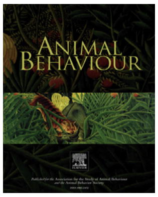
Animal Behaviour 135 (2018) 25–35

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Full length article

Social information cascades influence the formation of mixed-species foraging aggregations of ant-following birds in the Neotropics

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ARTICLE INFO

Article history:
Received 26 January 2017
Initial acceptance 16 June 2017
Final acceptance 25 September 2017

MS. number: A17-00090R

Keywords:
army ant swarm
eavesdropping
Eciton burchellii
foraging aggregation
information cascade
mixed-species group
Neotropical bird
social information

Animals frequently make decisions based on social information obtained from other animals, which can influence interspecific interactions and affect individual fitness. For example, animals eavesdrop on other animals to find profitable food resources, yet the types of cues they use and how these cues influence decisions to approach a resource remain poorly understood. In tropical systems, arthropods inadvertently flushed by army ant, *Eciton burchellii*, swarms are an important food resource for many bird species, which form mixed-species foraging aggregations at swarms. Competition at swarms is intense and birds vocalize to defend foraging areas, inadvertently producing acoustic social information about the swarm's location. Eavesdropping birds may use these acoustic cues, which provide information about the bird aggregation (i.e. species participating in the aggregation, the size of the aggregation and/or diversity of the aggregation) to assess potential benefits (food resources) and costs (competition for food) of joining an aggregation. To test this hypothesis, we used an acoustic playback experiment to simulate aggregations of birds foraging at ant swarms and we measured community-wide and guild-specific responses of forest birds to playbacks. We included three types of acoustic social information in playbacks that potentially interact to affect an eavesdropping bird's probability of attraction to a swarm: (1) aggregation size, (2) aggregation species richness and (3) degree of specialization on ant swarms for food of birds vocalizing in the aggregation (hereafter 'dependency'). Using Bayesian generalized linear mixed models, we found that playbacks of obligate ant-following species elicited greater community-wide responses (i.e. attracted more individuals and species) to simulated aggregations compared to playbacks of other, less dependent guilds. We also found that interactions between dependency, species richness and aggregation size influenced the overall community response to playbacks and that species from one guild generally responded to the guild above them (i.e. from less to more specialized). Our results suggest that species evaluate multiple types of acoustic cues representing the costs and benefits of foraging in a mixed-species aggregation at a swarm. We hypothesize that species change from information receivers to information producers upon joining a swarm, ultimately producing an information cascade that further affects the dynamics of feeding aggregations at swarms.

Animals must make decisions continuously to locate food, avoid predators and assess the quality of habitat and mates, and these decisions have profound effects on individual fitness (McNamara & Houston, 1986), population demography (Kristan, 2003) and community composition (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010). Decision making, however, is a complex process (McNamara & Houston, 1986) and therefore animals often use information gleaned from the behaviour of other animals (social information) to aid them in their behavioural decisions (Danchin, Giraldeau, Valone, & Wagner, 2004; Seppänen, Forsman, Mönkkönen, & Thomson, 2007). For example, animals use social information to increase foraging success (Galef & Giraldeau, 2001), reduce predation risk (Magrath, Haff, Fallow, & Radford, 2014; Seppänen et al., 2007) and identify high-quality habitat patches

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https://doi.org/10.1016/j.anbehav.2017.10.024

and mates (Valone & Templeton, 2002). Given the potential fitness benefits of social information use, the ability to identify and use social information may be under strong selection and can have implications across multiple spatial scales in which individual behavioural decisions translate into interspecific interactions and ultimately to community structure (Goodale et al., 2010; Seppänen et al., 2007).

One prevalent form of social information use is eavesdropping, whereby individuals use acoustic cues intended for another receiver to inform their behavioural decisions (Peake, 2005; Valone, 2007; Wagner & Danchin, 2010). Heterospecific eavesdropping on acoustic social information (i.e. alarm calls of other species) is commonly used by animals to gain information about the presence of shared predators (e.g. Magrath et al., 2014; Peres, 1993; Shriner, 1998; Sridhar, Beauchamp, & Shanker, 2009; Thiollay, 1999). Studies on social information in a foraging context have been limited primarily to visual social information use (e.g. observing another animal's foraging behaviour or location; see Galef & Giraldeau, 2001 for a review). Nevertheless, acoustic social information may be equally or more important than visual social information for finding food in environments where dense vegetation, cryptic prey and/or patchy resource distribution makes it challenging for animals to visually locate food resources or other individuals using those food resources (Powell, 1985; Westrip & Bell, 2015). Although acoustic social information is important in structuring species associations in a predation context (Magrath et al., 2014; Martínez, Gomez, Ponciano, & Robinson, 2016) and for finding other group members (Cordeiro et al., 2015; Goodale & Kotagama, 2005), its influence in the context of food finding remains unclear (Gu et al., 2017).

Ant-following birds of the Neotropics provide an ideal system to explore the role of acoustic social information in finding food resources and structuring animal foraging aggregations. Birds compete for foraging opportunities at swarms of the predatory ant species *Eciton burchellii* (hereafter army ants) and form aggregations of 1–20 species and up to 60 individual birds (Chaves-Campos, 2005; Willis & Oniki, 1978). Army ants are a conspicuous and widespread component of Neotropical forests. They have a dichotomous life cycle, alternating between a nomadic phase and a statary phase (Schneirla, 1971). During the nomadic phase, army ants swarm through leaf litter and inadvertently flush terrestrial arthropods en masse, creating an easily accessible and profitable food resource for more than 200 associate bird species (Rettenmeyer, Rettenmeyer, Joseph, & Berghoff, 2011). During the statary phase, however, the colony is relatively sedentary and swarming is greatly reduced (Rettenmeyer et al., 2011). Thus, army ant colonies are a profitable, but patchy resource, and certain bird species have evolved to specialize on following army ants as a foraging strategy (Brumfield et al., 2007). Availability of flushed prey is highest at the front and centre of the advancing swarm (Willis & Oniki, 1978), and birds compete (within and between species) for these profitable positions with vocalizations and physical aggression. Vocalizations produced at swarms could inadvertently provide acoustic social information to birds away from the swarm, indicating (1) a swarm's profitability and (2) a swarm's competitive environment, ultimately affecting the probability that an individual joins a swarm.

The behavioural decision of an individual to approach or avoid a swarm likely represents a balance between the potential benefits (i.e. concentrated food resources) and costs (i.e. competitive interactions) of foraging at that swarm. For example, previous studies have found that birds are attracted to playbacks of obligate ant-following birds (species that depend almost exclusively on army ants for food), suggesting that nonobligate species may eavesdrop on the vocalizations of obligate species to discover swarms (Batcheller, 2017; Chaves-Campos, 2003). Conversely, although obligate species are likely a highly reliable cue indicating the presence of an ant swarm (Chaves-Campos, 2003), they also tend to have higher body mass and exhibit behavioural dominance at swarms, which could represent a high cost of competition that deters eavesdropping birds from approaching a swarm (Batcheller, 2017). Because of the link between dominance and dependency (i.e. obligate ant followers tend to be the largest and most dominant attendants whereas no dominance is evident in other species), vocalizations of obligate species could be predicted to either attract (Chaves-Campos, 2003) or repel (Batcheller, 2017) eavesdropping birds. In addition to providing information about the competitive environment at a swarm, acoustic social information produced at a swarm could also convey information about resource profitability. For example, larger or more diverse bird aggregations at swarms may reflect larger, higher-density swarms that flush a larger quantity or greater diversity of prey resources, signifying increased resource profitability to eavesdropping birds. Presumably, more prey or more diverse prey would allow for increased attendance and/or finer niche partitioning of available prey resources (Willis & Oniki, 1978), allowing for a greater diversity and quantity of attending birds. Understanding whether eavesdropping birds use acoustic social information in general and how they use different characteristics of a bird aggregation (i.e. the number of individuals and species present in the aggregation and their competitive ability) to decide whether to join and follow swarms will shed light on how animals assess the costs and benefits of foraging at a profitable but highly contested resource.

