



# Mechanisms of noise disruption: masking, not distraction or increased vigilance, compromises wild bird communication

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Noise from human activity is a global concern that threatens wildlife, including by disrupting acoustic communication. This disruption is often assumed to be caused by masking, where signals are difficult to hear in the presence of noise of similar frequency to the signals. However, other mechanisms can also lead to reduced responses to signals: animals may be distracted by noise and so miss the signal, or noise may increase their vigilance and so lead them to use personal information instead of responding to signals from others. Previous experimental work on superb fairy-wrens, *Malurus cyaneus*, found evidence that masking disrupted responses to conspecific alarm calls but could not rule out distraction. We therefore designed experiments using responses to heterospecific alarm calls to distinguish masking from distraction. We tested responses to low- and high-frequency heterospecific alarm calls during low- and high-frequency noise. Fairy-wrens responded to both heterospecific alarm calls during nonoverlapping noise, but not during overlapping noise, regardless of noise frequency, and vigilance was similar during the two types of noise. We conclude that the alarm call response was compromised by masking, not distraction or increased vigilance. Overall, the assessment of mechanisms helps predict the consequences of noise pollution and provides suggestions on managing anthropogenic noise at the community level, such as avoiding noise whose frequency overlaps either conspecific or heterospecific calls.

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A global increase in environmental noise due to human activities has become a major concern for wildlife (Francis & Barber, 2013). Increasing noise leads to changes in behaviour and a reduction in fitness (Barber et al., 2010; Cox et al., 2018; Duquette et al., 2021; Francis & Barber, 2013; Gomes et al., 2021; Shannon et al., 2016; Solé et al., 2023). Among the many effects of noise, a disruption of acoustic communication is the most direct, and experimental studies of many taxa have shown that noise can lead to a failure to respond to acoustic signals (Dooling & Blumenrath, 2013; Kunc et al., 2016; Morley et al., 2014). A failure to respond to signals is important because it can reduce reproductive success if, for example, courtship signals are missed, and can lessen survival if, for instance, receivers do not respond to alarm calls warning of danger (Dooling & Blumenrath, 2013; Duquette et al., 2021; Liao et al., 2024). However, despite the importance of receiving signals, it is usually unclear what mechanisms explain the failure to respond to acoustic signals in noise.

Most research has focused on the effects of noise on communication, rather than on the mechanisms of how noise disrupts communication. There are three possible mechanisms that could explain why an animal fails to respond to acoustic signals when there is background noise (Kern & Radford, 2016b; Kight & Swaddle, 2011; Zhou et al., 2019). The first mechanism is auditory masking, which is defined as the increased detection threshold of acoustic signals due to the presence of noise. That is, the presence of noise makes it more difficult for individuals to hear signals than in quiet conditions (Moore, 2012, Chapter 3). Masking is strongest when noise is of high amplitude compared to the signal and when the frequency of noise and signal overlap (Gelfand, 2017, Chapter 10). Second, distraction caused by noise can lead to an animal missing a signal. Noise can reallocate an animal's attention so it may miss signals, regardless of whether the signals are acoustic or address another sensory system (Chan & Blumstein, 2011; Chan et al., 2010). In addition, distraction might increase the latency of response in noisy conditions (Chan et al., 2010). Third, increased vigilance in noisy conditions may indirectly affect an animal's response to signals. Noise may prompt animals to become vigilant, and so they may rely more on personal rather than social

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information to assess the environment (Kern & Radford, 2016a; Klett-Mingo et al., 2016; Meillere et al., 2015; Merrall & Evans, 2020). As a result, for example, animals may stop responding to the alarm calls of others because their extra vigilance means that they can assess danger themselves (Kern & Radford, 2016a). The three mechanisms are not mutually exclusive and can be difficult to distinguish because they can lead to the same behavioural changes. Auditory masking is often assumed to be the primary reason for a failure to respond to acoustic signals in noise (Clark et al., 2009; Lohr et al., 2003; Templeton et al., 2016), but empirical tests of the different mechanisms are rare. Since disruption of signal reception by noise could lead to severe outcomes, such as failure to receive warnings of predators (Templeton et al., 2016; Tilgar et al., 2022), distinguishing mechanisms is important when predicting effects of noise and providing suggestions to ameliorate its effects.

In our previous study on mechanisms of noise effects on behaviour, masking, rather than distraction or increased vigilance, most likely explained why superb fairy-wrens, *Malurus cyaneus*, failed to respond to conspecific alarm calls (Zhou et al., 2019). The experimental study entailed broadcasting high-frequency aerial (flee) alarm calls of fairy-wrens together with filtered background noise that either did or did not overlap in frequency with the alarm calls. No difference was found in vigilance during the two types of noise, and so the increased vigilance hypothesis was excluded. Birds failed to flee from alarm calls during the high-frequency 'overlapping noise', but still fled during the lower-frequency 'nonoverlapping' noise. These results are consistent with masking, under the assumption that both high- and low-frequency noise are equally distracting (or not distracting), which is also assumed in similar studies of mechanisms (Reed et al., 2021; Templeton et al., 2016). However, the results cannot rule out the possibility that higher-frequency noise is more distracting than low-frequency noise, so that distraction, rather than masking, could explain the pattern of response.

