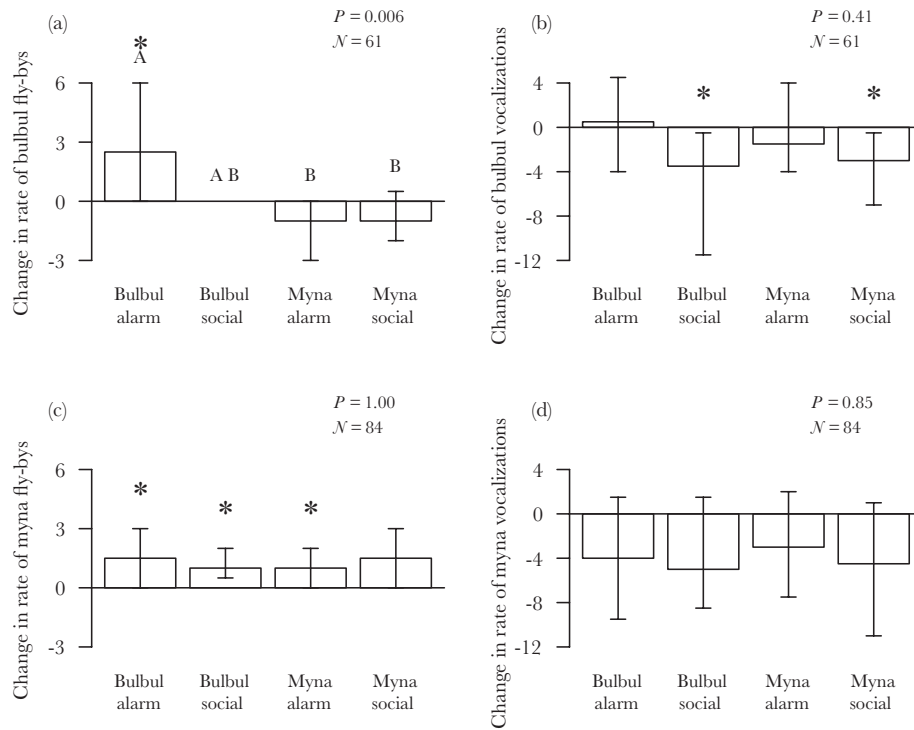
**Figure 2**
Change from baseline (2-min silence before playback) in the rate (min⁻¹) of (a) bulbul fly-bys, (b) bulbul vocalizations, (c) myna fly-bys, and (d) myna vocalizations by treatment between min 2 and min 3 of playback. $Y$ axis is the nonparametric point estimate of the mean (Wilcoxon 1945). Different letters above bars indicate significantly different pairwise comparisons. Asterisks indicate responses that significantly changed from baseline. $P$ values describe goodness-of-fit for the generalized linear model of treatment onto change in rate of behavior. Bars are estimated 95% Wilcoxon signed-rank confidence interval (Wilcoxon 1945).

**Table 1**

**Summary of bulbul or myna responses to conspecific and heterospecific playbacks indicating those playback types evoking a significant response**

|  | Conspecific alarm calls | Conspecific social vocalizations | Heterospecific alarm calls | Heterospecific social vocalizations |
|---|---|---|---|---|
| Bulbul responses |  |  |  |  |
|   Change in rate of fly-bys | ✓ |  |  |  |
|   Change in rate of vocalizations |  | ✓ |  | ✓ |
| Myna responses |  |  |  |  |
|   Change in rate of fly-bys | ✓ |  | ✓ | ✓ |
|   Change in rate of vocalizations |  |  |  |  |

Terms "conspecific" and "heterospecific" are used in reference to each respective avian species.

Avian behaviors were not significantly influenced by a specific exemplar used within a playback type (all $P > 0.08$) or location (all $P > 0.12$). The use of exemplars was not unevenly distributed among trials (all $P > 0.31$). The responses (fly-bys or vocalizations) during playback of either species (bulbuls or mynas) did not have a significant effect on the way in which birds responded during playback (all $P > 0.08$).

