

## Research



**Cite this article:** Dominguez JS *et al.* 2023 What's the rumpus? Resident temperate forest birds approach an unfamiliar neotropical alarm call across three continents. *Biol. Lett.* **19**: 20230332.

<https://doi.org/10.1098/rsbl.2023.0332>

Received: 19 July 2023

Accepted: 18 September 2023

### Subject Category:

Animal behaviour

### Subject Areas:

behaviour, cognition, ecology, evolution

### Keywords:

alarm call, avian mixed-species flocks, vocalization, heterospecific eavesdropping, avian alarm calls, sentinel species

### Author for correspondence:

Jonah S. Dominguez

e-mail: [disconsolatedragon@gmail.com](mailto:disconsolatedragon@gmail.com)

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.6858134>.

# What's the rumpus? Resident temperate forest birds approach an unfamiliar neotropical alarm call across three continents

Jonah S. Dominguez<sup>1,2</sup>, Marko Rakovic<sup>5</sup>, Donglai Li<sup>6</sup>, Henry S. Pollock<sup>3</sup>, Shelby Lawson<sup>4</sup>, Ivana Novcic<sup>7</sup>, Xiangting Su<sup>6</sup>, Qisha Zeng<sup>6</sup>, Roqaya Al-Dhufari<sup>1</sup>, Shanelle Johnson-Cadle<sup>3</sup>, Julia Boldrick<sup>3</sup>, Mac Chamberlain<sup>1</sup> and Mark E. Hauber<sup>1,2,4,8</sup>

<sup>1</sup>Department of Evolution, Ecology & Behavior, School of Integrative Biology, <sup>2</sup>Program in Ecology, Evolution, and Conservation Biology, <sup>3</sup>Department of Natural Resources and Environmental Sciences, and <sup>4</sup>Carl R Woese Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

<sup>5</sup>Department of Biology and Inland Waters Protection, University of Belgrade-Institute for Multidisciplinary Research, Despota Stefana Boulevard 142, Belgrade 11060, Serbia

<sup>6</sup>Provincial Key Laboratory of Animal Resource and Epidemic Disease Prevention, College of Life Sciences, Liaoning University, Shenyang, People's Republic of China