There are surprisingly few studies of the effect of noise frequency on distraction, and these have been on humans and have produced varied results. It is often assumed that any noise leads to a similar degree of distraction, regardless of the type or frequency range (Allen et al., 2021; Furnham & Strbac, 2002; Mehri et al., 2018). However, the type of noise can affect the level of distraction experienced by humans. For example, discontinuous background noise made a reading comprehension task more difficult than continuous noise, and speech made the task more difficult than tones (Jackson & Wogalter, 1997). Furthermore, the frequency of noise can affect how annoying it is perceived to be, and distraction was one of the factors included in an annoyance questionnaire (Zhang et al., 2003). However, there is no consensus on what frequencies are more annoying. High-frequency noise was more annoying than low-frequency noise in one study (Key & Payne, 1981) whereas noise with low-frequency characteristics was found more annoying in another study (Huang et al., 2008). For other animal species, it is unknown whether noise frequency affects distraction, but work on humans suggests that it is possible. Furthermore, the species-specific range of frequency sensitivity could affect the level of distraction, aside from noise simply being audible. This means that our previous results on fairy-wrens (Zhou et al., 2019) could be due to masking or to greater distraction, in that case by higher-frequency noise, which overlaps fairy-wrens' alarm calls.

In this study, we took advantage of the different frequencies of heterospecific alarm calls to design an experiment to test the mechanism through which noise affects responses of fairy-wrens to alarm calls. Like many birds and mammals, fairy-wrens eavesdrop on heterospecific alarm calls, and so gain important information on danger (Fallow et al., 2011, 2013; Magrath et al., 2007, 2009a, 2015, 2020). We studied the responses specifically to aerial alarm calls,

which warn conspecifics of flying predators that pose a current threat and prompt immediate flight to cover. The rapid and conspicuous response to these alarm calls allows a clear assay of response under different noise conditions (Zhou et al., 2019). Here, we broadcast the aerial alarm calls of New Holland honeyeaters, *Phylidonyris novaehollandiae*, and white-browed scrubwrens, *Sericornis frontalis*, because fairy-wrens are equally likely to flee in response to these calls under quiet conditions, yet the calls are of different acoustic frequency (Magrath et al., 2009a). The honeyeaters produce low-frequency alarm calls compared to scrubwrens. We therefore conducted a crossover experiment where these low- or high-frequency alarm calls were broadcast during either low- or high-frequency ambient noise. As a result, the experiment could discriminate the effects of masking (a reduced response when noise frequency overlapped the alarm call) from distraction (a reduced response to alarm calls during low- or high-frequency noise, independent of overlap with the alarm call frequencies). To our knowledge, this study is the first to investigate the mechanism of how noise can compromise heterospecific eavesdropping.

## METHODS

### Study Site and Species

We conducted the study in the Australian National Botanic Gardens, Canberra, Australia (35°16'44"S, 149°6'32"E) from June to September 2019. The 40 ha Gardens contain different habitats, including rainforest, natural bushland, woodland and lawn. Superb fairy-wrens, white-browed scrubwrens and New Holland honeyeaters are common in the Gardens, as are their shared predators, such as collared sparrowhawks, *Accipiter cirrhocephalus*, and pied currawongs, *Strepera graculina* (Magrath et al., 2000; McLachlan & Magrath, 2020). Fairy-wrens in the Gardens are accustomed to people and are individually colour-banded for long-term study (Cockburn et al., 2016).

Superb fairy-wrens are small (9–10 g) passerines that feed primarily on the ground. They hold territories during the breeding season (September – January). During the nonbreeding season, fairy-wrens often join foraging groups that contain adjacent breeding groups and move across two to three territories (Higgins et al., 2001; Rowley, 1965). Fairy-wrens produce high-frequency aerial alarm calls (mean  $\pm$  SD peak frequency =  $9.1 \pm 0.4$  kHz) that are given in response to flying predators (Magrath et al., 2007), but not in response to playback of aerial alarm calls (Zhou et al., 2019, 2024). Aerial alarm calls containing multiple, repeated elements prompt flight to cover as they indicate immediate danger (Magrath et al., 2007). The aerial alarm calls of scrubwrens are of relatively high frequency ( $7.1 \pm 0.4$  kHz) (Magrath et al., 2007), while those of New Holland honeyeaters are much lower ( $4.0 \pm 0.2$  kHz) (Magrath et al., 2009b). Like fairy-wrens, alarm calls signalling more urgent danger include more elements (Fallow & Magrath, 2010; McLachlan & Magrath, 2020), and fairy-wrens flee immediately to cover in response to playback of four-element scrubwren and honeyeater alarm calls, the same response as to conspecific four-element alarms calls (Magrath et al., 2009a).

### Experimental Design

We used playback experiments to investigate the mechanism of how noise affects fairy-wren alarm communication. In the first experiment, as in Zhou et al. (2019), we determined whether vigilance level differs during playback of the two types of noise alone: high frequency (6–10 kHz) or low frequency (2–6 kHz). In the second experiment, we examined whether masking or distraction disrupts alarm call reception, by using playbacks of alarm calls