## DISCUSSION

We found a communication network between red-vented bulbuls and common mynas in Mo'orea, French Polynesia. Mynas responded to bulbul alarm calls, but bulbuls did not respond to myna alarm calls. Therefore, eavesdropping is asymmetric in this system. Both bulbuls and mynas responded to conspecific alarm calls by increasing the rate of flights near the speaker, which

indicates that individuals are approaching the speaker possibly in order to visually ascertain the level of threat that a predator imposes.

Niche differences owing to differences in diet may result in a partial overlap of predators between mynas and bulbuls and may be responsible for asymmetric eavesdropping between bulbuls and mynas. Possible avian predators on Mo'orea include rats (*Rattus rattus*, *Rattus exulans*), feral cats (*Felis domesticus*), and swamp harriers (*Circus approximans*, Blanvillain et al. 2003). Despite both mynas and bulbuls being of similar sizes, both species may not fall prey equally to all predators, a pattern that could lead to asymmetric eavesdropping (Magrath et al. 2009). We observed mynas both in trees and on the ground and, therefore, may be vulnerable to all the aforementioned predators. By contrast, we mostly observed bulbuls to remain in trees; bulbuls might be vulnerable primarily to aerial predators, such as swamp harriers. Therefore, a threat to

**Table 2**

**Results of generalized linear models (Gaussian error distribution) for change in rate of fly-bys and vocalizations with type of playback**

| | Estimate | Standard error | $t$ | $P$ | $N$ |
|---|---|---|---|---|---|
| Bulbul fly-bys ($N_{tot} = 61$) | | | | | |
| Bulbul social | −1.25 | 0.65 | −1.92 | 0.06 | 11 |
| Myna alarm | −1.98 | 0.57 | −3.56 | 0.001 | 18 |
| Myna social | −1.76 | 0.57 | −3.07 | 0.003 | 18 |
| Bulbul vocalizations ($N_{tot} = 61$) | | | | | |
| Bulbul social | −3.64 | 1.91 | −1.26 | 0.21 | 11 |
| Myna alarm | −5.56 | 2.88 | −0.02 | 0.98 | 18 |
| Myna social | −2.83 | 2.55 | −1.11 | 0.27 | 18 |
| Myna fly-bys ($N_{tot} = 84$) | | | | | |
| Bulbul social | −0.11 | 0.54 | −0.20 | 0.84 | 19 |
| Myna alarm | −0.09 | 0.52 | −0.17 | 0.87 | 22 |
| Myna social | −0.90 | 0.52 | −0.17 | 0.87 | 22 |
| Myna vocalizations ($N_{tot} = 84$) | | | | | |
| Bulbul social | 0.03 | 2.96 | 0.01 | 0.99 | 19 |
| Myna alarm | 0.42 | 2.85 | 0.15 | 0.88 | 22 |
| Myna social | −1.90 | 2.85 | −0.67 | 0.51 | 22 |

Estimates were made with bulbul alarm-call playback as the reference level.

mynas may not always be a threat to bulbuls. Thus, myna alarm calls have low reliability from the perspective of bulbuls and bulbuls may therefore have been selected to ignore myna's alarm calls (Magrath et al. 2009). If this situation is indeed the case, then from the perspective of mynas a threat to bulbuls is always a threat to mynas. Therefore, mynas should respond to bulbul alarm calls in a manner similar to conspecific alarm calls, which is what we found; mynas increased the rate of fly-bys in response to both conspecific and bulbul alarm calls. However, a clearer understanding of the predators of each species is necessary to definitely conclude that a difference in vulnerabilities to predators is the cause of asymmetry.