In this study, we used a factorial playback experiment to simulate avian aggregations composed of different numbers of individuals and species foraging at ant swarms. We tested (1) whether ant-following birds eavesdrop on acoustic social information to locate and follow swarms and (2) how acoustic social information associated with different characteristics of the aggregation (i.e. dependency, aggregation size and aggregation richness) may interact to influence attraction of eavesdropping birds to swarms. We predicted that playbacks simulating bird aggregations that (1) were larger, (2) had higher species richness and (3) were composed of species more dependent on ant swarms would attract greater numbers of eavesdropping individuals and species, except in the case of large groups of obligate ant followers, which we predicted would attract fewer species as a result of their dominance at swarms.

METHODS

Classification of Ant-following Birds

Ant-following birds may be categorized into three dependency guilds: (1) obligate ant followers that forage almost exclusively at swarms and have evolved behavioural adaptations, such as bivouac checking (Swartz, 2001), to monitor and locate active swarms; (2) facultative ant followers that have fixed territories, yet regularly follow ant swarms and will leave their territory to forage at an active swarm; and (3) occasional ant followers that have fixed territories and attend swarms only when army ants cross into their territories (Willis & Oniki, 1978).

Study Site and Selection of Playback Locations

We conducted the experiment during the dry season (February–March 2014) in a tropical moist forest along Pipeline Road (9°9′35″N, 79°44′36″W) in Parque Nacional Soberanía in central Panama. We selected six locations to serve as replicates to conduct playbacks that were distributed within secondary tropical moist forest (Robinson, Brawn, & Robinson, 2000). Each point was located ≥200 m from the road to control for potential edge effects on bird responses to playbacks. Based on previous estimates of home range sizes of ant-following birds (Chaves-Campos & DeWoody, 2008; Robinson et al., 2000; Willson, 2004), we spaced points ≥500 m apart to decrease spatial dependence and eliminate the probability of resampling the same individuals at each point.

Experimental Design

We used a factorial playback experiment to simulate birds vocalizing at swarms to determine the degree to which ant-following birds use three different cues: aggregation size, aggregation richness and dependency (see Table 1 for list of species). We chose two aggregation sizes (small = two individuals; large = eight individuals) based on observations of aggregations at our field site (H. S. Pollock, personal observation). Although we acknowledge that bird aggregations at ant swarms vary greatly in size (e.g. Chaves-Campos, 2005), we are confident that eight vocalizing individuals constitutes a fairly large swarm at our field site. We also chose two levels of aggregation richness (low = one species; high = two species) and four dependency guilds (obligate, facultative, occasional and control = nonfollower). We used only two levels of richness because at our study site the obligate dependency guild had only two common species (ocellated antbird, *Phaenostictus mcleannani*; bicoloured antbird, *Gymnopithys bicolor*). Therefore, for every other dependency guild, we also chose two species whose dependency could reliably be classified based on the literature (Willis & Oniki, 1978) and previous research experience (H. S. Pollock & C. E. Tarwater, personal observation). Combining all three factors in all possible combinations resulted in 16 total treatments ($N = 2 \times 2 \times 4$; Supplementary Table S2). Based on a priori experience with more than 9 playback experiments (Kelley, n.d.), and because of logistical constraints, we estimated that six replicates would be sufficient to identify differential responses to the social information factors and their two-way interactions. The final data set, therefore, consisted of 96 total playback trials ($N = 16 \times 6$).

We conducted playback trials during a 3 h period after sunrise, approximately between 0600 and 0900 hours local time. We restricted sampling to the first 3 h of the day to maximize the probability of attraction to simulated swarms because attendant birds generally join swarms during this time (Chaves-Campos, 2003; Willis, 1972). We also took care not to conduct playbacks in the presence of any pre-existing swarm activity or incipient aggregations of ant-following birds by evaluating the area for 5 min prior to the start of a trial. Treatments were conducted in randomized order for each point and only one playback was conducted at each point per day.

Each trial consisted of three phases: (1) a 10 min pre-stimulus period to establish a baseline of nearby bird activity, (2) a 10 min stimulus period during which a given playback was broadcast and (3) a 10 min post-stimulus period to ensure detection of late-responding individuals. During each phase, we conducted an unlimited distance point count (Matsuoka et al., 2014), using the speakers as the centre of the point. Speaking into an Olympus recorder (Model VN-701PC), we noted in real-time the distance, height and direction of all individual birds that we could identify by sight or sound. Because locations were similar in vegetation structure, we did not expect detectability of species to vary between locations. We recorded WAV files of each trial using an Edirol recorder (Roland Corporation, model R-05) attached to a tripod set at a height of 1.5 m to create an auditory log for later verification of species' identities.

Playbacks

To create the playbacks, we obtained recordings (in WAV format) of eight focal species (Table 1) using archives at the Cornell Lab of Ornithology's Macaulay Library (www.macaulaylibrary.org; see Supplementary Table S2 for individual recordings used), as well as personal recordings from individuals (K. Allaire, A. Kirschel, J. P. Kelley, A. E. Martinez & C. E. Tarwater). Because geographical variation in vocalizations is common among birds, including antbirds (Isler, Isler, & Brumfield, 2005; Kelley, & Tarwater, n.d.-a), we restricted the sound files that we used for playbacks to individuals that were recorded within Panama and Costa Rica, including only song and call variants that we had previously heard on Pipeline Road (H. S. Pollock, J. P. Kelley & C. E. Tarwater, personal observations), and confirmed that preliminary playback experiments reliably elicited conspecific responses from focal species (Pollock & Tarwater, n.d.).

Given that we needed to simulate multiple individuals (i.e. two or eight) in our playbacks, we used the sound software program Reaper (Version 4.581, https://www.reaper.fm/) to create and edit multiple track recordings for each treatment. We manually created separate tracks for each individual bird and then overlaid these tracks, thereby creating playback recordings of multiple tracks that simulated several individual birds vocalizing simultaneously. Playbacks contained a combination of calls and songs, and vocalization rates for each species that were based on previous observations of multiple individuals vocalizing at and away from swarms (J. P. Kelley & C. E. Tarwater, personal observations). We filtered all recordings below 0.5 kHz to remove low-frequency background noise and removed the vocalizations of other bird species that could confound the interpretation of the target signal. All files were saved at 24-bit rate and 44 000 Hz. We standardized recordings to the same amplitude in Reaper and then used a sound

Table 1
Species used in the playback experiment and their dependencies on *E. burchellii* swarms

Species	Family	Dependency[1]	Mass (g)[2]	Vertical stratum
Blue-black grosbeak, *Cyanocompsa cyanoides*	Cardinalidae	Control	32.5	Understory–midstory
White-breasted wood-wren, *Henicorhina leucosticta*	Troglodytidae	Control	14.8	Understory
Song wren, *Cyphorhinus phaeocephalus*	Troglodytidae	Occasional	24.6	Understory
Streak-chested antpitta, *Hylopezus perspicillatus*	Grallariidae	Occasional	43.0	Understory
Plain-brown woodcreeper, *Dendrocincla fuliginosa*	Furnariidae	Facultative	38.8	Understory–midstory
Spotted antbird, *Hylophylax naevioides*	Thamnophilidae	Facultative	17.8	Understory
Bicoloured antbird, *Gymnopithys bicolor*	Thamnophilidae	Obligate	29.4	Understory
Ocellated antbird, *Phaenostictus mcleannani*	Thamnophilidae	Obligate	51.1	Understory

[1] Dependency classification based on data from Willis and Oniki (1978) and personal observations (C. E. Tarwater & J. P. Kelley). The two control species rarely or never forage at swarms, the two occasional species forage opportunistically at swarms that traverse their territories, the two facultative species maintain fixed territories but also frequently forage at swarms, and the two obligate species obtain their food almost exclusively at swarms.