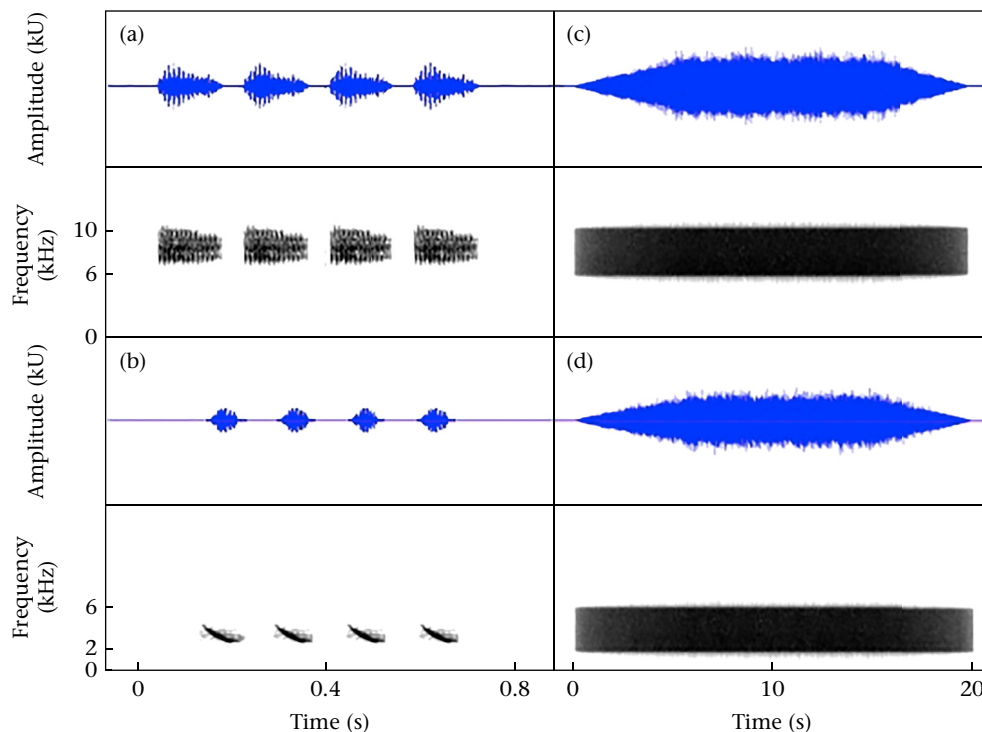
alone (as controls) and alarm calls together with either low-frequency or high-frequency noise. There were six treatments: (1) scrubwren alarm alone; (2) honeyeater alarm alone; (3) scrubwren alarm + high-frequency noise; (4) scrubwren alarm + low-frequency noise; (5) honeyeater alarm + high-frequency noise; and (6) honeyeater alarm + low-frequency noise. Treatments (3) and (6) had noise frequencies that overlapped with the concurrent alarm call; treatments (4) and (5) had noise frequencies that did not overlap with the concurrent alarm call. If masking is the mechanism that stops birds responding to alarm calls, fairy-wrens should flee in response to the nonoverlapping playbacks but not to overlapping playbacks. However, if high-frequency noise is more distracting than low-frequency noise, then fairy-wrens should flee in response to honeyeater alarms during low-frequency noise but not during high-frequency noise. We already knew that low-frequency noise was not distracting because our previous study found that it did not reduce the probability of fleeing in response to the fairy-wren's high-frequency alarm calls (Zhou et al., 2019). It is possible, however, that both masking and distraction occur, with high-frequency noise being more distracting. In that case, each alarm would be masked by the corresponding frequency noise, but only honeyeater alarms would additionally be affected by the non-masking (in that case, high-frequency) noise. In addition, we measured latency to flee to test whether distraction could have subtle effects on the timing of response, even if noise did not affect the probability of response. A longer latency to flee indicates greater distraction.

#### Preparation of Experimental Sound Files

We prepared 16 exemplars each of aerial alarm calls from 16 different white-browed scrubwrens and 16 different New Holland honeyeaters (Fig. 1a, b). Each alarm call was recorded from a

different individual, prompted using gliding models of collared sparrowhawks (as in Magrath et al., 2007; McLachlan et al., 2019; Zhou et al., 2019). The calls were recorded using a Sennheiser ME66 or ME67 directional microphone and Marantz PMD670 recorder sampling at 44.1 kHz and 16 bits. Each alarm call playback track included four elements and was made by copying and pasting one element at a natural interval (period of silence between elements: scrubwren, 40 ms; honeyeater, 64 ms). We filtered out background sound below 5 kHz for scrubwren alarm calls and filtered out sound below 2 kHz and above 5.5 kHz for honeyeater alarm calls, so that no extraneous sounds occurred at the frequency of the other species' alarm calls. All alarm call tracks were calibrated to a mean element amplitude of 52 dB SPL at 10 m, by re-recording playbacks at 10 m, along with a calibration tone that had its amplitude measured with the Brüel & Kjær 2240 sound level meter (as in Zhou et al., 2019).

We prepared 16 exemplars of filtered ambient noise of high and low frequencies (Fig. 1c, d). We used the original ambient recordings of the Gardens to create 20 s tracks (Zhou et al., 2019). To prevent abrupt changes in noise that might startle the birds, we applied a 7 s fade-in at the beginning and a 5 s fade-out at the end of each track, leaving 8 s in the middle with a constant average amplitude. Then we filtered noise to either 6–10 kHz ('high-frequency noise') or 2–6 kHz ('low-frequency noise'). The ambient noise spectra showed a natural drop of power as frequency increased, particularly at low frequencies, so we used the 'Equalization' function in Audacity (<https://audacityteam.org>) to adjust the low-frequency noise to make its spectrum relatively flat and like that of the high-frequency noise. This is different from the previous study, in which the low-frequency noise acted only as a 'nonmasking' noise matched by mean amplitude to the high-frequency masking noise. Finally, we calibrated the two types of noise to be 58 dB SPL at 10 m, measured with a Brüel & Kjær 2240



**Figure 1.** Examples of sounds used for playbacks, including waveform and spectrogram of (a) white-browed scrubwren aerial alarm call, (b) New Holland honeyeater aerial alarm call, (c) high-frequency noise and (d) low-frequency noise. Note the different timescales for alarm calls and noise. Playbacks were calibrated as needed in experiments, and some treatments entailed alarm calls mixed with noise. The amplitude is on a linear scale and expressed as the uncalibrated digital amplitude, given 16-bit wave files, where the absolute maximum, and range of the Y axis, is 32768. Spectrograms were prepared in Raven Pro 1.5 and used a Blackman window type, 5.8 ms window size and 95% overlap.

sound level meter (following the same calibration method as in Zhou et al., 2019). We used 58 dB SPL because this was the lowest amplitude of noise that completely masked 52 dB SPL conspecific alarm calls. We assumed that this would also mask heterospecific calls, because a previous study of fairy-wrens found that masking affected the reception of heterospecific alarm calls more severely than reception of conspecific calls (Zhou et al., 2024). There have been no previous studies on the effect of different amplitudes of background noise on masking heterospecific calls. Our results (below) confirmed our expectation that 58 dB SPL noise fully masked both heterospecific alarm calls.