Asymmetric eavesdropping may also result from differences in the degree to which each species has learned to associate a predator with heterospecific alarm calls (Fallow et al. 2013). A lack of response of bulbuls to myna alarm calls suggests that bulbuls may not have learned to associate myna's calls with predators. Both mynas and bulbuls originate from India where they have historically been sympatric (Ali and Ripley 2002) and presumably have had enough time for selection to act on learning capabilities. Given a long evolutionary history with mynas, bulbul learning may have been inhibited if myna alarm calls are not consistently associated with a threat. This explanation may be the case if not all predators of mynas are predators of bulbuls.

A difference in gregariousness between heterospecifics has also been hypothesized to drive asymmetric eavesdropping on alarm calls. Ridley et al. (2014) found the more social of 2 species to be insensitive to alarm calls of a heterospecific as a more social species is likely to have an established conspecific system for communicating threat. The nonsocial heterospecific, which has limited conspecific information, showed greater response to heterospecific alarm calls (Ridley et al. 2014). In our results, mynas, being more social than bulbuls, responded to bulbul alarm calls where bulbuls did not respond to myna alarm calls. Therefore, a difference in gregariousness between bulbuls and mynas may not be the primary driver of asymmetric eavesdropping between mynas and bulbuls. Consequently, asymmetric eavesdropping of alarm calls in this system may be better explained by a difference in relevance of alarm calls to each species. However, more work needs to be done to clearly understand the predators of mynas and bulbuls.

Mynas did not respond to conspecific social calls through vocalizations or fly-bys, nor did they change their rate of vocalizing in response to any of our playback stimuli. Together these results suggest that songs may be more of a contact call as opposed to a territorial response, which is supported by mynas being highly gregarious (Counsilman 1974b).

In response to conspecific social vocalizations, bulbuls decreased the rate of vocalizing but did not significantly change the rate of flights near the playback speaker. In a territorial response, we would expect to have seen an increase in the rate of fly-bys or an increase in vocalizations as a measure of counter-singing. Counter-singing is thought to be a signal of directed aggression in songbirds. Instead, bulbuls may have decreased their rate of singing on hearing a conspecific social vocalization in order to gather more information about the caller, a low-risk method of assessment that can be performed from a distance. Eavesdropping on potential rival threats has been found in great tits (*Parus major*) and European nightingales (*Luscinia megarhynchos*), which were found to act more aggressively towards males that were heard to have dominated an acoustic interaction (Naguib and Todt 1997; Peake et al. 2001).

Past studies indicate that animals eavesdrop on heterospecific social communications in order to assess competitors (Naguib and Todt 1997), determine the likelihood that predators are nearby (Møller 1992), and identify the location of suitable habitat and resources (Goodale et al. 2010). In our study, bulbuls responded to myna social calls by decreasing their rate of vocalizing, a behavior that would decrease the chances of being detected by mynas, which have been known to harass heterospecifics (Counsilman 1974a).

There are some conservation implications of our findings. Given that communities are often composed of several species, understanding the influence of interspecific eavesdropping is important for understanding the distributions of species and may have valuable implications for conservation and management (Goodale et al. 2010). Furthermore, by ascertaining the extent of interdependencies of various species, we can better understand the effect that removal of 1 species might have on the others. For instance, secondary effects of species removals or population reductions (Zavaleta et al. 2001) may partially be due to interspecific eavesdropping. If a species heavily relies on heterospecific alarm communications for avoiding predation, removal of the

heterospecific may detrimentally affect the eavesdropping species. This effect may be negative if the goal is to eradicate an invasive that a native species has come to rely on for predator warnings. However, reliance on interspecific information can also beneficially be exploited when attempting to eradicate multiple invasive species. Ideally, ascertaining the relative extent to which each invasive species relies on the other would precede any steps at eradication. An efficient strategy would then be to focus eradication efforts on the invasive species that is most heavily relied on by the other invasive species.