<sup>7</sup>Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia

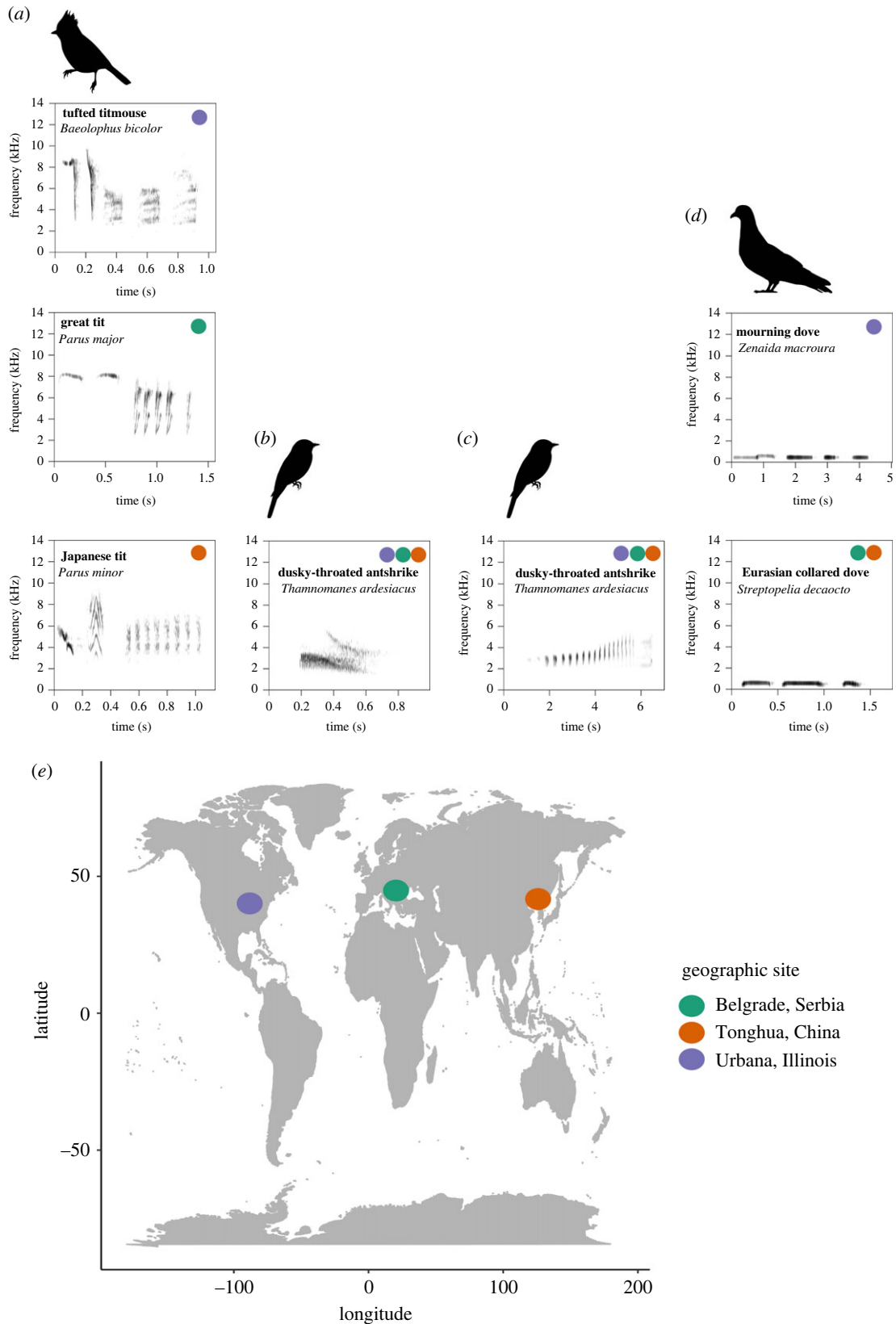
<sup>8</sup>Advanced Science Research Center and Program in Psychology, Graduate Center of the City University of New York, 85 Saint Nicholas Terrace, New York, NY 10031, USA

JSD, 0009-0007-6490-0330; HSP, 0000-0002-8698-691X; SL, 0000-0002-7628-8042

Alarm signals have evolved to communicate pertinent threats to conspecifics, but heterospecifics may also use alarm calls to obtain social information. In birds, mixed-species flocks are often structured around focal sentinel species, which produce reliable alarm calls that inform eavesdropping heterospecifics about predation risk. Prior research has shown that Neotropical species innately recognize the alarm calls of a Nearctic sentinel species, but it remains unclear how generalizable or consistent such innate signal recognition of alarm-calling species is. We tested for the responses to the alarm calls of a Neotropical sentinel forest bird species, the dusky-throated antshrike (*Thamnomanes ardesiacus*), by naive resident temperate forest birds across three continents during the winter season. At all three sites, we found that approaches to the Neotropical antshrike alarm calls were similarly frequent to the alarm calls of a local parid sentinel species (positive control), while approaches to the antshrike's songs and to non-threatening columbid calls (negative controls) occurred significantly less often. Although we only tested one sentinel species, our findings indicate that temperate forest birds can recognize and adaptively respond globally to a foreign and unfamiliar tropical alarm call, and suggest that some avian alarm calls transcend phylogenetic histories and individual ecological experiences.

