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Research article

Strangers like me: birds respond equally to a familiar and an unfamiliar sentinel species' alarm calls, but respond less to non-core and non-sentinel's alarm calls

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Alarm signals have evolved to communicate imminent threats to conspecifics but animals may also perceive other species' alarm displays to obtain adaptive information. In birds, mixed-species foraging flocks are often structured around a focal sentinel species, which produces reliable alarm calls that inform eavesdropping non-sentinel heterospecifics about predation risk. Ongoing work has revealed that several species can recognize the alarm calls of certain sentinel species even without prior encounters, including when these are from distant biogeographic regions. Similar work has yet to examine whether naive subjects' responses to unfamiliar sentinel alarm calls differ from responses to non-sentinel alarm calls. Here we played the alarm calls of three subtropical Asian bird species that participate in mixed species flocks, to temperate North American birds. Birds responded most to the alarm call of an allopatric core sentinel and a local sympatric sentinel control species, less so to an allopatric non-core sentinel, and least so to an allopatric non-sentinel and a negative control stimulus. These patterns provide evidence that broad phylogenetic and geographic recognition is a pertinent aspect of sentinel alarm calls in general.

Keywords: alarm calls, communication, heterospecific eavesdropping, mixed-species flocks, sentinel species

Introduction

Antipredatory behaviors in birds are a key mechanism for survival (Lima 1993). Among these are alarm calls, which are vocal cues that can function to alert conspecifics to specific threats. Alarm calls may convey a wide variety of meanings, including the presence of a predator, the type of predator, the extent of its threat, and/or the best course of response to take (Evans et al. 1993, Gill and Bierema 2013). In many cases, alarm calls are also heard by heterospecifics, who may eavesdrop and glean information for their own survival or other fitness benefit (Magrath et al. 2015, Lawson et al. 2020). While

alarm calls can evoke a wide variety of responses intraspecifically, heterospecific alarm calls often evoke vigilant responses (Magrath et al. 2015). These can include approach and mobbing that can help protect both the caller and responders from predators.

Mixed species flocks form when birds of two or more species gather together to forage (Sridhar et al. 2009). Sentinel species, also called nuclear species, represent the backbone of these mixed species flocks (Zou et al. 2018) as they are typically more vigilant than other members of the flock and produce alarm calls earlier in response to predators (Ragusa-Netto 2010). As a result, participation in these mixed-species flocks produces significant fitness benefits for non-sentinel species through eavesdropping on sentinel alarm calls, providing an evolutionary pressure for non-sentinels to recognize sentinel vocalizations (Magrath et al. 2015).

Mixed-species flocks have been widely studied, but sentinels in particular have been relatively understudied compared to other species-members of such flocks (Mangini et al. 2023). Researchers have proposed that sentinels may gain fitness benefits from evolving alarm calls that are easily recognizable by heterospecifics within their local flocks (Baigrie et al. 2014). Engaging in sentinel behavior can allow these actors to gain access to insects flushed by other members of the flock, and in some cases may reduce predation risk (Diamond 1987, Johnson et al. 2003). In return, species that associate with them will typically gain anti-predator benefits due to the sentinels' high vigilance (Diamond 1987, Limparungpatthanakij et al. 2017). As a result, sentinels are likely able to more easily entice other species to associate with them if their alarm is readily recognizable.

However, not all sentinels are equally reliable. While sentinels are defined by their alarm calls and vigilant behavior, not all sentinels produce alarm calls when there are other sentinels also present in the flock (Carlson et al. 2020). Core sentinels typically produce alarm calls more reliably, regardless of other members of a flock, while non-core sentinels produce alarm calls less reliably when in the presence of core sentinels (Goodale and Kotagama 2005, Limparungpatthanakij et al. 2017, Zou et al. 2018, Moeliker et al. 2020).