In conclusion, we found asymmetric eavesdropping on heterospecific alarm calls between mynas and bulbuls. We speculate this asymmetry is due to differences in predator types between the 2 species. However, further studies in the predators of mynas and bulbuls are necessary to make a definitive conclusion. We also found heterospecific eavesdropping to nonalarm communication, the reason for which is not entirely clear. Reasons for eavesdropping to heterospecific social communications include the assessment of competitors, the lack of predators locally, and the location of suitable habitat and resources. Given these non-exhaustive or exclusive reasons, we suggest future research on the eavesdropping of heterospecific nonalarm communication would be profitable.

## Appendix 1
### Sources of exemplars used in playback experiments

| Website | Name of website | Exemplar number | Treatment |
|---------|-----------------|-----------------|-----------|
| http://www.xeno-canto.org/sounds/uploaded/UUXSJGNURV/XC157864-Bulbul%20Red-vented%20%28Pycnonotus%20cafer%29%20alarm%20Mahatma%20RNP.mp3 | Xeno-Canto | 1 | Bulbul alarm vocalization |
| http://www.xeno-canto.org/sounds/uploaded/UUXSJGNURV/XC157864-Bulbul%20Red-vented%20%28Pycnonotus%20cafer%29%20alarm%20Mahatma%20RNP.mp3 | Xeno-Canto | 2 | Bulbul alarm vocalization |
| http://www.biosecurity.govt.nz/files/pests/red-vented-bulbul/red-vented-bulbul-soundv2.mp3 | NZ Biosecurity | 1 | Bulbul nonalarm vocalization |
| http://www.xeno-canto.org/sounds/uploaded/VKGELLURFO/XC161254-Red%20Vented%20Bulbul%20-Goncoi%2C%20ALdona%2C%20Goa%20_May%2019%202012%204.28%20pm.mp3 | Xeno-Canto | 2 | Bulbul nonalarm vocalization |
| http://www.xeno-canto.org/sounds/uploaded/VKGELLURFO/XC161471-goa%20goncoi%20aldona%20red-vented%20bulbul%2012%20sept%202012%206.33%20pm%20CP.mp3 | Xeno-Canto | 3 | Bulbul nonalarm vocalization |
| http://www.xeno-canto.org/sounds/uploaded/YTUXOCTUEM/XC149692-Pycnonotus_cafer-FL%20song%20calls%20%5Bcom%20tailorb%5D%20Gir%20NP%2028Jan13%20LS113400.mp3 | Xeno-Canto | 4 | Bulbul nonalarm vocalization |
| http://www.xeno-canto.org/sounds/uploaded/EHGWCIGILC/XC146251-red-vented-bulbul.mp3 | Xeno-Canto | 5 | Bulbul nonalarm vocalization |
| http://www.biosecurity.govt.nz/files/pests/red-vented-bulbul/red-vented-bulbul-soundv2.mp3 | NZ Biosecurity | 6 | Bulbul nonalarm vocalization |
| http://www.xeno-canto.org/species/Acridotheres-tristis | Xeno-Canto | 1 | Myna alarm vocalization |
| http://www.xeno-canto.org/species/Acridotheres-tristis | Xeno-Canto | 2 | Myna alarm vocalization |
| http://www.xeno-canto.org/species/Acridotheres-tristis | Xeno-Canto | 3 | Myna alarm vocalization |
| http://avocet.zoology.msu.edu/recordings/3737 | Michigan State University's Avian Vocalization Center | 1 | Myna nonalarm vocalization |
| http://avocet.zoology.msu.edu/recordings/3737 | Michigan State University's Avian Vocalization Center | 2 | Myna nonalarm vocalization |
| http://avocet.zoology.msu.edu/recordings/5753 | Michigan State University's Avian Vocalization Center | 4 | Myna nonalarm vocalization |
| http://avocet.zoology.msu.edu/recordings/6548 | Michigan State University's Avian Vocalization Center | 6 | Myna nonalarm vocalization |

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