## 1. Introduction

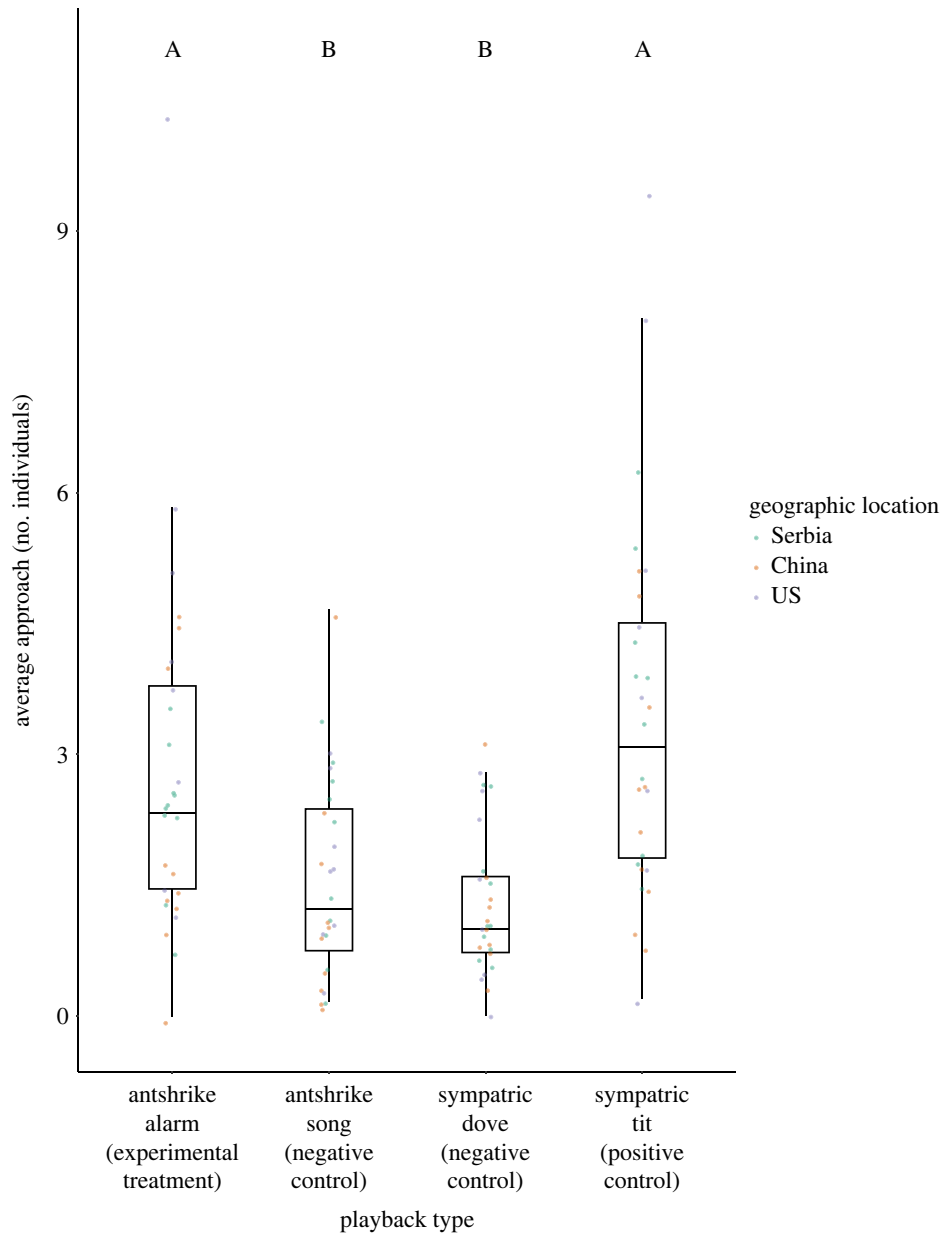
Alarm calls are auditory cues produced by animals in response to predators or other potential threats [1] and may encode a wide variety of meanings, including the type of predator, the extent of threat or the adaptive behavioural response to the predator [2,3]. While alarm calls have typically evolved to inform conspecifics, heterospecifics may eavesdrop on alarm calls, thus reducing their own risks [1]. Mixed-species flocks are the aggregations of multiple bird species for the purposes of foraging and protection from predators [4]. Within these flocks, certain species can fill the role of 'sentinels', with highly recognizable alarm calls upon which other flock members eavesdrop [5,6].



**Figure 1.** Spectrograms of playbacks and world map of playback sites. (a) Alarm calls of sympatric tit species, serving as positive control. (b) The alarm call of the dusky-throated antshrike, a foreign sentinel species. (c) The loudsong of the dusky-throated antshrike. (d) The loudsong of a sympatric dove species, serving as negative control. (e) World map of three sites. Playbacks are marked with coloured dots for each site where they were played.