[2] Masses obtained from Dunning (2007).

meter (CEM Instruments, model DT-85A) to normalize the amplitude of all playbacks to 85 dB at a distance of 1 m from the playback speakers to standardize the strength of the stimulus. We do not have information on the natural sound levels of all focal species used in this study, and thus in the absence of this information we took a conservative approach by standardizing all treatments to the same loudness level. Using a single speaker with multiple tracks raises the possibility that the simulation of multiple individuals could be interpreted by a receiver as an increase in signal frequency given by a single individual. To address this potential confound, we panned each track to emit different proportions of the recording from the left and right speakers of a dual-speaker system. Speakers were placed 5 m apart, allowing us to simulate multiple individuals vocalizing from different locations and more accurately approximate the spatial arrangement of birds at a swarm. For each trial, we recorded the time of day to control for temporal effects on bird activity (e.g. foraging or vocal behaviour) (Kelley & Tarwater, n.d.-b).

Responses to Playbacks

We defined a positive response to playbacks as individuals that approached within 15 m (the maximum distance at which birds are still considered part of a mixed-species bird flock; Jullien & Thiollay, 1998) of the playback speaker during both the stimulus or post-stimulus trial period (to account for individuals that exhibited a high response latency and approached after cessation of the stimulus). Only 34 individuals exhibited ambiguous responses (i.e. remained within 15 m of the speakers during all trial phases) and these individuals were excluded from the analyses. We acknowledge that (1) some individuals that were classified as responding to playbacks may have been simply passing through the area and (2) some individuals that were responding to playbacks may not have been detected. Yet, these false positive and false negative responses should be randomly distributed across treatments and therefore should not influence general response patterns. In addition, individuals that ceased to call from the pre-trial stage to the stimulus/post-trial stage could either have remained in the area undetected or could have moved out of the area, so these individuals were excluded from the analysis. Individuals moving away from speakers during and after playback were considered to respond negatively to the stimulus.

Statistical Analysis

All analyses were conducted in the R programming environment (R Core Team, 2016, version 3.2.4) using Bayesian generalized mixed models (GLMMs) implemented with the MCMCglmm package (Hadfield, 2010). We included dependency, number of individuals and richness of species in the playbacks as fixed effects and calendar day (day since start of year) and trial start time as random effects in each model. For each model's covariance matrix of the two random effects and the residuals, we specified $V = 1$ and nu $= 0.002$ as very weak priors.

We first examined whether ant-following birds eavesdrop on acoustic social information to locate and follow swarms by comparing the proportion of total individuals detected during the pre-stimulus phase to the proportion of individuals detected during the stimulus and post-stimulus phases. We ran this model for 100 000 iterations with a burn-in of 10 000 and a thinning interval of 100 and visually checked model diagnostics (i.e. mixing properties and autocorrelation of the MCMC trace).

We then examined how different types of acoustic social information interact to influence eavesdropping birds' attraction to swarms using two metrics: (1) community-wide attraction, by assessing the responses of the total number of individuals and total species to playbacks; (2) guild-specific attraction, by assessing responses of each dependency guild (control, occasional, facultative and obligate followers) to playbacks. To assess community-wide attraction to playback, we retained the three factors (dependency, aggregation size and aggregation richness) as well as all two-way interactions. Three-way interactions were not included because of sample size constraints. We used the proportion of responding individuals and the proportion of responding species (relative to the total number of individuals and species detected in each 30 min trial) as our response variables. For the guild-specific analyses, we retained the same fixed effects included in the community-wide analysis, and used the proportion of responding individuals in each dependency category (control, occasional, facultative and obligate) relative to the number of total individuals detected across all trial phases as our response variable. We used the total pool of individuals detected for each specific trial as the basis for deriving trial-specific proportions of individuals and species available to join at each point. We were thus able to explore any potential guild-specific differences in attraction to playbacks. The large numbers of nonresponses of eavesdropping birds in dependency guilds with relatively low population sizes (e.g. obligates) resulted in poorly mixed MCMC traces and/or absolute parameter estimates >20; therefore, for all zero values (nonresponses) in nonfollower, facultative and obligate responses, we set values to unity and set the total number of individuals (the denominator) to an arbitrarily large value of 1000), which changed the proportion joining from 0 to 0.001. Using simulation as well as data with few zero responses, we confirmed that this approach did not alter inference.

For both the community-wide and guild-specific analyses, we ran models for 2 000 000 iterations with a 200 000 burn-in and a thinning interval of 1000 for each response variable. Visual inspection of final trace plots indicated good mixing properties. For all response variables, these settings resulted in parameters estimates with effective sample sizes >1000 and MCMC chains that exhibited no observable autocorrelation. Effective sample size for all parameter estimates (across all models run) was 1800 (range 1380–2186). To ensure that models had converged and would be repeatable, we repeated this process two additional times to obtain three model runs for each response variable. We then calculated the Gelman–Rubin statistic, which compares within- and between-chain variance between models by providing a metric called the potential scale reduction factor (PSR) that becomes <1.1 when models converge (Gelman & Rubin, 1992). The PSR was 0.9997–1.0089 for all terms across all models. We then randomly selected one of the three models for prediction, plotting and inference. For plotting, we reran this model with only the meaningful predictors (pMCMC < 0.05). Effects are presented as posterior mean (PM), 95% credible interval (lower and upper CI) and pMCMC (the probability that the posterior distribution crosses zero).

All research was approved by the Smithsonian Tropical Research Institute Institutional Animal Care and Use Committee under permit number 2015-0102-2018.

RESULTS

Ant-following Birds Use Acoustic Social Information to Locate and Follow Swarms

We found clear evidence that ant-following birds use acoustic social information to locate and join swarms. Across the trials, playbacks elicited positive responses during the stimulus and post-stimulus period from 15.2% (CI: 12.5–18.8%) of individuals detected in the vicinity of playbacks, significantly higher than the percentage of individuals that randomly ‘responded’ during the pre-stimulus period (7.8%, CI: 6.3–9.9%) (pMCMC < 0.001).

Community-wide Responses to Acoustic Social Information

In the community-wide analysis, the dependency guild of species included in the playback was an important predictor of the proportion of individuals and species responding to playbacks. Although there were no significant differences in responses of eavesdropping birds to facultative and occasional playbacks relative to control playbacks, we did find that playbacks of obligate species attracted a significantly greater proportion of individuals and species than control playbacks (Table 2).

Our models also revealed an interaction between dependency and richness of the species in the playbacks on attraction of eavesdropping birds. Higher-richness playbacks of occasional species attracted a greater proportion of individuals and species than nonfollower playbacks (individuals: Table 2, Fig. 1a; species: Table 2, Fig. 1b). Similarly, higher-richness playbacks of obligate species attracted a greater proportion of individuals than nonfollower playbacks (Table 2, Fig. 1a).

Guild-specific Responses to Acoustic Social Information

Overall, we found that interactions between the different acoustic cues (dependency, aggregation size, aggregation richness) influenced the probability of attraction to swarms. We found that playbacks with higher aggregation richness and larger aggregation size (irrespective of dependency) increased attraction of obligate birds to simulated swarms. In turn, playbacks simulating high aggregation richness of obligate species positively influenced attraction of facultative species, and larger aggregations of facultative species positively influenced attraction of occasional species.

Attraction of Nonfollowers

Playbacks of high aggregation richness of occasional followers increased attraction of nonfollowing individuals, whereas playbacks of large aggregations of obligate species decreased attraction of nonfollowers (Table 3, Fig. 2a).

Attraction of Occasional Species

Playbacks of larger aggregations of facultative species attracted more occasional followers than control playbacks (Table 3, Fig. 2c). Similarly, playbacks of larger aggregations of obligate species also tended to attract more occasional followers than control playbacks, although this pattern was not statistically significant (Table 3, Fig. 2c).

Attraction of Facultative Species

Playbacks of obligate species attracted a greater proportion of facultative individuals than did occasional or control (nonfollower) playbacks (Table 3). Furthermore, we also found an interaction between aggregation richness and dependency of species in the playbacks: high-richness aggregations of obligates also attracted more individuals compared to controls (Table 3, Fig. 2d).