For playbacks of alarm calls together with noise, an alarm call was mixed in the middle of noise during the 8 s constant amplitude period, using the 'mixdown session to new file' function in Adobe Audition CC 2019. We mixed the tracks to produce a single file that could be broadcast from one speaker, to avoid any effect of masking release if an alarm call and noise came from different directions ('spatial release of masking'; Brumm, 2013). The mixdown function does not change the quality of the alarm calls and noise and has also been used in previous work on fairy-wren communication in noise (Zhou et al., 2019, 2024).

#### *Playback Field Methods*

Each experiment entailed matching playback treatments by site, so that all treatments were presented at each site. We chose 16 sites with open foraging areas across the Gardens, as in Zhou et al. (2019). In each site, we broadcast a unique set of playback sounds to avoid pseudoreplication (Kroodsma et al., 2001). We matched playbacks by site, rather than individual, to control for factors that could potentially affect sound transmission, reception or response, such as vegetation and substrate, ambient noise or the local abundance of predators. At the beginning of the playback experiments, fairy-wrens were not breeding and could move over several breeding territories. We ensured that no bird received a specific treatment more than once. In experiment 1, 26 individuals received 32 playbacks, with six birds receiving both treatments and 20 birds receiving a single treatment. In experiment 2, 36 individuals received 96 playbacks, with four birds receiving all six treatments, two birds receiving five treatments, seven birds receiving four treatments, two birds receiving three treatments, eight birds receiving two treatments and 12 birds receiving a single treatment.

We randomly generated the order of playbacks at each site using R but rejected a random order if it resulted in too many specific treatments in a given position in the order. The outcome was that treatments occurred a similar number of times at each order (experiment 1 had two treatments, each broadcast first eight times; experiment 2 had six treatments, with each occurring two or three times in each position in the order).

In both experiments, equal numbers of males and females received each treatment. All the playbacks were broadcast to adults, which are known to respond to the alarm calls of both heterospecifics at the study site (Magrath et al., 2007, 2009a), where they have had the opportunity to learn to recognize these calls earlier in life (Magrath & Bennett, 2012; Magrath et al., 2009a, 2009b, 2015; Potvin et al., 2018). We excluded males with blue breeding plumage because they can be more responsive to alarm calls than females and males in nonbreeding plumage, both of which are brown (McQueen et al., 2017). To avoid birds habituating to alarm calls, we avoided conducting playbacks at adjacent sites on the same day. A maximum of two playbacks were conducted at each site on a given day with at least a 1 h interval. Completion of a whole set of treatments at a site took a mean of 5.9 days (range 1–21) for experiment 1 and 14.3 days (range 5–38) for experiment 2, further reducing risks of habituation.

For each trial, we followed a focal fairy-wren, which was the closest individual to the observer, from 5–15 m away. We followed our standard playback methods for fairy-wrens (Magrath et al., 2009a; Murray & Magrath, 2015; Zhou et al., 2019). The focal bird was observed for at least 5 min and the playback was then carried out only if there had been no alarm calls from conspecifics or heterospecifics, no predators nearby and no obvious disturbance such as by visitors walking nearby. Playbacks were carried out only if the focal bird was 0.5–10 m from cover and there was no obstruction between the loudspeaker and the focal bird. If the playback was disrupted before the alarm call was broadcast, then it was stopped and repeated after at least 5 min. If there was disturbance after the alarm call was initiated, then the playback was repeated after at least 1 h or the next day if there were already two playbacks conducted at the site; this was necessary in five cases out of 96 playbacks during experiment 2. We also recorded the number of other fairy-wrens present during the playback but dropped it from statistical models because it had no significant effect on response to playback. We broadcast playbacks from a Roland Edirol R-05 HR digital recorder, connected to a custom amplifier and a Peerless 810921 tweeter loudspeaker (frequency response 2–11 kHz). All playback equipment was mounted around the observer's waist. In addition, a Panasonic HC-V770M 168 camcorder (filming at 50 frames/s at 1920×1080p) was mounted over the observer's shoulder using a Wizmount CU2pack; this was used to record the behaviour of the focal bird during playbacks. Playbacks were conducted only during relatively constant, low-level natural background noise, without prominent noise such as from wind, aircraft and leaf blowers. The level of background noise during playbacks ranged from 29.6 to 45.8 dB SPL. We measured background noise for 30 s after each playback using a Sennheiser ME62 omnidirectional microphone and Marantz PMD670 recorder with a constant gain. These recordings were then measured using the 'Average Power' function in Raven Pro 1.5 and finally calibrated against a recording of a 1 kHz tone of known amplitude.

#### *Scoring Responses to Playback*

We scored the responses of focal fairy-wrens to playback from muted videos, so the scorer was blind to the treatment. Methods followed Ratnayake et al. (2021). In brief, we used Adobe Premier CC 2019 to add visual markers for the start of noise, the start of alarm calls and the focal individual (if there was more than one bird in the frame). The videos were then muted and randomly renamed by another person before scoring.

In experiment 1, we broadcast two types of noise without alarm calls. Vigilance was measured as the proportion of video frames when the focal bird's head was up and as the mean number of frames for each look up (look duration) over the whole 20 s noise playback, following methods in Zhou et al. (2019). The two measurements are commonly used for indicating vigilance level, which compares the total time of a bird looking as well as the duration of each look (Merrall & Evans, 2020; Sweet et al., 2021).