The alarm calls of certain sentinel species are recognizable across geographic and species barriers. For instance, Sandoval and Wilson (2022) demonstrated the alarm call of the black-capped chickadee (*Poecile atricapillus*; a common Nearctic sentinel species of mixed winter foraging flocks) was recognized innately by Neotropical birds, and Dominguez et al. (2023) showed that the alarm call of the dusky-throated antshrike *Thamnomanes ardesiacus* (a Neotropical sentinel) was recognized by north temperate zone birds, implying that the recognition on unfamiliar sentinel species' calls was not restricted to members of the local foraging flocks or geographic zones. However, these studies have only tested whether foreign sentinel alarm calls were recognizable by unfamiliar heterospecifics. It remains to be tested whether the alarm calls of foreign non-sentinel mixed-flock members produce similar responses or the alarm call of sentinel species focally elicits these responses.

Our goal here was to fill in knowledge gaps regarding whether the alarm calls of non-sentinel members of mixed flocks produce similar alert responses as sentinel alarm calls or if the alarm call of sentinel species alone elicits these responses. We predicted that a core sentinel species has more recognizable alarm calls than both a non-core sentinel and a non-sentinel member species of the same mixed-species flock. To test this, we conducted a playback experiment with the alarm calls of three subtropical Asian mixed-species flocking species with varying roles by broadcasting their calls to naive birds native to temperate forests in North America. We used a local, North American sentinel species' alarm calls as our positive control and the songs of the Asian sentinel as the negative control.

Material and methods

Playback species selection

To select species for the playbacks, we focused on taxa that had many digital recordings available for us in online bioacoustic collections. For our novel (foreign) species stimuli, we selected species all native to Asia that lacked migratory connectivity to North America. Our species for playbacks consisted of 1) a positive control: the alarm call of the tufted titmouse *Baeolophus bicolor* (hereafter titmouse), a core sentinel species native to our study area in temperate North America (Courter and Ritchison 2010, Zou et al. 2018), 2) the alarm call of the grey-cheeked fulvetta *Alcippe morrisonia*; hereafter fulvetta, a core sentinel in Taiwan (Zou et al. 2018, Kirwan et al. 2021), 3) the alarm call of the the black-naped monarch *Hypothymis azurea* (hereafter monarch), a non-core sentinel species in Taiwan (i.e. it can act as the sentinel of a flock, yet does not reliably produce alarm calls when in the presence of core sentinels; Goodale and Kotagama 2005, Limparungpatthanakij et al. 2017, Zou et al. 2018, Moeliker et al. 2020), 4) the alarm call of the Eurasian tree sparrow *Passer montanus* (hereafter sparrow), a non-sentinel that participates in mixed species flocks in Taiwan (Barlow et al. 2020) and 5) a negative control: the song of the fulvetta, to account for birds responding to geographically novel stimuli (i.e. Asian stimulus played in North America; Fig. 1). The Eurasian tree sparrow has been introduced to a region that includes western Illinois, USA, and breeds there regularly, but it does not breed nor was it present at our study sites in Champaign county, eastern Illinois (Burnett et al. 2017). Responses to novel stimuli are potentially unpredictable when exposing birds to alarm calls they have not encountered before, and so we included the negative control in order to have a baseline response that should solely be due to an acoustic stimuli being geographically unfamiliar: that is, if birds respond to a novel alarm with no difference from a novel song (an intraspecific sexual signal), then those responses are likely solely due to the sound being a foreign vocalization, and not due to any meaning conveyed by the alarm call.