Attraction of Obligate Species

In contrast to the other guilds, we found that dependency had no detectable impact (simple or interactive) on attraction of individuals of obligate species. However, aggregation richness interacted with aggregation size to influence attraction of obligate followers to playbacks. Specifically, irrespective of the dependency guild of species used in the playbacks, playbacks of large, high-

Table 2
Evaluation of the effects of acoustic social information on attraction of individuals and species to playbacks

Model terms	Posterior mean	95% CI lower	95% CI upper	n_{eff}	pMCMC
Proportion of total individuals					
(Intercept)	−2.02	−2.71	−1.30	1643	0.0006
Dependency$_{\text{occasional}}$	−0.43	−1.39	0.60	1800	0.4078
Dependency$_{\text{facultative}}$	0.01	−0.92	0.95	1525	0.9778
Dependency$_{\text{obligate}}$	**0.99**	**0.16**	**1.83**	**1800**	**0.0156**
Aggregation size$_{\text{large}}$	−0.14	−1.13	0.83	1657	0.7622
Richness$_{\text{high}}$	−0.92	−2.10	0.05	1800	0.0833
Dependency$_{\text{occasional}}$ * aggregation size$_{\text{large}}$	−0.28	−1.69	0.91	1800	0.6411
Dependency$_{\text{facultative}}$ * aggregation size$_{\text{large}}$	1.15	−0.07	2.38	1800	0.0578
Dependency$_{\text{obligate}}$ * aggregation size$_{\text{large}}$	−0.29	−1.38	0.76	1800	0.0578
Dependency$_{\text{occasional}}$ * richness$_{\text{high}}$	**1.50**	**0.21**	**2.72**	**1800**	**0.0167**
Dependency$_{\text{facultative}}$ * richness$_{\text{high}}$	0.42	−0.69	1.57	1800	0.4867
Dependency$_{\text{obligate}}$ * richness$_{\text{high}}$	**1.17**	**0.07**	**2.26**	**1933**	**0.0333**
Aggregation size$_{\text{large}}$ * richness$_{\text{high}}$	0.49	−0.23	1.25	1800	0.1933
Proportion of total species					
(Intercept)	−2.36	−3.02	−1.62	1800	0.0006
Dependency$_{\text{occasional}}$	−0.85	−1.95	0.32	1666	0.1556
Dependency$_{\text{facultative}}$	−0.07	−1.04	0.83	1800	0.8900
Dependency$_{\text{obligate}}$	**0.92**	**0.10**	**1.74**	**1668**	**0.0356**
Aggregation size$_{\text{large}}$	0.24	−0.66	1.25	1656	0.6033
Richness$_{\text{high}}$	−0.64	−1.68	0.30	1800	0.2033
Dependency$_{\text{occasional}}$ * aggregation size$_{\text{large}}$	−0.76	−2.05	0.57	1803	0.2456
Dependency$_{\text{facultative}}$ * aggregation size$_{\text{large}}$	0.66	−0.51	1.79	1800	0.2578
Dependency$_{\text{obligate}}$ * aggregation size$_{\text{large}}$	−0.54	−1.54	0.45	1703	0.2856
Dependency$_{\text{occasional}}$ * richness$_{\text{high}}$	**1.76**	**0.33**	**3.06**	**1622**	**0.0044**
Dependency$_{\text{facultative}}$ * richness$_{\text{high}}$	0.59	−0.64	1.67	1741	0.3078
Dependency$_{\text{obligate}}$ * richness$_{\text{high}}$	**0.87**	**−0.07**	**1.93**	**1819**	**0.0922**
Aggregation size$_{\text{large}}$ * richness$_{\text{high}}$	0.28	−0.41	1.01	1629	0.4478

Estimates of Bayesian GLMMs on the influence of dependency, aggregation size and species richness on attraction of individuals and species to simulated ant swarms. Response is the proportion of individuals and species relative to the total number of detected individuals and species in each experimental trial, respectively. Effects are relative to the model intercept (dependency = control; aggregation size = small; richness = low). Reported are posterior means, lower and upper 95% credible intervals (CI), effective sample size (n_{eff}) and pMCMC (the probability that the posterior distribution crosses zero). Bold font indicates pMCMC < 0.05.

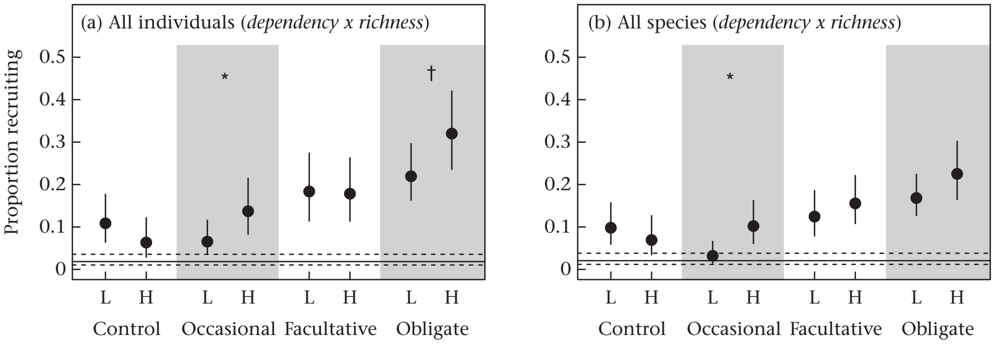

Figure 1. Community-wide responses to experimental playbacks. Proportion of (a) individuals and (b) unique species that responded to different treatment types, relative to the number of total individuals and species detected per trial, respectively. Panels show the significant two-way interaction between dependency and richness and its influence on the total proportion of eavesdropping birds that responded to playbacks. Only two-way interactions that were found to be significant are shown. Error bars indicate 95% credible interval. L: low aggregation richness; H: high aggregation richness. Solid and dashed lines along the bottom of each graph indicate the proportion that randomly approached the speaker during the pre-stimulus period (±95% credible interval), pooling all trials. Treatment combinations are grouped by dependency guild: control (nonfollower) and facultative = no shading; occasional and obligate = shaded. Asterisks indicate significant pairwise differences (pMCMC < 0.05) within each shaded or unshaded block (e.g. between low and high aggregation richness for occasional treatment in (a)). †pMCMC < 0.1.

richness (two species) aggregations positively influenced attraction of obligate followers (Table 3, Fig. 2e). Across all trials, only 27 obligate individuals responded to playbacks, possibly hampering our abilities to detect treatment effects. We summarize the results of our playback experiment in Table 4.

DISCUSSION

Our findings support the hypothesis that forest birds of the Neotropics eavesdrop on acoustic social information of heterospecific bird species to locate and approach a profitable food resource (i.e. ant swarms). Furthermore, we demonstrate that probability of joining a swarm depends on a combination of different cue types (i.e. number of individuals and number of species in a bird aggregation and dependency of species present in a bird aggregation) and their interactions. As predicted, we observed that playbacks simulating bird aggregations with greater dependency (obligate > facultative > occasional > nonfollower), higher species richness and larger aggregation size typically attracted more species/individuals. Interestingly, we also observed that each guild had a positive response to the playback of the dependency guild directly above it (occasional responded to facultative, facultative to obligate), except in the case where nonfollowers negatively responded to obligates (Fig. 3). These guild-specific responses suggest that an information cascade is occurring, whereby species from a dependency guild that is less specialized are influenced by information from the dependency guild that is more specialized. Our results indicate that the decision of an eavesdropping bird to join and follow an ant swarm is a function of the interactions between different types of acoustic social information and likely represents the perceived costs/benefits of foraging at the swarm. Our results provide experimental evidence that individuals most likely do not process a simple stream of one type of information but more likely integrate overlapping streams of social information (Bonnie & Earley, 2007).

Ant-following Birds Use Acoustic Social Information to Locate and Join Swarms

Overall, playbacks of birds that follow swarms attracted approximately double the number of individuals from the available pool of individuals (compared to nonfollowers). Our general result is consistent with previous evidence from mixed-species groups (Goodale & Kotagama, 2005) and aggregations of frugivorous birds (Gu et al., 2017).