In experiment 2, we broadcast scrubwren or honeyeater alarm calls either alone or together with low- or high-frequency noise. We first categorized the response of the focal individual as flee or not flee. Fleeing was defined as stopping foraging and flying immediately in response to playback. If the bird fled, we measured latency to flee as the time from the onset of playback to the instant when the bird's feet left the ground.

#### *Statistical Analysis*

We conducted all statistical analyses in R version 4.2.0 (R Core Team, 2022). For experiment 1, we used linear mixed models

(LMMs) to investigate whether the proportion of time looking and look duration was different during low-frequency noise and high-frequency noise. Both measurements were logarithmically transformed to improve fit for the models. The fixed factors were the noise frequency (low- or high-frequency noise) and natural background noise level (a continuous variable), with treatment order and site included as random factors. LMMs were conducted using the 'lmer()' function of the 'lme4' package (Bates et al., 2015).

For experiment 2, we used bias-reduced generalized linear models (BRGLMs) to test whether birds responded differently to alarm calls played alone and alarm calls played during the different types of noise. Here the response variable was dichotomous: flee or not flee. BRGLM models can fit the uniform responses of some playback treatments, where the focal birds all responded or did not respond, which cannot be achieved using generalized linear mixed models. We conducted two BRGLMs, both with binomial distributions and logit link functions, using the 'brglm()' function of the 'brglm2' package (Kosmidis, 2020). The first BRGLM tested the interaction effect of noise frequency and alarm call type, which included only the four treatments with alarm calls and noise together. The factors were treatment order, site, noise frequency (low- or high-frequency noise), alarm call type (scrubwren or honeyeater), natural background noise level and the interaction between noise frequency and alarm call type. A second BRGLM including all six treatments was used to compare the four treatments with controls of alarm call alone. The model tested the responses to playbacks of alarm calls according to the presence and type of noise. The factors were treatment order, site, alarm call type (scrubwren or honeyeater), treatment type (alarm alone, alarm with overlapping noise and alarm with nonoverlapping noise) and natural background noise level.

For analysing the latency to respond to alarm calls in experiment 2, we included playbacks with alarm alone and alarm with nonoverlapping noise, and only cases where birds fled. We excluded the alarm with overlapping noise treatments because almost no birds fled. We used LMMs for the continuous variable of time latency, with treatment type (alarm alone and alarm with nonoverlapping noise), alarm call type (scrubwren or honeyeater) and natural background noise level (a continuous variable) as fixed factors and treatment order and site as random factors. The latency to respond was logarithmically transformed to improve fit for the models.

#### Ethical Note

The study was approved by the Australian National University Ethics Committee (protocol A2019/09) and designed to minimize any adverse effects on the birds. The noise stimulus used was recorded from the natural habitat of the study species and amplified to a moderate volume within the range of natural sound levels. Most birds exhibited no behavioural changes before, during or after playback of noise alone. To mitigate the potential impact of alarm call playbacks, each site had a maximum of two playbacks per day, with a minimum 1 h interval. Birds quickly resumed foraging after the playbacks.

## RESULTS

### Experiment 1: Vigilance during Noise

None of the birds fled during playback of either high-frequency or low-frequency noise, and vigilance was also similar during the two types of noise. There was no significant difference in the proportion of time that birds had their head raised (LMM:  $\chi^2_1 = 1.042$ ,  $P = 0.307$ ; Table 1) nor in the duration of each look ( $\chi^2_1 = 0.146$ ,

$P = 0.702$ ; Table 1) during the two types of noise (Fig. 2). There was also no significant effect of the level of natural background noise on response to the playbacks (proportion of time looking:  $\chi^2_1 = 0.511$ ,  $P = 0.475$ ; look duration:  $\chi^2_1 = 0.922$ ,  $P = 0.337$ ; Table 1).

### Experiment 2: Noise Masking versus Distraction

Overlapping, but not nonoverlapping, noise dramatically reduced the probability of fleeing in response to alarm calls, regardless of the alarm call type (Fig. 3). There was a significant interaction between noise frequency (high- or low-frequency noise) and alarm call type (scrubwren or honeyeater) in the likelihood of fleeing (BRGLM with the four alarm+noise treatments: log odds ratio =  $7.37 \pm 1.62$ ,  $z = 4.55$ ,  $P < 0.0001$ ; Table 2). Every bird fled in response to both heterospecific alarm calls during nonoverlapping noise, but no bird fled in response to scrubwren alarms and only 1/16 fled in response to honeyeater alarms during overlapping noise. Consistently, almost all birds fled in response to alarm calls alone (14/16 to scrubwren alarms and 15/16 to honeyeater alarms). As a result, the proportion fleeing during nonoverlapping noise was similar to that during alarm calls alone (secondary BRGLM with all six treatments: log odds ratio =  $-1.21 \pm 0.88$ ,  $z = -1.37$ ,  $P = 0.359$ ; Table 2), but it was greatly reduced during overlapping noise (log odds ratio =  $3.67 \pm 0.83$ ,  $z = 4.44$ ,  $P < 0.0001$ ; Table 2).

Nonoverlapping sound did not significantly affect the latency to flee in response to alarm calls (LMM: alarm alone versus alarm + nonoverlapping noise:  $\chi^2_1 = 3.322$ ,  $P = 0.068$ ; Fig. 4, Table 3). The nonsignificant tendency was for birds to respond more quickly (by about 60 ms) to alarm calls during noise compared to alarm calls alone, which is contrary to the noise distraction hypothesis, which predicts a delayed response in noise (Chan et al., 2010).