Tits and chickadees (avian family Paridae) are well established as alarm-calling sentinel taxa in temperate zone mixed-species flocks [7,8]. The ability to recognize parid alarm calls, however, is not restricted to sympatric species [9,10]. Sandoval & Wilson [10] found that naive Neotropical bird species recognized and responded to alarm calls of an allopatric North American parid, the black-capped chickadee

(*Poecile atricapillus*), demonstrating that these tropical species had an innate ability to recognize unfamiliar temperate alarm calls. Our study's aim was to explore how generally the ability to innately recognize allopatric alarm calls extends across avian lineages and geographical localities, as these earlier studies focused on a single geographical region and only on parid alarm calls.



**Figure 2.** Average approach of birds to various playbacks conducted at temperate sites in North America, Europe, and Asia. Playback type was a significant predictor of response, independent of geographical site.

## 2. Methods

### (a) Species selection

The species we selected to serve as treatments in our playback experiment included: (1) a positive control, which consisted of the mobbing alarm calls of a local parid species, which typically serves as sentinels in temperate winter mixed-species flocks, (2) an experimental treatment, which consisted of the mobbing alarm calls of a known sentinel species in Neotropical mixed-species flocks [11], the dusky-throated antshrike (*Thamnomanes ardesiacus*; hereafter: antshrike); (3) a negative control, which consisted of the contact calls of a local dove species (family: Columbidae); and (4) a second negative control, which consisted of the loudsong of the antshrike, to account for the novelty of the antshrike calls (our focal treatment) potentially eliciting a response (figure 1).

### (b) Playback locations

We used eight locations in the USA, and 10 each in Serbia and China as our northern temperate zone study sites in late winter

(see below) when tropical migrants breeding in the temperate zone were absent. We visited locations in a random order. We conducted six replicates of each playback type at each location. Our USA playback locations came from a mixture of wooded sites and public parks in the area of Champaign-Urbana, Illinois (40.1°N, 88.2°W). Data collection ran from 20 January to 4 March 2023. Our Serbian playback locations came from a large suburban forest in Belgrade (44.8°N, 20.4°E); data collection ran from 13 February to 14 March 2023. Our Chinese site was in Tonghua city, Jilin province (41.7°N, 125.9°E); data collection ran from 2 March to 7 April 2023.

### (c) Playback construction

We used calls from 21 unique individuals of each playback species to create seven exemplars per playback treatment, with each exemplar containing calls from three different individuals of the given focal species. The number of notes in parid alarm calls can signify different levels of danger [12,13], with more 'dee' notes signalling a graver threat. To control for this, we standardized titmouse 'chick-a-dee' calls to have two introductory notes and three 'dee' notes, and both tit species' 'chicka' calls

to have two introductory notes and 5–7 ‘dee’ notes as this was most commonly found naturally in recordings. We then drew a random example of our titmouse (and other call/song) files for each playback occasion and location. For the antshrike, we used the ‘chirr’ call, which is used in response to predators [11]. Vocalizations from individuals were placed in a random order, and then repeated to obtain 5 min playback files. Amplitude was adjusted so sounds played from our speaker at full volume were approximately 80 SPL dB (at 1 m; see electronic supplementary material, Methods).

#### (d) Field protocol

For consistency our speaker was set to always face north. We recorded all birds that entered within a 15 m range of the speaker during the 5 min playback period as having approached the speaker. These birds were mostly absent at the trial start. We calculated approach rate as the number of individuals detected as having approached during the trial. We also recorded vocalization rate, which was the percentage of approaching individuals present that vocalized; it was positively correlated with approach rates ( $R = 0.25$ ,  $p \ll 0.0001$ ), indicating that approach rate can serve as a behavioural proxy for playback response.

#### (e) Statistical analyses

We used R v. 4.2.2 for all analyses [14]. For each playback location and playback type, we calculated average approach rates and used the non-parametric Friedman ANOVA and Kruskal–Wallace Conover’s all-pair tests to assess statistical differences between geographical locations and playback types, using R Package PMCMRplus [15]. Because several days of data collection had approach rates of zero, we also constructed a zero-inflated model using the R package glmmTMB [16], with playback type, geographical site and temperature ( $C^\circ$ ) as independent variables, playback location as a random effect and approach rate as our response variable. We tested whether there was any influence between playback type and geographical site but the interaction terms were not significant and not included in the final models. Due to responding species varying by site and date, we could not analyse species level responses across sites (electronic supplementary material, table S1).