Community-wide Responses to Acoustic Social Information

The dependency of the bird species was the most important predictor of attraction to the simulated swarms. Despite the relatively low abundance of obligate ant followers, playbacks of obligate species attracted a larger proportion of the bird community (with respect to both total number of individuals and species) than facultative, occasional or nonfollower playbacks (see Figs 1 and 2), suggesting that obligate species are key players in attracting heterospecifics to swarms and influence the species composition of bird aggregations at swarms. Our findings corroborate the results of other studies to examine heterospecific eavesdropping in ant-following birds, which found that playbacks of obligate ant-following species attracted significantly more individuals and species than control (nonfollower) playbacks in Costa Rica and Ecuador (Batcheller, 2017; Chaves-Campos, 2003). Because obligate species depend exclusively on ant swarms for food and have special behavioural adaptations such as bivouac checking (Swartz, 2001) that allow them to locate active swarms, it is likely that they are information producers (sensu Barnard & Sibly, 1981) and are a particularly reliable indicator of swarm presence to eavesdropping birds. The biological relevance of core aggregation species functioning as a source of social information is further strengthened by the fact that facultative ant followers were the strongest responders to playbacks of obligate species (Table 2). Facultative species regularly forage at swarms (Willis & Oniki, 1978), and thus it is logical that they would be the guild most likely to join and follow a swarm once it has been discovered by obligate species. Conversely, we found little evidence that the competitive dominance of obligate species discouraged other species from joining swarms. Our results corroborate a recent study by O'Donnell (2017), who found that obligate species were core aggregation members at swarms that facilitated other species finding and foraging at swarms. However, given the extreme variability in the size and composition of avian foraging aggregations at swarms (up to 20 species and 60 individuals) it is possible that there is a threshold size or composition of an aggregation at which the cost of competition becomes prohibitively high to approach the swarm. For example, O'Donnell (2017) found some evidence for negative associations among species at swarms, suggesting that the cost of competition for food at swarms can be

Table 3
Evaluation of the effects of acoustic cues on species level of dependency

Model terms	Posterior mean	95% CI lower	95% CI upper	n_{eff}	pMCMC
Proportion of nonfollowing individuals					
(Intercept)	−3.56	−4.74	−2.34	2186	0.0006
Dependency$_{\text{occasional}}$	−1.14	−3.28	0.84	1506	0.2756
Dependency$_{\text{facultative}}$	0.26	−1.17	1.81	1800	0.7556
Dependency$_{\text{obligate}}$	1.16	−0.04	2.66	1800	0.0700
Aggregation size$_{\text{large}}$	0.95	−0.55	2.42	1621	0.1811
Richness$_{\text{high}}$	−1.13	−2.92	0.44	1674	0.1767
Dependency$_{\text{occasional}}$ * aggregation size$_{\text{large}}$	−2.23	−4.84	−0.06	1800	0.0556
Dependency$_{\text{facultative}}$ * aggregation size$_{\text{large}}$	−0.37	−2.26	1.66	1800	0.7100
Dependency$_{\text{obligate}}$ * aggregation size$_{\text{large}}$	**−1.99**	**−3.65**	**−0.35**	**1800**	**0.0189**
Dependency$_{\text{occasional}}$ * richness$_{\text{high}}$	**3.07**	**0.66**	**5.45**	**1584**	**0.0078**
Dependency$_{\text{facultative}}$ * richness$_{\text{high}}$	0.69	−0.93	2.59	1534	0.4133
Dependency$_{\text{obligate}}$ * richness$_{\text{high}}$	0.43	−1.27	2.15	1800	0.6367
Aggregation size$_{\text{large}}$ * richness$_{\text{high}}$	0.28	−1.02	1.65	1660	0.6733
Proportion of occasional individuals					
(Intercept)	−3.22	−4.41	−2.05	1659	0.0006
Dependency$_{\text{occasional}}$	0.29	−1.17	1.81	1800	0.6844
Dependency$_{\text{facultative}}$	−0.92	−2.76	0.71	1800	0.2956
Dependency$_{\text{obligate}}$	0.30	−1.01	1.73	1800	0.6956
Aggregation size$_{\text{large}}$	−1.17	−2.85	0.54	1388	0.1933
Richness$_{\text{high}}$	−0.09	−1.77	1.63	1800	0.9433
Dependency$_{\text{occasional}}$ * aggregation size$_{\text{large}}$	1.11	−0.74	3.04	1664	0.2689
Dependency$_{\text{facultative}}$ * aggregation size$_{\text{large}}$	**2.63**	**0.59**	**5.02**	**1800**	**0.0156**
Dependency$_{\text{obligate}}$ * aggregation size$_{\text{large}}$	1.49	−0.23	3.34	1800	0.0989
Dependency$_{\text{occasional}}$ * richness$_{\text{high}}$	0.22	−1.50	2.41	1800	0.8333
Dependency$_{\text{facultative}}$ * richness$_{\text{high}}$	0.37	−1.85	2.26	1800	0.7444
Dependency$_{\text{obligate}}$ * richness$_{\text{high}}$	0.55	−1.24	2.41	1800	0.5867
Aggregation size$_{\text{large}}$ * richness$_{\text{high}}$	0.37	−0.73	1.61	1532	0.5200
Proportion of facultative individuals					
(Intercept)	−6.49	−8.10	−4.93	1800	0.0006
Dependency$_{\text{occasional}}$	−0.65	−2.77	1.33	1380	0.5178
Dependency$_{\text{facultative}}$	1.94	−0.01	4.19	1800	0.0656
Dependency$_{\text{obligate}}$	**2.06**	**0.30**	**4.00**	**1800**	**0.0278**
Aggregation size$_{\text{large}}$	−0.18	−2.10	1.97	1800	0.8657
Richness$_{\text{high}}$	−0.83	−2.86	1.25	1580	0.4167
Dependency$_{\text{occasional}}$ * aggregation size$_{\text{large}}$	−0.21	−2.77	2.38	1800	0.8911
Dependency$_{\text{facultative}}$ * aggregation size$_{\text{large}}$	1.58	−0.81	4.21	1800	0.2167
Dependency$_{\text{obligate}}$ * aggregation size$_{\text{large}}$	−0.66	−3.20	1.57	1800	0.5978
Dependency$_{\text{occasional}}$ * richness$_{\text{high}}$	1.06	−1.39	3.69	1800	0.4000
Dependency$_{\text{facultative}}$ * richness$_{\text{high}}$	−0.37	−2.75	2.12	1800	0.7533
Dependency$_{\text{obligate}}$ * richness$_{\text{high}}$	**2.64**	**0.41**	**5.08**	**1974**	**0.0244**
Aggregation size$_{\text{large}}$ * richness$_{\text{high}}$	0.15	−1.50	1.79	1800	0.8722
Proportion of obligate individuals					
(Intercept)	−6.65	−7.83	−5.50	1800	0.0006
Dependency$_{\text{occasional}}$	−0.36	−1.99	1.23	1800	0.6400
Dependency$_{\text{facultative}}$	−0.23	−1.94	1.38	2030	0.7867
Dependency$_{\text{obligate}}$	0.71	−0.67	2.18	1800	0.3467
Aggregation size$_{\text{large}}$	−0.70	−2.13	0.77	1942	0.3278
Richness$_{\text{high}}$	−0.75	−2.28	0.79	1800	0.3500
Dependency$_{\text{occasional}}$ * aggregation size$_{\text{large}}$	0.23	−1.70	2.22	1800	0.8278
Dependency$_{\text{facultative}}$ * aggregation size$_{\text{large}}$	0.43	−1.37	2.58	1800	0.6678
Dependency$_{\text{obligate}}$ * aggregation size$_{\text{large}}$	0.45	−1.34	2.14	1800	0.5900
Dependency$_{\text{occasional}}$ * richness$_{\text{high}}$	0.28	−1.74	2.15	1976	0.7789
Dependency$_{\text{facultative}}$ * richness$_{\text{high}}$	0.01	−2.00	1.96	1800	0.9756
Dependency$_{\text{obligate}}$ * richness$_{\text{high}}$	0.88	−0.71	2.81	1800	0.3344
Aggregation size$_{\text{large}}$ * richness$_{\text{high}}$	**1.50**	**0.24**	**2.75**	**1935**	**0.0178**

Estimates of Bayesian GLMMs for the influence of dependency, aggregation size and species richness on attraction of species with different swarm dependencies to simulated ant swarms. Response is the proportion of nonfollowers and occasional followers, facultative followers and obligate followers relative to the total number of detected individuals in each dependency level in each experimental trial. Effects are relative to the model intercept (dependency = nonfollower, aggregation size = small, richness = low). Reported are posterior means, lower and upper 95% credible intervals (CI), effective sample size (n_{eff}) and pMCMC (the probability that the posterior distribution crosses zero). Bold font indicates pMCMC < 0.05.

high. Our playbacks might not have simulated a large enough aggregation of dominant individuals of obligate species to reach this threshold, and future experiments should explore this possibility.

