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What's the Rumpus? Resident Temperate Forest Birds Approach An Unfamiliar Neotropical Alarm Call Across Three Continents

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

[1]University of Illinois at Urbana-Champaign, Department of Evolution, Ecology & Behavior, School of Integrative Biology, Urbana, IL 61801, USA

[2]University of Illinois at Urbana-Champaign, Program in Ecology, Evolution, and Conservation Biology, Urbana, IL 61801, USA

[3]Department of Biology and Inland Waters Protection, University of Belgrade-Institute for Multidisciplinary Research, Despota Stefana Blvd. 142, 11060 Belgrade, Serbia

[4]Provincial Key Laboratory of Animal Resource and Epidemic Disease Prevention, College of Life Sciences, Liaoning University, Shenyang, China

[5]University of Illinois at Urbana-Champaign, Department of Natural Resources and Environmental Sciences, Urbana, IL 61801, USA

[6]University of Illinois at Urbana-Champaign, Carl R Woese Institute for Genomic Biology, Urbana, IL, 61801, USA

[7]Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia

[8]Advanced Science Research Center and Program in Psychology, Graduate Center of the City University of New York, 85 St. Nicholas Terrace, New York, NY 10031, USA

Abstract

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.

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 size of threat, or the adaptive behavioral 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].

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 and Wilson (2022) 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 geographic localities, as these earlier studies focused on a single geographic region and have focused only on parid alarm calls.

Methods

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).

Playback Locations

We used eight locations in the U.S.A., 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 U.S.A. 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 January 20th to March 4th, 2023. Our Serbian playback locations came from a large suburban forest in Belgrade (44.8° N, 20.4° E); data collection ran from February 13th to March 14th, 2023. Our Chinese site was in Tonghua city, Jilin province (41.7° N, 125.9° E); data collection ran from March 2nd to April 7th, 2023.

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 signaling 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 ~ 80 SPL dB (at 1 m; see Supplementary Methods).

Field Protocol

For consistency our speaker was set to always face north. We recorded all birds that entered within a 15 meter range of the speaker during the 5 min playback period as having approached the speaker. These birds were mostly not present 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 behavioral proxy for playback response.

Statistical Analyses

We used R v4.2.2 for all analyses [14]. For each playback location and playback type, we calculated average approach rates and used the nonparametric Friedman ANOVA and Kruskal-Wallace Conover's All-Pair tests to assess statistical differences between geographic 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, geographic site, and temperature (C°) 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 geographic 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 analyze species level responses across sites (Supplemental Table 1).

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 ($P << 0.0001$, $Z = 7.23$; Figure 2). Birds consistently responded to the alarm calls of the foreign antshrike at rates comparable to the alarm calls of the sympatric parid ($P = 0.50$, $Z = 0.68$; Table 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 ($T = -0.941$, $P= 1.0$).

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 treatment species, temperate residents' responses were comparable to 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 both 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 geographic regions and species boundaries.