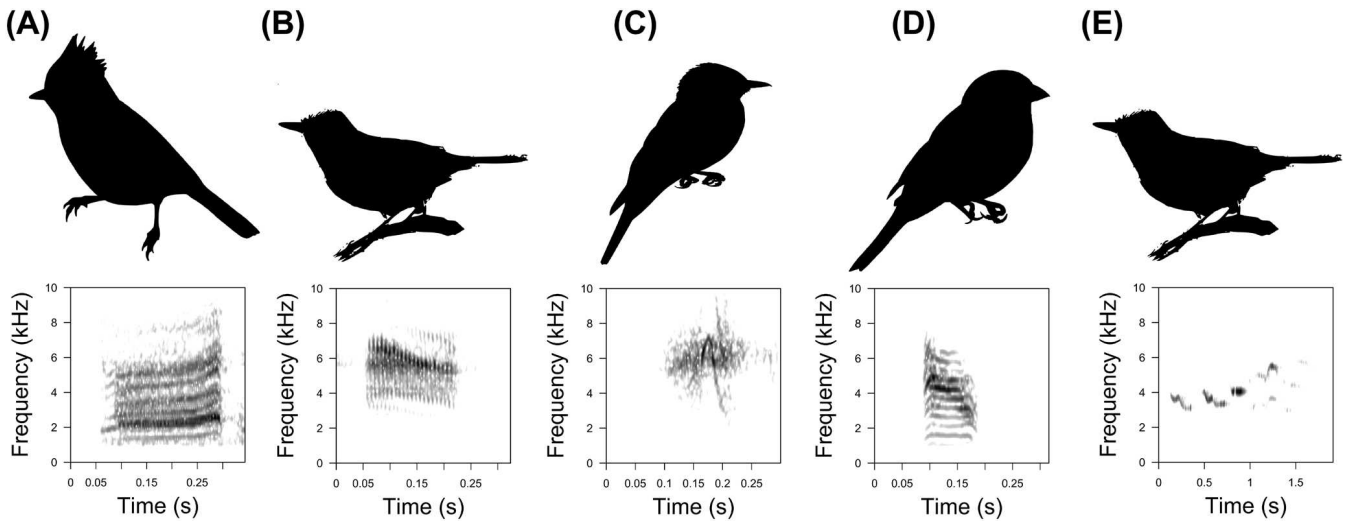

Figure 1. Spectrograms of the vocalizations used in this experiment. (A) The alarm call of the tufted titmouse *Baeolophus bicolor*. (B) The alarm call of the grey-cheeked fulvetta *Alcippe morrisonia*. (C) The alarm call of the black-naped monarch *Hypothymis azurea*. (D) The alarm call of the Eurasian tree-sparrow *Passer montanus*. (E) The song of the grey-cheeked fulvetta.

Playback stimuli

We sourced audio files from the public birdsong repository of xeno-canto.org, supplementing them from Cornell University's Macaulay Library as needed. We used a hi-pass filter to remove ambient noise frequencies below 1 kHz for all playbacks and adjusted playback amplitude to generate a volume of 80 dB at 1 m from the speaker, a FoxPRO NX4, using a RadioShack Sound Level Meter 33-2055.

For the alarm call of the fulvetta, fulvettas produce a single alarm call, modulating volume in response to intensity of the threat (Chen and Hsieh 2002). By standardizing the amplitude, we ensured that all playbacks should convey the same threat. For the alarm call of the monarch, we used the 'wheet-wheet' alarm call, which is uttered in bursts (Moeliker et al. 2020). For the titmouse alarm calls, we used the scold calls, which are known to produce a mobbing response from birds and should elicit strong avian responses (Langham et al. 2006). For the alarm call of the sparrow, we used the 'quer-quer' alarm call, which is structurally similar to the alarm call of the congeneric house sparrow *P. domesticus*. While sparrows possess this clearly identifiable alarm call, they do not typically produce alarm calls when participating in mixed-species flock (Barlow et al. 2020).

We standardized the playbacks' notes to have a 3-2-3 call note structure, with gaps of 1.5 to 3 s based on the natural intervals of silence in natural calls. For the fulvetta song, we used the entire song, repeated three times for a structure of 1-1-1 songs. In all cases playbacks consisted of a 12s loop, which we then spliced together repeatedly to obtain 5-min playback files, with 30s of silence at the start to allow for us to take the observers' position at the onset of the trials. Each playback contained calls from at least two different individuals. We generated three playback files per playback type to reduce acoustic pseudoreplication.