Our factorial design allowed us to document interactions between different types of social information (aggregation size, aggregation richness and dependency guild) and how they may reflect trade-offs between foraging opportunities and competitive interactions. We found an interaction effect between aggregation richness and dependency on community-wide responses to playbacks: higher-aggregation richness treatments of occasional and obligate playbacks attracted a greater proportion of responding individuals and species of eavesdropping birds (Table 1, Fig. 1a and b). A more diverse mixed-species aggregation may indicate an increased diversity of prey types to exploit, and potentially, less competition with conspecifics (Powell, 1985).

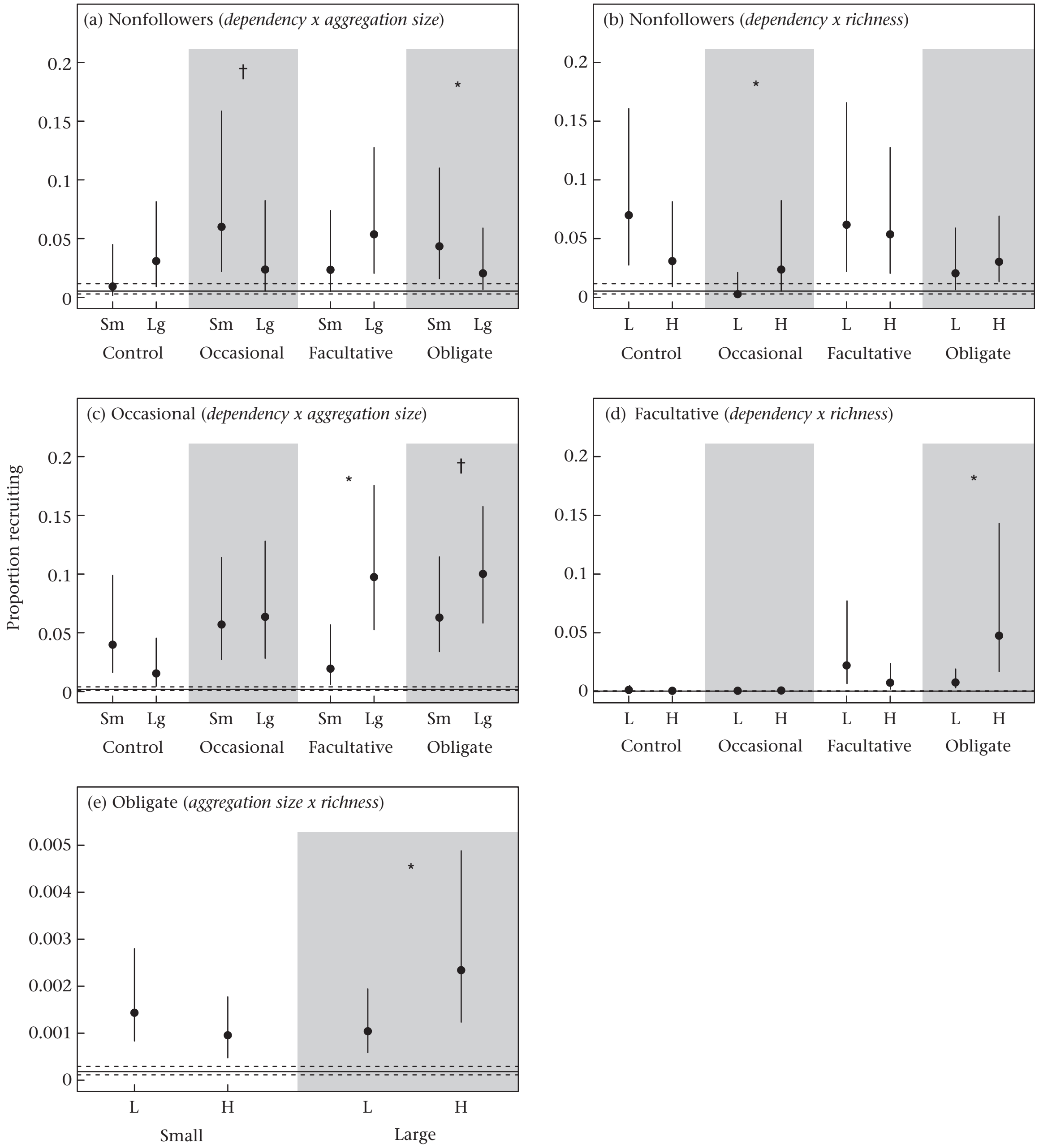

Figure 2. Guild-specific responses to experimental playbacks. Posterior means from reduced Bayesian models (implemented in MCMCglmm). Proportion of (a) nonfollowers (dependency × aggregation size), (b) nonfollowers (dependency × richness), (c) occasional (dependency × aggregation size), (d) facultative (dependency × richness) and (e) obligate (aggregation × richness) species that responded to the different treatments (aggregation size: small (Sm) versus large (Lg); aggregation richness: high (H) versus low (L)). Panels show only interaction terms with significant results from Table 3. Error bars indicate 95% credible interval. Solid and dashed lines along the bottom of each graph indicate the proportion that randomly approached the speaker during the pre-stimulus period (±95% credible interval), pooling all trials. Note the different response scales among panels. In (a)–(d), treatment combinations are grouped by dependency guild: control and facultative = no shading; occasional and obligate = shaded. Asterisks indicate significant pairwise difference ($pMCMC < 0.05$) within each shaded or unshaded block (e.g. between low and high aggregation richness for occasional treatment in (a)). †$pMCMC < 0.1$.

Guild-specific Responses to Acoustic Social Information

We also found interactions between dependency guild and either aggregation size or species richness in guild-specific responses to playbacks. In spite of having low population densities in general (Willis & Oniki, 1978), a greater proportion of obligate species responded to playbacks simulating large, high-richness aggregations (Table 2, Fig. 2e), potentially due to an increase in perceived resource profitability coupled with an obligate species' ability to competitively exclude other birds from resources at swarms (Willis & Oniki, 1978). A greater proportion of occasional followers also responded to playbacks of larger aggregation sizes of facultative birds (Table 2, Fig. 2c). Generally, these results are consistent with the benefits of being in larger groups where more individuals may indicate a larger swarm and thus a higher abundance of food resources (Clark & Mangel, 1984). Previous work has shown that the presence of more individuals indicates a larger food patch that may be exploitable and provide for greater foraging benefits (Morgan & Fernández-Juricic, 2007; Pitcher, Magurran, & Winfield, 1982). Alternatively, enhanced responses to large,

Table 4
Effects of aggregation size, richness and dependency level on the attraction of individuals and species and the four dependency guilds to simulated swarms

Response variable	Predictor variable					
	D_{obligate}	Size * richness	$D_{\text{occcasional}}$ * richness	D_{obligate} * richness	D_{obligate} * size	$D_{\text{Facultative}}$ * size
Individuals	+		+	+		
Species	+		+	+		
Control			+		−	
Occasional						+
Facultative	+			+		
Obligate	+	+				

D = dependency guild; size = aggregation size; richness = aggregation richness. Asterisks denote an interaction between predictor variables. A +/− is included if either the singular or interaction term positively (+) or negatively (−) influenced the response variable.