## DISCUSSION

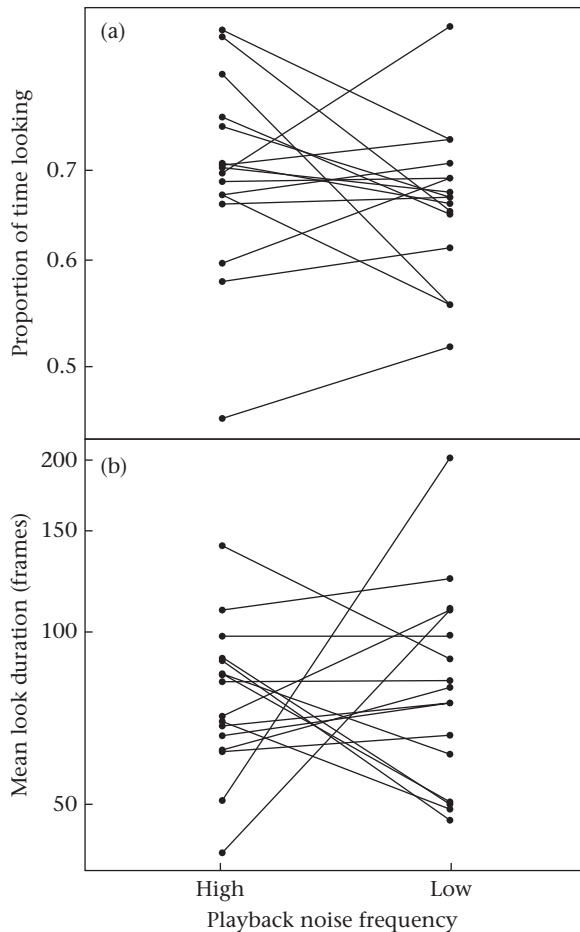
Our results show that acoustic masking was the primary mechanism compromising alarm communication in fairy-wrens. We used playback of two heterospecific alarm calls, at different frequencies, combined with two types of ambient noise, at different frequencies, to discriminate mechanisms. The flee response to alarm calls was only compromised by overlapping noise, regardless of frequency. In addition, neither low- nor high-frequency noise delayed the response to nonoverlapping alarm calls compared to quiet conditions. These results show that masking prevented birds from perceiving alarm signals in noise and that responses were not affected by distraction from either low- or high-frequency noise. Together with the finding of no difference in visual vigilance according to the two types of broadcast noise, our results demonstrate that masking, instead of distraction or increased visual vigilance, explains the lack of response to alarm calls in noisy conditions.

**Table 1**

Comparison of vigilance (proportion of time looking and duration of each look) by fairy-wrens during playback of high- versus low-frequency noise in experiment 1

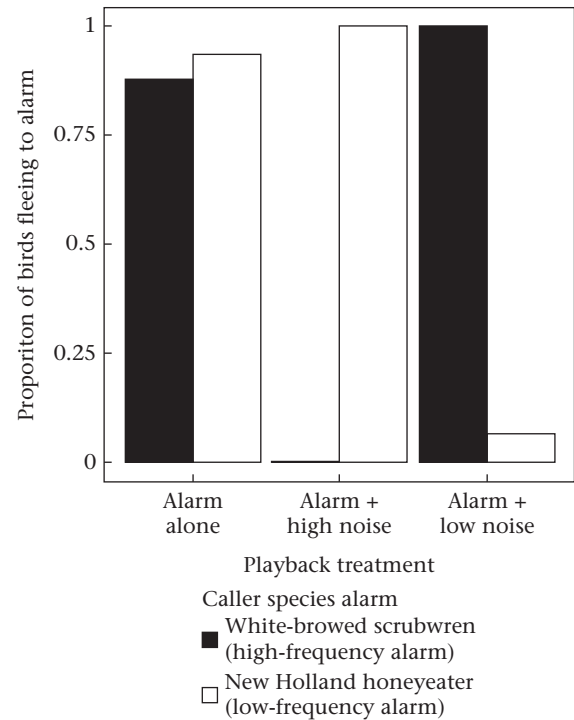
Fixed effects	Estimate $\pm$ SE	$\chi^2_1$	P
<b>Proportion of time looking</b>			
Background noise level (dB SPL)	0.006 $\pm$ 0.008	0.511	0.4747
Noise frequency (High – Low)	-0.044 $\pm$ 0.043	1.042	0.3074
<b>Duration of each look</b>			
Background noise level (dB SPL)	0.019 $\pm$ 0.019	0.922	0.3370
Noise frequency (High – Low)	0.048 $\pm$ 0.770	0.147	0.7016

Both measurements are logarithmically transformed. Background noise level was recorded immediately after playback of each noise frequency. The proportion of time looking is shown in Fig. 2a; the mean duration of each look is shown in Fig. 2b.



**Figure 2.** The vigilance level of the focal bird in high- and low-frequency noise. (a) The proportion of time spent looking during noise and (b) the mean duration of each look based on the number of frames (1 frame = 20 ms). The two values from each location are joined by a line, reflecting the matched experimental design. Note that the Y axis is on a log scale. The results of statistical comparison are shown in Table 1.

Field studies of other species also suggest that noise affects response to acoustic signals via masking, although it is usually not possible to exclude other mechanisms. Reduced signal response in overlapping noise was found in lazuli buntings, *Passerina amoena*, spotted towhees, *Pipilo maculatus* (Reed et al., 2021), northern cardinals, *Cardinalis cardinalis* (Grade & Sieving, 2016), great tits, *Parus major* (Templeton et al., 2016), and several species of owls (Mason et al., 2016; Senzaki et al., 2016). These studies tested only the effect of broadband natural or anthropogenic noise and found signal receivers responded less as the amplitude of noise increased, which was consistent with the pattern of masking, but does not rule out other mechanisms. For studies that investigated the effect of different frequency spectra of noise, such as in great tits (Tilgar et al., 2022) and superb fairy-wrens (Zhou et al., 2019), a reduced response to alarm calls was found during overlapping noise compared to nonoverlapping noise, which is stronger evidence for masking. However, different types of noise might be more or less distracting, and in all these studies it is possible that birds failed to respond to the signal because they were distracted by the noise. To understand fully the extent to which noise disruption can affect communication, it is crucial to distinguish between the mechanisms. In this study, we took advantage of the variation in acoustic frequency among the heterospecific alarm calls on which fairy-wrens eavesdrop. By using a crossover playback design, our study