Field site locations

We selected 12 field sites across Champaign-Urbana, Illinois, USA, to collect our data during early summer of 2023, which included a combination of wooded public parks and managed forests. We chose these types of sites due to the high variety of bird species present as well as moderate levels of human disturbance. No Asian bird songs or calls have ever been played back at these sites before to our knowledge (Dominguez et al. 2023). We visited each site in a random order. A total of 10 replicates of each playback per field site were attempted; however, due to logistic constraints, this number was not reached for all 12 locations (8–10 replicates per site). Data were collected from 15 May to 14 June 2023, during the northern breeding season at our locality. We visited each site twice each day, once directly following sunrise, and once in the late afternoon. We made sure to have at least seven hours between each trial to prevent habituation of the birds to playbacks.

Field protocol

Before each trial, we recorded the temperature and wind speed utilizing the Apple Inc. Weather app. Additionally, we recorded the cloud cover on a scale from 0–4 (0 – no clouds visible, 1 – minimal clouds visible, 2 – cloud cover over half

Table 1. Anova of linear-mixed model values for examining the overall approach of birds in response foreign alarm calls compared to the alarm calls of native species, and coefficients of the model. Field site included as a random effect (n = 538 trials).

	χ^2	df	p value
Playback type	207.49	4	< 0.0001
Temperature (C°)	32.79	1	< 0.0001
Windspeed (km h^{-1})	44.21	1	< 0.0001
Cloud cover	4.87	1	0.027

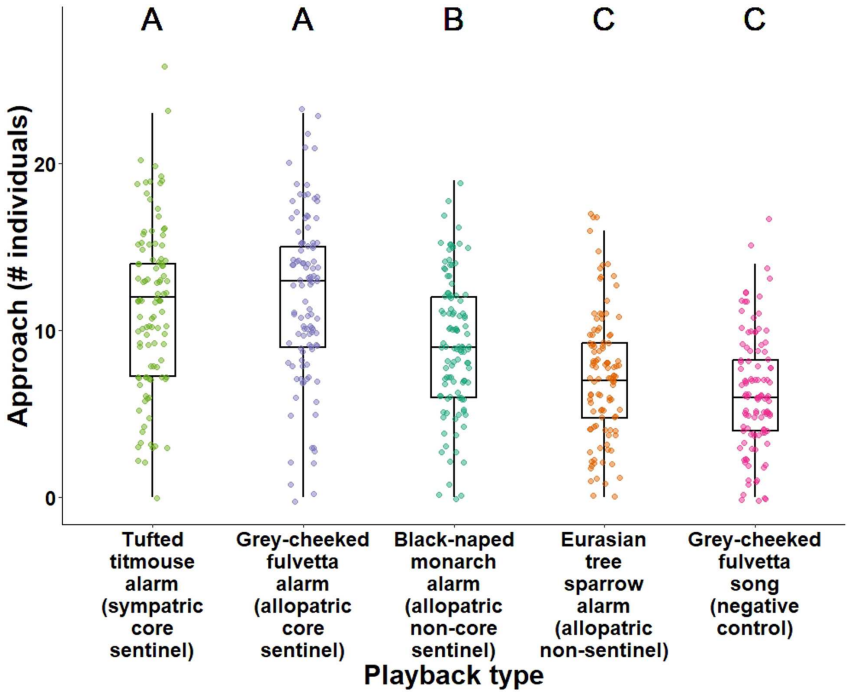

Figure 2. Per-trial approach of birds in response to the vocalizations of a variety of birds. Letters indicate statistically different groups, box plots indicate 10, 25, 50, 75 and 90th percentiles, and the dots are all the data points (n = 538 trials)

the sky, 3 – mostly cloudy with few gaps of clear sky, 4 – full cloud cover). We set the speaker to face north at each site in an unobstructed position. We randomly selected one of our playback files for each playback occasion. We took position 15 m away from the speaker and began trials.