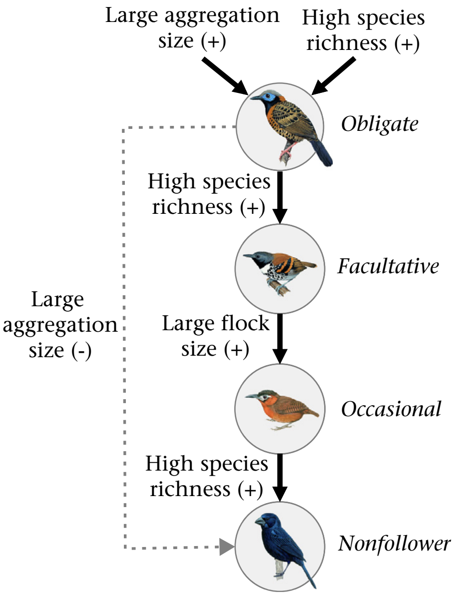

Figure 3. Schematic illustrating the flow of different types of social information (aggregation size, species richness, dependency) cascading in mixed-species bird aggregations at ant swarms. Dependency guilds are indicated within circles. Positive effects are indicated by solid lines or as (+); negative effects are indicated by dotted lines or as (-). For example, larger aggregations with higher species richness positively increased attraction of obligate species, more diverse aggregations of obligate species increased attraction of facultative species, large aggregations of facultative species increased attraction of occasional species. Obligate = ocellated antbird, *Phaenostictus mcleannani*; facultative = spotted antbird, *Hylophylax naevioides*; occasional = song wren, *Cyphorhinus phaeocephalus*; nonfollower = blue-black grosbeak, *Cyanocompsa cyanoides*. Images are reproduced with permission from J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie and E. de Juana (Eds.). (2017). *Handbook of the Birds of the World Alive*. Barcelona, Spain: Lynx Edicions. (Retrieved from http://www.hbw.com/ on 13 February 2017).

higher-richness aggregations may simply be a result of disturbance foraging, whereby visual and vocal activity attracts individuals to an area (mixed-species flocks, sensu Powell, 1985). Birds in particular (including ant-following birds) are known to cue in to disturbances such as foraging monkeys (Boinski & Scott, 1988; Fontaine, 1980; reviewed in Heymann & Hsia, 2015), tamanduas excavating termite nests (Pollock, 2017) and even humans (Alexander Skutch and 'Jimmy' the bicoloured antbird; Skutch, 1980). Ant swarms may therefore simply represent a more predictable form of disturbance that is exploited by birds and various other taxa (Rettenmeyer et al., 2011). The only negative interaction observed was a lower proportion of nonfollowers responding to playbacks simulating large aggregations of obligate species. While nonfollowing birds are not affected by other guilds, they may actively avoid larger groups of obligate birds, potentially to avoid the presence of superior competitors (Fletcher, 2008; Forsman, Hernquist, Taipale, & Gustafsson, 2008). In general, many nonfollowers are smaller insectivores relative to behaviourally dominant obligate ant followers.

One potential criticism of our analysis is that we did not partition conspecific and heterospecific responses to playbacks, primarily because we did not detect enough conspecific responders to model conspecific responses to playbacks separately using our Bayesian analytical framework. However, we did compare raw numbers of conspecific responders and found no differences across the different treatment groups. Furthermore, our analyses for guild-specific responses suggest that species from one guild responded to the guild above it (from less specialized to more specialized). Had species responded only to conspecifics, we would expect guilds to have the strongest responses to members of the same guild themselves. However, we did not see this in our results and we therefore are confident that conspecifics did not influence the conclusions derived from our analysis.

Attraction of Eavesdropping Birds to Swarms Is Based on a Social Information Cascade

Overall, our results strongly suggest that the attraction of eavesdropping birds to ant swarms is based on an information cascade among the guilds. We found that attraction of each guild was positively influenced by the presence of the dependency guild directly above it in the degree of specialization on ant swarms: obligate species increased attraction of facultative species, which increased attraction of occasional species, which increased attraction of nonfollowers (Fig. 3).

We propose that, as individual birds join a swarm, they themselves become producers of information, which in turn may reflect the changing costs and benefits of foraging at the swarm. We found a nonrandom pattern in this cascade of information: individuals of lower-dependency guilds consistently responded to cues of the immediately higher-dependency guild. We suggest that species may respond to different guilds at foraging aggregations as a way of identifying diverse aggregations that may reflect a diversity of exploitable prey resources (Rettenmeyer et al., 2011).

We acknowledge that the concept of eavesdropping birds responding to the initial responders rather than the playbacks themselves ('the snowball effect') was likely to influence our results to a certain extent. Responding birds often vocalized while approaching playbacks, which could serve as additional acoustic social information that could further influence attraction of other eavesdropping birds. Although we could not evaluate this effect on a trial-by-trial basis, we argue that the presence of a snowball effect would only reinforce more strongly the idea that an information cascade is occurring in this system. Indeed, facultative species were usually the first to approach playbacks of obligate species and would often vocalize, potentially becoming information producers and attracting occasional species, which often recruited later to playbacks. These observations are consistent with our finding that obligate species positively influenced attraction of facultative species, which in turn positively influenced the attraction of occasional species. Unfortunately, it is impossible to distinguish whether eavesdropping birds were responding to the playbacks themselves or to other vocalizing birds that initially responded. However, our results clearly indicate that obligate species are core members whose vocalizations are critical for aggregation formation and induce the strongest responses, which in turn cascade to lower-dependency guilds.

Our study is limited in that we did not measure actual costs and benefits to individual birds, but rather we assumed that individuals' positive or negative responses to playbacks were a proxy for the cost–benefit ratio of joining an aggregation. For example, if a bird responded to playback, we assumed that the benefit of joining an aggregation was greater than the cost. Future studies are needed that measure actual costs (i.e. frequency of competitive interactions) and benefits (i.e. prey capture rates) of foraging at aggregations of different size, richness and dependency. We predicted that larger, higher-richness aggregations would confer greater foraging opportunities that would be reflected in more individuals and species approaching playbacks, and indeed that is what we found, although intense competition has been documented at swarms with larger aggregations (Willis & Oniki, 1978). We did not create treatments combining different dependency guilds, something likely to occur in nature, and we predict that such combinations might generate even stronger responses (as they may represent greater diversity of foraging strategies reflective of a diversity of prey diet) than those used in our study. We suggest that future studies should assess multiple types of social information in a cost–benefit framework to determine the relative importance of different types of social information that underlie the formation and maintenance of mixed-species foraging aggregations. Understanding how animals make behavioural decisions can shed light on how individual behaviour can scale up to influence interspecific interactions and subsequent community composition of mixed-species groups (Goodale et al., 2010).

Acknowledgments

We dedicate this paper to Ken Allaire, who generously provided numerous local recordings of focal species' vocalizations that were used in creating playbacks and was an integral part of the Panama ornithological community. We also thank the Macaulay Library at the Cornell Lab of Ornithology and especially A. Kirschel for also providing access to personal recordings of focal species. We thank J. Brawn, Z. Cheviron and J. Touchton for logistical support and helpful comments on the manuscript, E. Parra for help constructing the speakers used in the experiment and O. Jaramillo for help identifying bird vocalizations. We also thank the Administración Nacional del Ambiente (ANAM) for providing us with research permits and allowing us to conduct our research in Parque Nacional Soberanía. We are grateful to E. Goodale and an anonymous referee whose comments improved the manuscript. This research was funded by National Science Foundation Grant PRFB 1309320 to A. E. Martínez. A.E.M., H.S.P., J.P.K. and C.E.T. conceived and designed the experiment; A.E.M. and H.S.P. collected the data; J.P.K. conducted data analyses; A.E.M., H.S.P., J.P.K. and C.E.T. wrote the paper.

Supplementary material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2017.10.024.

References

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour, 29*, 543–550.

Batcheller, H. J. (2017). Interspecific information use by army-ant following birds. *Auk, 134*, 247–255.

Boinski, S., & Scott, P. E. (1988). Association of birds with monkeys in Costa Rica. *Biotropica, 20*, 136–143.

Bonnie, K. E., & Earley, R. L. (2007). Expanding the scope for social information use. *Animal Behaviour, 74*, 171–181.

Brumfield, R. T., Tello, J. G., Cheviron, Z. A., Carling, M. D., Crochet, N., & Rosenberg, K. V. (2007). Phylogenetic conservatism and antiquity of a tropical specialization: Army-ant following in the typical antbirds (Thamnophilidae). *Molecular Phylogenetics & Evolution, 45*, 1–13.