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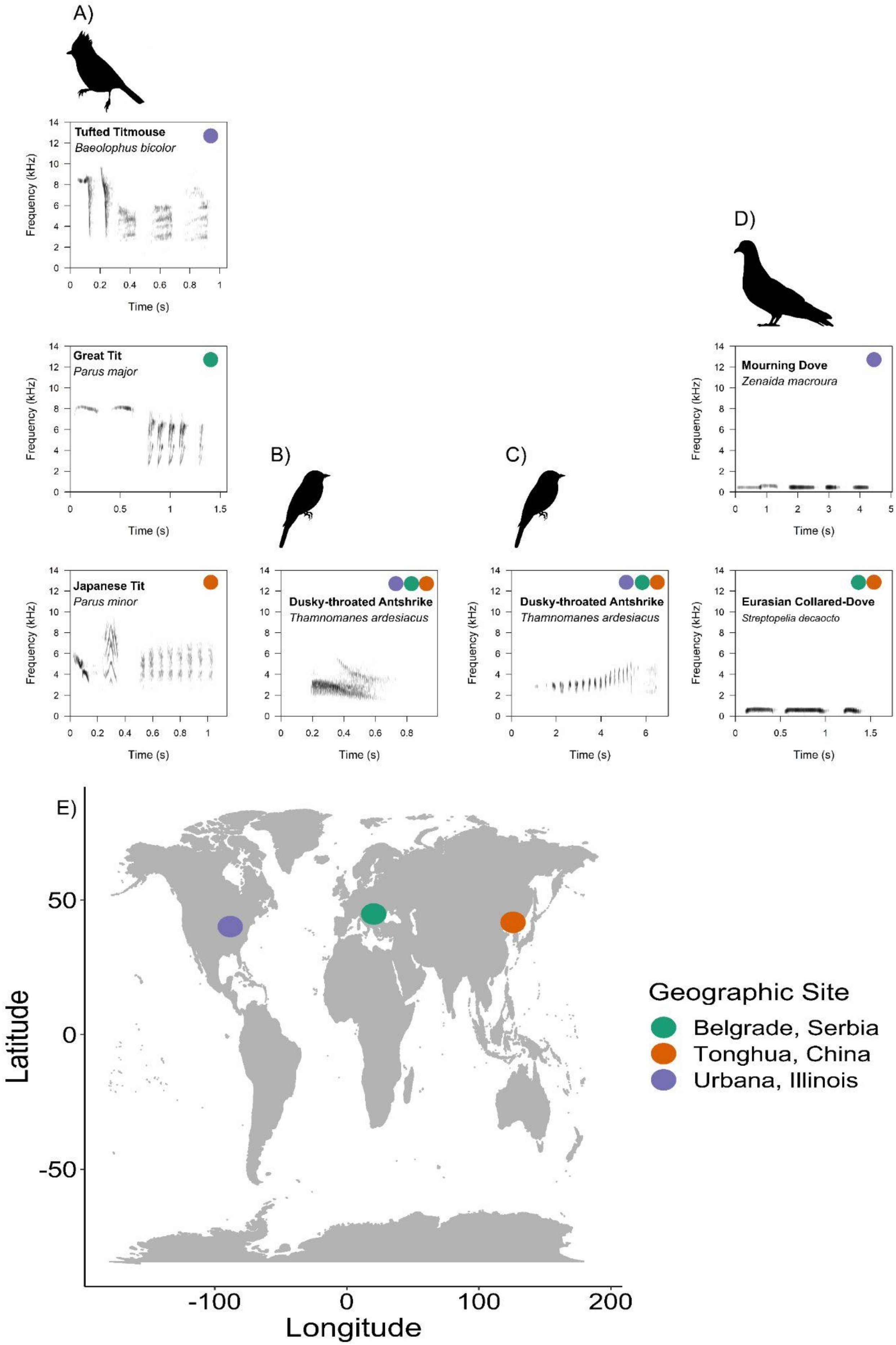

A)
Tufted Titmouse
Baeolophus bicolor
Great Tit
Parus major
Japanese Tit
Parus minor
B)
Dusky-throated Antshrike
Thamnomanes ardesiacus
C)
Dusky-throated Antshrike
Thamnomanes ardesiacus
D)
Mourning Dove
Zenaida macroura
Eurasian Collared-Dove
Streptopelia decaocto
Frequency (kHz)
Time (s)
E)
Latitude
Longitude
Geographic Site
Belgrade, Serbia
Tonghua, China
Urbana, Illinois

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 colored dots for each site where they were played.