**Figure 3.** The proportion of fairy-wrens fleeing in response to playback of scrubwren alarm calls (peak frequency  $\pm$  SD =  $7.1 \pm 0.4$  kHz) or honeyeater alarm calls ( $4.0 \pm 0.2$  kHz) alone or mixed with low-frequency (range 2–6 kHz) or high-frequency (6–10 kHz) noise. The frequency of scrubwren alarm calls is overlapped with high-frequency noise whereas the frequency of honeyeater alarm calls is overlapped with low-frequency noise. The results of statistical analyses are shown in Table 2.

shows that the impact of noise on alarm call reception was primarily caused by auditory masking rather than distraction.

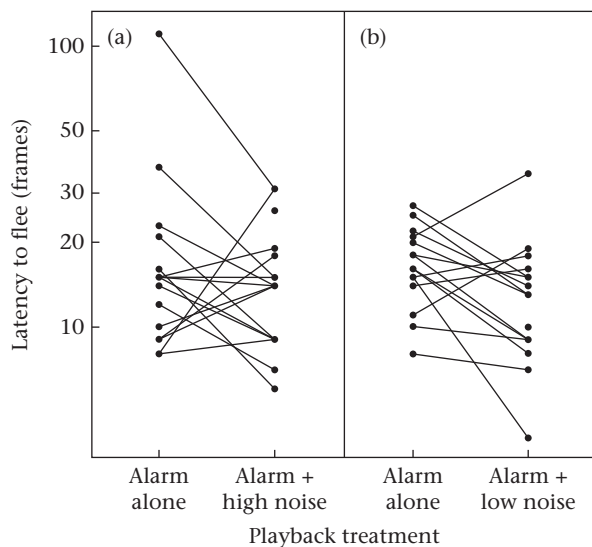
Our experiment revealed no evidence that noise was a source of distraction, despite evidence from other studies that noise distraction can compromise response to acoustic information. Foraging efficiency was equally reduced in Daubenton's bats, *Myotis daubentonii*, and in gleaning pallid bats, *Antrozous pallidus*, when using echolocation during noise, regardless of whether frequency overlapped with their echolocation calls or not (Allen et al., 2021; Luo et al., 2015). Similarly, female ezo brown frogs, *Rana pirica*, responded less to male advertisement calls during both overlapping and nonoverlapping noise (Senzaki et al., 2018). In all these studies, the behaviour was therefore consistent with distraction and not masking. We suggest three reasons why there may have been minimal distraction of fairy-wrens in our study. First, aerial alarm calls are signals of immediate danger. It is likely that animals evolve to pay specific attention to alarm signals because responses (or lack thereof) have direct survival consequences. Second, we used roughly continuous natural ambient noise calibrated to moderate amplitude, which still sounded similar to wind or cicada calls, and so may be more familiar to birds and less distracting than loud anthropogenic noise or discontinuous noise. Third, the bandwidth of the two playback noises that we used was relatively narrow (4 kHz) compared to the original whole-frequency ambient noise (0–20 kHz) and noise used in other studies that have found distraction (Allen et al., 2021; Chan et al., 2010; Luo et al., 2015; Senzaki et al., 2018). Therefore, it is possible that other frequency profiles may be more distracting. Overall, there is limited knowledge about the effect of noise or signal attributes on the potential for distraction, so we suggest further studies investigating how different noise types affect the response to different signals and cues.

**Table 2**

The proportion of fairy-wrens fleeing in response to scrubwren (SW) or New Holland honeyeater (NHHE) alarm calls, either alone or mixed with high- or low-frequency noise in experiment 2 (shown in Fig. 3)

Fixed effects	Log odds ratio $\pm$ SE	Z	P
<b>Interaction (model with the 4 alarm+noise treatments only)</b>			
Background noise level (dB SPL)	-0.002 $\pm$ 0.163	-0.150	0.8807
Noise frequency (Low – High) * Alarm call type (SW – NHHE)	7.366 $\pm$ 1.619	4.551	<b>&lt;0.0001</b>
<b>Pairwise comparisons (model with all 6 treatments)</b>			
Background noise level (dB SPL)	0.049 $\pm$ 0.139	0.352	0.7245
Alarm call type (NHHE – SW)	-0.618 $\pm$ 1.060	-0.583	0.5598
Treatment type (Alarm – Nonoverlapping)	-1.207 $\pm$ 0.883	-1.366	0.3589
Treatment type (Alarm – Overlapping)	-3.675 $\pm$ 0.828	4.442	<b>&lt;0.0001</b>
Treatment type (Nonoverlapping – Overlapping)	4.883 $\pm$ 1.020	4.788	<b>&lt;0.0001</b>

The first bias-reduced generalized linear models (BRGLM) testing the interaction between noise frequency and alarm call type, which included only the four treatments with alarm calls mixed with noise. The second BRGLM was used for pairwise comparison, including all treatments: with alarm calls alone (the control treatments) as well as alarm calls mixed with noise. Background noise level was recorded immediately after each playback. Significant outcomes are shown in bold.