We recorded each bird species and the number of individuals that were present or entered a 15 m radius during the five minute period of the playback as having approached the speaker. Additionally, we recorded each audible response within the study's range (~ 50 m). No birds were typically present at the trial start as we flushed them while setting up the speaker. To verify that approaching the speaker was a consistent measure of behavioral displays during the playbacks, we used the number of birds that vocalized during the trial and compared it with the number of birds that approached during the trial and found that these metrics were positively correlated ($R = 0.36$, $p < 0.001$), indicating that approach rate can serve as a proxy for different behavioral metrics during the playbacks. If an individual was out of the 15 m radius, we noted them as 'out of range.' This was used to note the general presence of species in the area as well as to note which species would reliably approach to certain calls and which would not. Of the individuals that approached, we noted the latency which the first member of each species took to be noted within the study radius. Finally, if an individual bird was seen flying high over the tree cover without landing within the study area we did not count this as 'in range' because this was beyond the 15 m radius around the playback set-up. All data were collected by the same observer.

Statistical analyses

We constructed mixed-linear models using all 538 trials with the R Package 'glmmTMB' (Brooks et al. 2017). As temperature or other weather conditions can potentially influence response to alarm calls (Cordonnier et al. 2023), we

Table 2: Comparisons between approach rates of birds in response to a variety of alarm calls using a generalized mixed model, corrected using Tukey correction for multiple comparisons.

Comparison	Estimate	t	p
Allopatric core sentinel alarm – Allopatric core sentinel song	5.6	11.37	< 0.001
Allopatric core sentinel alarm – Allopatric non-core sentinel alarm	2.78	5.60	< 0.001
Allopatric core sentinel alarm – Non-sentinel alarm	4.88	9.87	< 0.001
Allopatric core sentinel alarm – Sympatric sentinel alarm	0.53	1.06	0.83
Allopatric core sentinel song – Allopatric non-core sentinel alarm	−2.85	−5.81	< 0.001
Allopatric core sentinel song – Non-sentinel alarm	−0.73	−1.49	0.57
Allopatric core sentinel song – Sympatric sentinel alarm	−5.09	−10.29	< 0.001
Allopatric non-core sentinel alarm – Non-sentinel alarm	2.12	4.31	< 0.001
Allopatric non-core sentinel alarm – Sympatric sentinel alarm	−2.24	−4.56	< 0.001
Non-sentinel alarm – Sympatric sentinel alarm	−4.36	−8.81	< 0.001

Table 3. Anova of linear-mixed model values for examining the mean latency of birds to approach in response foreign alarm calls compared to the alarm calls and vocalizations of native species, and coefficients of the model. Field site included as a random effect (n = 523 trials).

	χ^2	df	p value
Playback type	79.64	4	< 0.0001
Temperature (C°)	0.26	1	0.61
Windspeed (km h^{-1})	1.77	1	0.18
Cloud cover	3.60	1	0.057

used temperature, cloud cover, wind speed, and playback as fixed effects, and field site as a random effect, and per-trial approach as the response variable.

We similarly constructed a linear mixed model for latency to approach. In this case we took the average time it took for birds to approach in that trial, or simply the mean of recorded latencies. When birds were present but did not approach, we marked them with a latency of 301 s, indicating a non-response. The resulting average trial latency did not statistically deviate from a normal distribution according to a Shapiro–Wilk's test (p = 0.056). As before, we used temperature, cloud cover, wind speed, and playback as fixed effects, and field site as a random effect. Alpha levels were set at 0.05.