### 3. Results

Playback type was a significant predictor of approach rate responses across all three continents (all  $p < 0.02$  all  $F > 3.6$ ). When looking at all sites together, playback was a strong predictor of response to alarm calls ( $p \ll 0.0001$ ,  $Z = 7.23$ ; table 1). Birds responded to the alarm calls of the foreign antshrike at rates comparable to the alarm calls of the sympatric parid ( $p = 0.50$ ,  $Z = 0.68$ ; figure 2). Relative to sentinel alarm calls, birds responded at significantly lower rates to both negative controls (columbid calls:  $T = -3.849$ ,  $p = 0.0012$ ; antshrike songs:  $T = -2.908$ ,  $p = 0.026$ ), with no significant difference between the responses to the two negative controls ( $T = -0.941$ ,  $p = 1.0$ ).

### 4. Discussion

We discovered that birds across a variety of Northern Hemisphere temperate locations responded by approaching the alarm calls of an unfamiliar species from the Neotropics. Despite having no exposure to our focal tropical treatment species, temperate residents’ responses were comparable to

**Table 1.** ANOVA of zero-inflated model values for examining the response of birds to foreign alarm calls compared to the alarm calls and vocalizations of native species, and coefficients of the model. Playback location included as a random effect ( $N = 645$  observations).

	$\chi^2$	d.f.	<i>p</i> -value
playback type	17.34	3	0.00060
geographic site/country	17.067	2	0.00020
temperature	1.86	1	0.17

those elicited by playbacks of local sentinel parid species. Several prior works considered the alarm responses of parid or non-parid species to parid sentinel alarm calls within a single study site [9,10], whereas our study demonstrated adaptive responses to a non-parid alarm call across three continents within the northern temperate zone. Interestingly, responses to heterospecific vocalizations (loudsongs and contact calls) of a locally extinct sentinel species in a foraging context appear to be learned in Neotropical birds [17]. Thus, alarm calls that occur in a predation context and have more direct ties to fitness may be under stronger selection to be recognized by heterospecifics.

In turn, our findings demonstrate that alarm calls of certain, phylogeographically distant species are innately recognizable. Nevertheless, one limitation of our study was that we only explored responses to a single tropical sentinel antshrike species, and it remains unclear whether innate alarm call recognition by heterospecific mixed-species flock members is generalizable to other sentinel species. Future work should therefore test responses to more sentinel species and to unfamiliar non-sentinel species to assess whether the latters’ alarm calls produce the same responses as those of sentinel species. Finally, it remains to be uncovered what bioacoustic aspects of the alarm calls serve to convey meaning across geographical regions and species boundaries.

**Ethics.** Our field sites came from managed sites within the university and from local parks. In all cases, we obtained necessary permits to conduct playback experiments at these sites under IACUC Protocol no.: 22195.

**Data accessibility.** All data used to generate figures and perform analysis can be found at: <http://dx.doi.org/10.6084/m9.figshare.23613672> [18].

The data are provided in the electronic supplementary material [19].

**Declaration of AI use.** We have not used AI-assisted technologies in creating this article.

**Authors’ contributions.** J.S.D.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, supervision, validation, visualization, writing—original draft, writing—review and editing; M.R.: data curation, investigation, supervision, writing—review and editing; D.L.: funding acquisition, project administration, supervision, writing—review and editing; H.S.P.: conceptualization, investigation, methodology, writing—review and editing; S.L.: conceptualization, methodology, software, writing—review and editing; I.N.: data curation, investigation, project administration, resources, supervision, validation, writing—review and editing; X.S.: data curation, investigation, writing—review and editing; Q.Z.: data curation, investigation, writing—review and editing; R.A.: investigation, methodology, writing—review and editing; S.J.-C.: investigation, writing—review and editing; J.B.: investigation, writing—review and editing; M.C.: investigation, methodology, writing—review and editing; M.E.H.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

**Funding.** J.S.D. was supported by a University of Illinois' Graduate College Fellowship. Additional support was provided by a National Science Foundation grant (grant no. 1953226 to M.E.H.). I.N. and M.R. were supported by the Ministry of Education, Science and

Technological Development of Serbia, no. 451-03-47/2023-01/200178 and 451-03-47/2023-01/200053. D.L. was supported by the Basic Scientific Research Projects of Liaoning Provincial Department of Education (grant no. LJKZ0093).