**Figure 4.** Latency to flee in response to alarm calls broadcast alone or during nonoverlapping noise for (a) New Holland honeyeaters and (b) scrubwrens in experiment 2. Latency was measured as the number of video frames from the start of the alarm call to when the bird's feet left the ground (1 frame = 20 ms). New Holland honeyeaters have low-frequency alarm calls that are not overlapped with high-frequency noise, while scrubwrens have high-frequency alarm calls that are not overlapped by low-frequency noise. Note that the Y axis is on a log scale. The results of statistical analysis are shown in Table 3. Playbacks where the noise overlapped alarm calls are excluded because most birds did not flee.

Nonoverlapping noise did not delay the response to alarm calls, which is further evidence against a subtle effect of distraction, especially as fairy-wrens tended to respond faster during noise compared to quiet conditions. This tendency is contrary to the noise distraction hypothesis, because if birds were distracted, they should have responded more slowly during noise (Chan et al., 2010; D'Addario & Donmez, 2019). This pattern suggests that fairy-wrens may have been more alert auditorily in a noisy environment. Previous studies of, for example, wood pigeons, *Columba palumbus* (Murton & Isaacson, 1962), semipalmated sandpipers, *Calidris pusilla* (Beauchamp, 2015), and Australian magpies, *Cracticus tibicen* (Ratnayake et al., 2021), have shown that animals exhibit higher vigilance levels in visually restricted environments than in areas with clearer lines of sight. Alongside visual barriers, auditory restriction caused by noise can increase auditory vigilance. For instance, mule deer, *Odocoileus hemionus*, reduce chewing activity in the evening and in noisy environments, probably to listen for acoustic cues from predators (Lynch et al., 2015). Similarly, the pattern that we observed may indicate that noise increases

**Table 3**

Comparison of latency to flee in response to alarm calls broadcast alone or with nonoverlapping noise, in experiment 2 (shown in Fig. 4)

Fixed effects	Estimate $\pm$ SE	$\chi^2_1$	P
Background noise level (dB SPL)	-0.027 $\pm$ 0.018	2.236	0.1349
Alarm call type (NHHE – SW)	-0.011 $\pm$ 0.133	0.007	0.9334
Treatment type (Alarm – Nonoverlapping)	-0.238 $\pm$ 0.133	3.322	0.0684

NHHE = New Holland honeyeater; SW = scrubwren. Latency was measured as the number of video frames from the start of the alarm call to when the bird's feet left the ground (1 frame = 20 ms). Latency is logarithmically transformed. Background noise level was recorded immediately after each playback.

auditory vigilance, potentially helping animals to detect predators more quickly, even if there is no immediate behavioural change. Future experiments are needed to explore the more subtle effects of noise and to assess the potential for noise to expedite predator detection.

Increased visual vigilance did not explain different responses according to noise frequency, as fairy-wrens showed a similar level of vigilance during high- and low-frequency noise; this is in line with previous work (Zhou et al., 2019). Some studies of other species have found increased vigilance during broadband noise, usually compared to relatively quieter conditions (Eastcott et al., 2020; Merrall & Evans, 2020; Sweet et al., 2021). We did not assess whether noise in general increased vigilance compared to quiet conditions but, if so, any increased vigilance did not have a substantial effect on response to alarm calls, given that every fairy-wren fled in response to alarm calls in nonoverlapping noise. However, to our knowledge there has been only one study, on California ground squirrels, *Otospermophilus beecheyi*, comparing vigilance across different noise frequencies. In that case, there was increased vigilance during low-frequency river sounds compared to high-frequency cicada choruses (Le et al., 2019). Future studies need to investigate the effect of noise frequency on animal vigilance, which is relevant because it indirectly affects foraging efficiency and may also affect response to auditory information on danger.

As an extra source of predator information, eavesdropping is important for animals' daily survival (Goodale & Magrath, 2024; Iqic et al., 2019; Lowney et al., 2020). Some previous studies, including of dwarf mongooses, *Helogale parvula* (Morris-Drake et al., 2017), black-capped chickadees, *Poecile atricapillus* (Damsky & Gall, 2016), and northern cardinals (Grade & Sieving, 2016), also found that noise reduced the response of animals receiving heterospecific alarm signals. However, those studies did not test mechanisms. Any masking of eavesdropping would disrupt information networks and may reduce fitness of community members (Goodale & Magrath, 2024). Furthermore, noise can specifically

make heterospecific eavesdropping more difficult than conspecific reception, which would exacerbate the problem of interspecific information flow (Zhou et al., 2024). The substantial masking effect of noise highlights the importance of conservation efforts focused on minimizing noise frequencies that overlap with calls of not just the targeted species but also the acoustic signals from the entire community.

In conclusion, our results show that masking alone can have important effects on the response to alarm calls, with likely consequences for individual survival. Moreover, given that eavesdropping on alarm signals from other species can be disrupted by noise masking, animals may suffer the consequences of noise at a broad range of frequencies, including natural background sounds and anthropogenic noise that often has prominent low frequencies. Assessing mechanisms is crucial for understanding the evolution of communication, forecasting the impacts of anthropogenic noise and proposing solutions to mitigate the outcomes of this worldwide pollutant (Francis & Barber, 2013). It would be valuable to conduct explicit tests of mechanism in other species, as well as assess the effects of noise with different noise characteristics, such as in amplitude, frequency, duration and temporal pattern. Animals are likely affected differently by specific characteristics of noise, and the mechanisms might differ across taxa (Gomes et al., 2021). Quantifying noise effects by sound characteristics and by species would help us understand more fully the problem of noise, especially its effect on responses to acoustic signals and other informative sounds.

#### CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

**You Zhou:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Andrew N. Radford:** Conceptualization, Funding acquisition, Methodology, Supervision, Validation, Writing – review & editing. **Robert D. Magrath:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

#### Data Availability

<https://data.mendeley.com/preview/rnb748ysmp?u=0423849d-c8e2-453e-9919-43949faef9b3>

#### Declaration of Interest

The authors declare no conflicts of interest.

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