Results

Playback type was a significant predictor of approach rate responses to the speaker (Table 1). While there was no statistical difference between the total responses between allopatric core sentinel alarm calls and sympatric sentinel calls (t = 1.06, df = 528, p = 0.82), the alarm calls of the allopatric non-core sentinel had lower responses than the alarm calls of the allopatric core sentinel (t = 5.60, df = 528, p < 0.0001) and had higher responses than the alarm calls of the non-sentinel (t = 4.31, df = 528, p = 0.002). There was no statistical difference between the alarm calls of the non-sentinel and the songs of the core sentinel (controls; t = −1.49, df = 528, p = 0.57; Fig. 2, Table 2).

The latency to approach was also predicted by playback type (p < 0.0001, Table 3). Latency to respond was longest for the non-sentinel alarm calls and the song of the allopatric core sentinel (non-sentinel – core sentinel song: t = 1.86, df = 513, p = 0.34; core sentinel alarm – core-sentinel song t = −6.81, df = 513, p < 0.0001). There was no statistical difference in the latency to respond for the alarm calls of the three sentinel species (core sentinel – non-core sentinel: t = −2.00, df = 513, p = 0.26; non-core sentinel – sympatric sentinel: t = 2.48, df = 513, p = 0.096; core sentinel – sympatric sentinel: t = 0.47, df = 513, p = 0.99; Fig. 3, Table 4).

Discussion

In line with our predictions for naive Nearctic forest species, the alarm calls of the Asian subtropical core sentinel species garnered stronger approach responses than the calls of a non-core sentinel, which in turn generated a higher response than a non-sentinel mixed-flock member species. These patterns provide strong evidence that the innate, cross-geographic recognition of alarm calls documented by Sandoval and Wilson (2022) and Dominguez et al. (2023) is a dependent on which

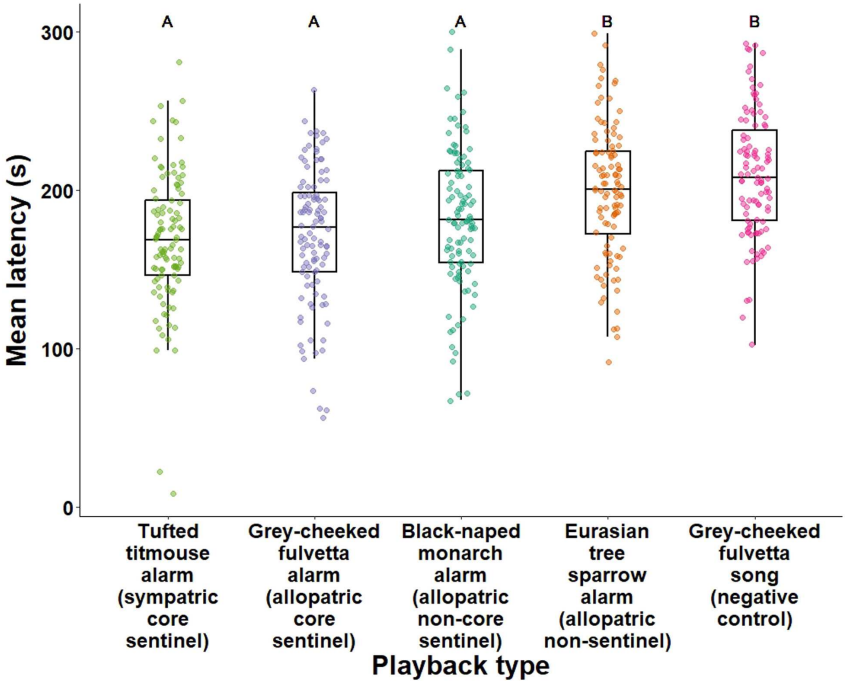

Figure 3. Mean latency to approach in response to the vocalizations of a variety of birds. Letters indicate statistically different groups, box plots indicate 10, 25, 50, 75 and 90th percentiles, and the dots are all the data points (n = 523 trials).

Table 4. Comparisons between latency of individual bird species to approach in response to a variety of alarm calls using a linear mixed model, corrected using Tukey correction for multiple comparisons.