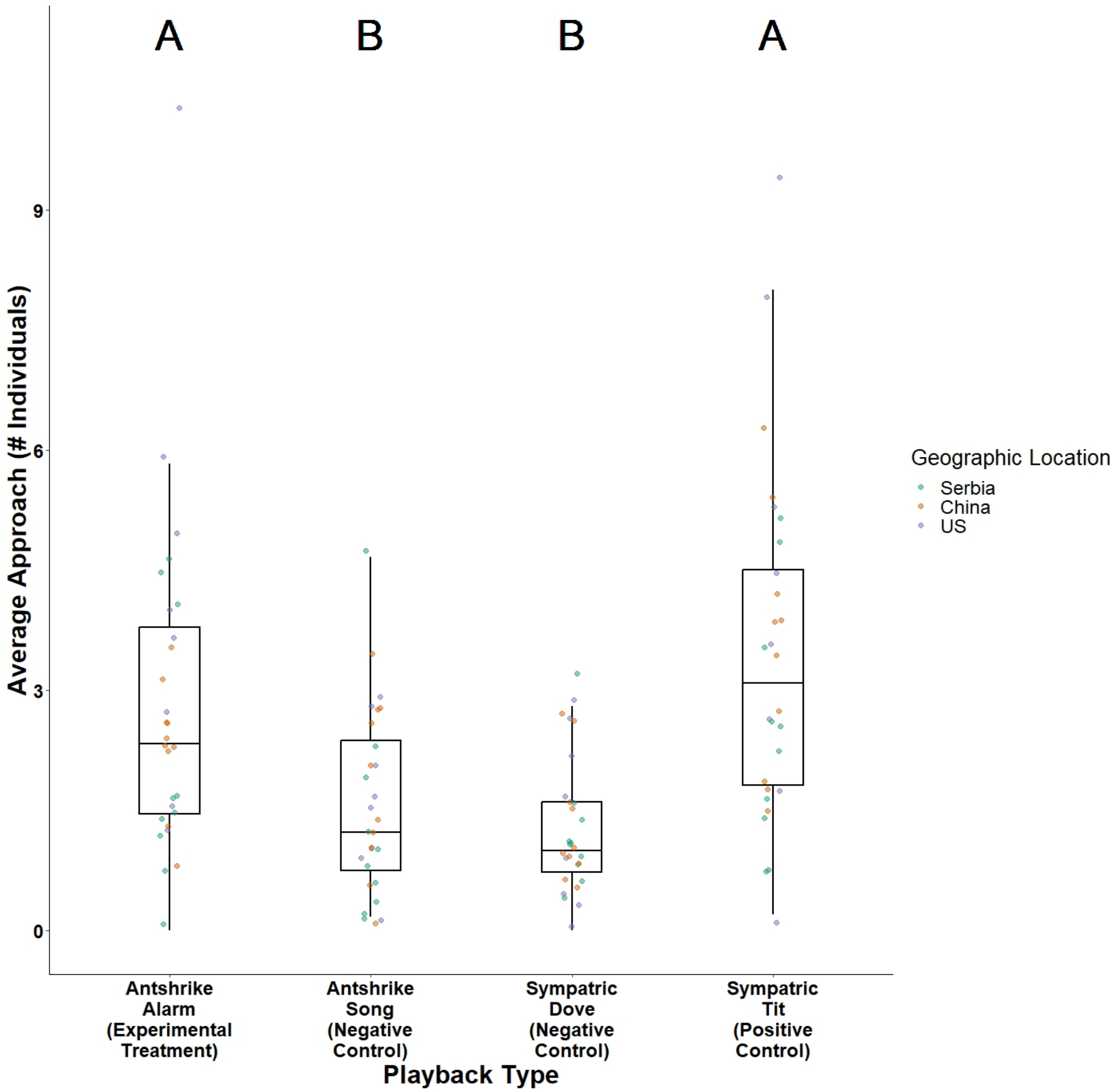

Figure 2: Average approach of birds to various playbacks conducted at temperate sites in North America, Europe, and Asia. Playback type was a significant predictor of response, independent of geographic site.

	$\chi 2$	Df	P Value
Playback Type	17.34	3	0.00060
Geographic Site/Country	17.067	2	0.00020
Temperature	1.86	1	0.17

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).

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