Chaves-Campos, J. (2003). Localization of army-ant swarms by ant-following birds on the Caribbean slope of Costa Rica: Following the vocalization of antbirds to find the swarms. *Ornitología Neotropical, 14*, 289–294.

Chaves-Campos, J. (2005). Bare-necked umbrellabird (*Cephalopterus glabricollis*) foraging at an unusually large assemblage of army ant-following birds. *Wilson Bulletin, 117*, 418–420.

Chaves-Campos, J., & DeWoody, J. (2008). The spatial distribution of avian relatives: Do obligate army-ant-following birds roost and feed near family members? *Molecular Ecology, 17*, 2963–2974.

Clark, C. W., & Mangel, M. (1984). Foraging and flocking strategies: Information in an uncertain environment. *American Naturalist, 123*, 626–641.

Cordeiro, N. J., Borghesio, L., Joho, M. P., Monoski, T. J., Mkongewa, V. J., & Dampf, C. J. (2015). Forest fragmentation in an African biodiversity hotspot impacts mixed-species bird flocks. *Biological Conservation, 188*, 61–71.

Danchin, É., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science, 305*, 487–491.

Dunning, J. B., Jr. (Ed.). (2007). *CRC handbook of avian body masses*. Chicago, IL: CRC Press.

Fletcher, R. J. (2008). Social information and community dynamics: Non-target effects from simulating social cues for management. *Ecological Applications, 18*, 1764–1773.

Fontaine, R. (1980). Observations on the foraging association of double-toothed kits and white-faced capuchin monkeys. *Auk, 97*, 94–98.

Forsman, J. T., Hernquist, M. B., Taipale, J., & Gustafsson, L. (2008). Competitor density cues for facilitating habitat selection and investment decisions. *Behavioral Ecology, 19*, 539–545.

Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour, 61*, 3–15.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science, 7*, 457–511.

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution, 25*, 354–361.

Goodale, E., & Kotagama, S. W. (2005). Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. *Journal of Tropical Ecology, 21*, 669–676.

Gu, H., Chen, J., Ewing, H., Liu, X., Zhao, J., & Goodale, E. (2017). Heterospecific attraction to the vocalizations of birds in mass-fruiting trees. *Behavioral Ecology and Sociobiology, 71*, 82. https://doi.org/10.1007/s00265-017-2312-6.

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software, 33*, 1–22.

Heymann, E. W., & Hsia, S. S. (2015). Unlike fellows: A review of primate–non-primate associations. *Biological Reviews, 90*, 142–156.

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., & de Juana, E. (Eds.). (2017). *Handbook of the birds of the world alive*. Barcelona, Spain: Lynx Edicions. Retrieved from: http://www.hbw.com/. on 13 February 2017.

Isler, M. L., Isler, P. R., & Brumfield, R. T. (2005). Clinal variation in vocalizations of an antbird (Thamnophilidae) and implications for defining species limits. *Auk, 122*, 433–444.

Jullien, M., & Thiollay, J. M. (1998). Multi-species territoriality and dynamic of neotropical forest understorey bird flocks. *Journal of Animal Ecology, 67*, 227–252.

Kelley, J. P. (n.d.). Neighbor–stranger discrimination in a tropical, suboscine bird: Importance of accounting for social environment in detecting hypothetically improbable patterns. Manuscript in preparation.

Kelley, J. P., & Tarwater, C. E. (n.d.-a). [Quantification of geographical variation in song traits in the black-crowned antshrike, *Thamnophilus atrinucha*]. Unpublished raw data.

Kelley, J. P., & Tarwater, C. E. (n.d.-b). How intruder age impacts aggression of territorial pairs: Experimental manipulation of perceived age of intruder males. Manuscript in preparation.

Kristan, W. B., III (2003). The role of habitat selection behavior in population dynamics: Source–sink systems and ecological traps. *Oikos, 103*, 457–468.

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2014). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews, 90*, 560–586.

Martínez, A. E., Gomez, J. P., Ponciano, J. M., & Robinson, S. K. (2016). Functional traits, flocking propensity, and perceived predation risk in an Amazonian understory bird community. *American Naturalist, 187*, 607–619.

Matsuoka, S. M., Mahon, C. L., Handel, C. M., Sólymos, P., Bayne, E. M., Fontaine, P. C., et al. (2014). Reviving common standards in point-count surveys for broad inference across studies. *Condor, 116*, 599–608.

McNamara, J. M., & Houston, A. I. (1986). The common currency for behavioral decisions. *American Naturalist, 127*, 358–378.

Morgan, T., & Fernández-Juricic, E. (2007). The effects of predation risk, food abundance, and population size on group size of brown-headed cowbirds (*Molothrus ater*). *Ethology, 113*, 1173–1184.

O'Donnell, S. (2017). Evidence for facilitation among avian army-ant attendants: Specialization and species associations across elevations. *Biotropica, 49*(5), 665–674. https://doi.org/10.1111/btp.12452.

Peake, T. M. (2005). Eavesdropping in communication networks. In P. K. McGregor (Ed.), *Animal communication networks* (pp. 13–37). Cambridge, U.K.: Cambridge University Press.

Peres, C. A. (1993). Anti-predation benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica, 61*, 61–76.

Pitcher, T. J., Magurran, A. E., & Winfield, I. J. (1982). Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology, 10*, 149–151.

Pollock, H. S. (2017). First observation of a disturbance foraging association between obligate ant-following birds and a tamandua anteater in central Panama. *Wilson Journal of Ornithology, 129*(4), 870–873.

Pollock, H. S. and Tarwater C. E. (n.d.). [Responses of antbird community to conspecific playbacks: A pilot study]. Unpublished raw data.

Powell, G. V. N. (1985). Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. *Ornithological Monographs, 36*, 713–732.

R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rettenmeyer, C. W., Rettenmeyer, M. E., Joseph, J., & Berghoff, S. M. (2011). The largest animal association centered on one species: The army ant *Eciton burchellii* and its more than 300 associates. *Insectes Sociaux, 58*, 281–292.

Robinson, W. D., Brawn, J. D., & Robinson, S. K. (2000). Forest bird community structure in central Panama: Influence of spatial scale and biogeography. *Ecological Monographs, 70*, 209–235.

Schneirla, T. C. (1971). *Army ants: A study in social organization*. San Francisco, CA: W. H. Freeman.

Seppänen, J. T., Forsman, J. T., Mönkkönen, M., & Thomson, R. L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology, 88*, 1622–1633.

Shriner, W. M. (1998). Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. *Animal Behaviour, 55*, 529–536.

Skutch, A. F. (1980). *A naturalist on a tropical farm*. Berkeley, CA: University of California Press.

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

Swartz, M. B. (2001). Bivouac checking, a novel behavior distinguishing obligate from opportunistic species of army-ant-following birds. *Condor, 103*, 629–633.

Thiollay, J. M. (1999). Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: An intertropical comparison. *Journal of Avian Biology, 30*, 282–294.

Valone, T. J. (2007). From eavesdropping on performance to copying the behavior of others: A review of public information use. *Behavioral Ecology and Sociobiology, 62*, 1–14.

Valone, T. J., & Templeton, J. J. (2002). Public information for the assessment of quality: A widespread social phenomenon. *Philosophical Transactions of the Royal Society B: Biological Sciences, 357*, 1549–1557.

Wagner, R. H., & Danchin, É. (2010). A taxonomy of biological information. *Oikos, 119*, 203–209.

Westrip, J. R., & Bell, M. B. (2015). Breaking down the species boundaries: Selective pressures behind interspecific communication in vertebrates. *Ethology, 121*, 725–732.

Willis, E. O. (1972). The behavior of spotted antbirds. *Ornithological Monographs, 10*, 1–162.

Willis, E. O., & Oniki, Y. (1978). Birds and army ants. *Annual Review of Ecology and Systematics, 9*, 243–263.

Willson, S. K. (2004). Obligate army-ant-following birds: A study of ecology, spatial movement patterns, and behavior in Amazonian Peru. *Ornithological Monographs, 55*, 1–67.