Comparison	Estimate	T	p
Allopatric core sentinel alarm – Allopatric core sentinel song	−39.13	−6.81	< 0.001
Allopatric core sentinel alarm – Allopatric non-core sentinel alarm	−11.42	−2.00	0.27
Allopatric core sentinel alarm – Non-sentinel alarm	−28.41	−4.94	< 0.001
Allopatric core sentinel alarm – Sympatric sentinel alarm	2.68	0.47	0.99
Allopatric core sentinel song – Allopatric non-core sentinel alarm	27.71	4.85	< 0.001
Allopatric core sentinel song – Non-sentinel alarm	10.72	1.86	0.34
Allopatric core sentinel song – Sympatric sentinel alarm	41.81	7.28	< 0.001
Allopatric non-core sentinel alarm – Non-sentinel alarm	−16.99	−2.98	0.025
Allopatric non-core sentinel alarm – Sympatric sentinel alarm	14.11	2.48	0.096
Non-sentinel alarm – Sympatric sentinel alarm	31.1	5.42	< 0.001

role a species occupies within a mixed-species flocks, and is not simply a universal component of avian alarm calls.

Regarding the latency response metrics, the alarm calls of the non-core sentinel monarch had the same mean latency to approach compared to the alarm calls of both the core local and the unfamiliar sentinel species. Still, these responses were stronger (the latencies were shorter) than those to the non-sentinel species and the negative control. Differential responses to different types of sentinels may require more detailed assessment and analyses of the response data; furthermore, future work should also compare responses between a wide variety of unfamiliar sentinel roles, types, and species.

One context that our study could not address was whether the local environment impacts the recognizability of foreign sentinel alarm calls. Our study utilized a single forested habitat type in temperate North America, and it is possible that sentinel alarm calls have evolved to be most effective, and thus more recognizable in their original habitat and not other habitat types or in areas with significant human disturbance (Potvin et al. 2014). Earlier work on alarm call responses has shown that birds dampen their responses to conspecific alarm calls in areas with higher noise pollution, leading to muddled responses that can impact foraging efficiency (Antze and Koper 2018). Due to the large number of bird species that participate in diverse mixed species flocks, it is important that future work should consider how these flocks' communication systems may be warped by climatic and other anthropogenic disturbances (Zou et al. 2018). For instance, while we only used the alarm calls of three unfamiliar bird species from a single geographic locale of a single habitat type, future work could compare the local responses to a variety of unfamiliar sentinels from a variety of source habitats.

One of the questions that remain – why do the alarm calls of sentinels produce stronger responses than other species' alarm calls? While some members of mixed species flocks do share alarm call similarities with sentinels (Ficken 2000), work done in parids found that alarm call similarity between caller and receiver cannot fully explain foreign alarm call recognition (Dutour et al. 2017, Sandoval and Wilson 2022). Work on sentinels has suggested that sentinels benefit from producing recognizable alarm calls, as it allows them to more easily manipulate flockmates (Baigrie et al. 2014). As a result, it may be beneficial to sentinel species to possess a common bioacoustic component of their alarm calls that is innately recognized by other, unfamiliar, and even phylogeographically distant bird species. Many avian aerial alarm calls possess common components, such as similar frequencies (Marler 1955). Previous work hypothesized that this may be the case for sentinel alarm calls (Sandoval and Wilson 2022, Dominguez et al. 2023); but these bioacoustic analyses require more behavioral experimentations and comparative sonogram analyses. Nonetheless, with these new data, we see strong evidence for our focal hypothesis, as multiple studies have now demonstrated the universal recognition of sentinel alarm calls, including our work here showing that unfamiliar sentinel alarm calls elicit stronger responses than non-sentinel alarm calls.

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Author contributions

Jonah S. Dominguez: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (lead); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Morgan Bolger:** Investigation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Autumn Bush:** Investigation (supporting). **Mark E. Hauber:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal);.

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Data availability statement

Data are available from the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.24201588.v1 (Dominguez et al. 2024).

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