**Acknowledgements.** The authors thank the University of Illinois Natural Areas Committee, the Experimental Forestry Management Team, and the Urbana Parks Department for permission to conduct experiments at managed sites.

## References

- Magrath RD, Haff TM, Fallow PM, Radford AN. 2015 Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biol. Rev.* **90**, 560–586. (doi:10.1111/brv.12122)
- Evans CS, Evans L, Marler P. 1993 On the meaning of alarm calls: functional reference in an avian vocal system. *Anim. Behav.* **46**, 23–38. (doi:10.1006/anbe.1993.1158)
- Gill SA, Bierema AM-K. 2013 On the meaning of alarm calls: a review of functional reference in avian alarm calling. *Ethology* **119**, 449–461. (doi:10.1111/eth.12097)
- Sridhar H, Beauchamp G, Shanker K. 2009 Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* **78**, 337–347. (doi:10.1016/j.anbehav.2009.05.008)
- Farley EA, Sieving KE, Contreras TA. 2008 Characterizing complex mixed-species bird flocks using an objective method for determining species participation. *J. Ornithol.* **149**, 451–468. (doi:10.1007/s10336-008-0284-z)
- Ragusa-Netto J. 2002 Vigilance towards raptors by nuclear species in bird mixed flocks in a Brazilian savannah. *Stud. Neotrop. Fauna Environ.* **37**, 219–226. (doi:10.1076/snfe.37.3.219.8573)
- Hurd CR. 1996 Interspecific attraction to the mobbing calls of black-capped chickadees (*Parus atricapillus*). *Behav. Ecol. Sociobiol.* **38**, 287–292. (doi:10.1007/s002650050244)
- Dolby AS, Grubb jr TC. 1998 Benefits to satellite members in mixed-species foraging groups: an experimental analysis. *Anim. Behav.* **56**, 501–509. (doi:10.1006/anbe.1998.0808)
- Dutour M, Léna J-P, Lengagne T. 2017 Mobbing calls: a signal transcending species boundaries. *Anim. Behav.* **131**, 3–11. (doi:10.1016/j.anbehav.2017.07.004)
- Sandoval L, Wilson DR. 2022 Neotropical birds respond innately to unfamiliar acoustic signals. *Am. Nat.* **200**, 419–434. (doi:10.1086/720441)
- Zimmer K, Isler ML. 2020 Dusky-throated antshrike (*Thamnomanes ardesiacus*). In *Birds of the world* (eds SM Billerman, BK Keeney, PG Rodewald, TS Schulenberg). Ithaca, NY: Cornell Lab of Ornithology. (doi:10.2173/bow.dutant2.01)
- Suzuki TN. 2014 Communication about predator type by a bird using discrete, graded and combinatorial variation in alarm calls. *Anim. Behav.* **87**, 59–65. (doi:10.1016/j.anbehav.2013.10.009)
- Courter JR, Ritchison G. 2010 Alarm calls of tufted titmice convey information about predator size and threat. *Behav. Ecol.* **21**, 936–942. (doi:10.1093/beheco/arq086)
- R Core Team. 2023 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>
- Pohlert T. 2022 *PMCMRplus: calculate pairwise multiple comparisons of mean rank sums extended*. See <https://CRAN.R-project.org/package=PMCMRplus>.
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017 glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378. (doi:10.32614/RJ-2017-066)
- Pollock HS, Martínez AE, Kelley JP, Touchton JM, Tarwater CE. 2017 Heterospecific eavesdropping in ant-following birds of the Neotropics is a learned behaviour. *Proc. R. Soc. B* **284**, 20171785. (doi:10.1098/rspb.2017.1785)
- Dominguez JS *et al.* 2023 Data from: What's the rumpus? Resident temperate forest birds approach an unfamiliar neotropical alarm call across three continents. Figshare. (doi:10.6084/m9.figshare.23613672)
- Dominguez JS *et al.* 2023 What's the rumpus? Resident temperate forest birds approach an unfamiliar neotropical alarm call across three continents. Figshare. (doi:10.6084/m9.figshare.c.6858134)