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The effect of temporal masking on alarm call communication in wild superb fairy-wrens

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Noise from human activity is a global concern that threatens wildlife, including by disrupting acoustic communication. This disruption appears predominantly caused by masking, where noise makes it difficult to hear acoustic signals. Previous studies have found a strong masking effect when noise and signals occur simultaneously. However, noise can also have a temporal masking effect, meaning that the signal is not detected even if noise occurs before or after the signal (forward and backward masking, respectively). As background noise is often intermittent, temporal masking by natural sounds and anthropogenic noise could pose a significant challenge for animal communication. Surprisingly, although commonly found in humans, temporal masking has been rarely studied in other species. To investigate whether temporal masking affects bird communication in the wild, we conducted a playback experiment on superb fairy-wrens, *Malurus cyaneus*, using single-element alarm calls before, during and after filtered white noise, as well as a control playback of alarm calls alone. We found that fairy-wrens stopped responding to alarm calls during noise, showing simultaneous masking, but were equally likely to flee if there was noise immediately before or after an alarm call as when there was no noise, suggesting a lack of temporal masking. However, among those fairy-wrens that fled, there was a 20 ms delay in the response to alarm calls after the noise, possibly because of subtle forward masking that delayed call reception. We conclude that temporal masking is unlikely to stop fairy-wrens' fleeing to alarm calls but might slightly delay call reception. We urge further studies of temporal masking in other species, using various sources of natural and anthropogenic noise, as only then will we know whether temporal masking is of general significance in compromising animal communication.

Environmental noise from abiotic and biotic sources is inevitable, and there is a rising concern that the increasing levels of global anthropogenic noise pose a threat to animal fitness. The most studied behavioural impact of noise is on acoustic communication (Dooling, 2019; Duquette et al., 2021; Gomes et al., 2021; Shannon et al., 2016). Noise can disrupt the ability of animals to receive sounds, including those that are important for survival such as alarm calls and the sounds of predators (Grade & Sieving, 2016; Morris-Drake et al., 2017; Rabin et al., 2006; Templeton et al., 2016). This interference is commonly caused by auditory masking (Barber et al., 2010; Lohr et al., 2003; Templeton et al., 2016; Zhou et al., 2019, 2024a). Auditory masking occurs when the presence of one sound makes the other sound difficult or impossible to detect. The quietest amplitude of the signal that can be heard in a given noise determines the masking threshold, below which receivers might fail to detect the signal (Gelfand, 2017). In general, the louder the masking sound compared to the signal, the stronger the masking effect. Also, masking is most effective when the two sounds share a similar frequency spectrum and occur simultaneously (Moore, 2012). In practice, masking leads to failure to detect the signal but could also increase the latency of detection if the signal is partially masked (Abou-Zeid et al., 2024; Bee & Micheyl, 2008; Lohr et al., 2003; Templeton et al., 2016). However, noise might disrupt signal reception even when it does not appear at the same time as the signal, through a process called temporal masking (Moore, 2012). As background noise is often intermittent, temporal masking caused by ambient sound and anthropogenic noise could pose a significant challenge for animal communication.

Temporal masking can affect reception of the signal if the masking sound occurs before (forward masking) or after (backward masking) the signal, and it has been widely found in humans (Silva,

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2014). Temporal masking follows similar rules relating to amplitude and frequency as simultaneous masking, where higher amplitudes of masking sounds and overlapping frequency ranges between the masking sounds and the signal lead to stronger effects (Gelfand, 2017; Moore, 2012). In addition, the effect of temporal masking is stronger with a shorter time interval between the masking sound and the signal, with the strongest effect occurring when there is no time gap between them (Moore, 2012). Generally, forward masking occurs with longer time intervals (up to 200 ms in humans) than backward masking (up to 10 ms in humans) (Elliot, 1962; Musiek & Chermak, 2015; Snodgrass et al., 2009). The mechanism of temporal masking is still unclear but predominantly can be explained by the time required by the hearing system to process signal information (Moore, 2012). As a result, people are unable to hear signals, such as tones, before or after filtered white noises that cover the frequency of the tones (Grose et al., 2016; Hartley et al., 2000; Krizman et al., 2017; Yoo & Bidelman, 2019). Furthermore, forward and backward masking appear to be explained by different neural processes, hence the mismatch of effective time interval (Moore, 2012).

Temporal masking can also affect nonhuman animals, but the effect has received little research attention. Previous studies have focused on temporal masking in animals that use echolocation, such as bottlenose dolphins, *Tursiops truncates* (Popov et al., 2020), false killer whales, *Pseudorca crassidens* (Supin et al., 2008), and free-tailed bats, *Tadarida brasiliensis* (Smotherman & Bakshi, 2019), which emit biosonar pulses and detect their echoes. Depending on the location of the target, the delay of the echo can be in milliseconds, resulting in forward masking from the pulse on the echo (Supin et al., 2008). The echolocating animals actively reduce the forward masking effect by improving the ability of receiving echoes (Smotherman & Bakshi, 2019). For birds, only one study, on budgerigars, *Melopsittacus undulates*, has studied temporal masking (Dooling & Searcy, 1980). The study used band-limited noises (0.5–9 kHz, 40 ms) as masking sounds and 2.86 kHz tones (5 ms) as signals. In the laboratory, signals were masked if the intervals were within 100 ms for forward masking and 10 ms for backward masking. In addition, budgerigars overall had a lower temporal masking threshold compared to humans, suggesting that budgerigars might be less affected by temporal masking. Other studies on avian temporal resolution and gap detection, which is for recognizing different signals with a short time interval in between, also found that birds are better at discriminating temporal structure than humans (Dooling et al., 2002; Vernaleo & Dooling, 2011; Wagner et al., 2003). Excellent temporal resolution is an important skill in birds because they often produce vocalizations with rapid temporal changes and can face complex soundscapes from conspecifics and heterospecifics.

In this study, we used a field playback experiment to test whether wild superb fairy-wrens, *Malurus cyaneus,* are vulnerable to temporal masking by noise. The experiment entailed playback of aerial alarm calls, which warn of predatory birds in flight and normally provoke immediate flight to cover (Leavesley & Magrath, 2005), with noise that occurred before, during or after the call. Aerial alarm calls are ideal for investigating masking and signal reception because elements are short (on average 104 ms for fairy-wrens) and the responses are quick and obvious with no prior training needed (Magrath et al., 2007). Also, alarm calls are closely related to survival and so, by testing the possibility of alarm calls being masked, we highlight the ecological importance of temporal masking (Caro, 2005). We predicted that fairy-wrens would stop fleeing to alarm calls before or after noise if there is temporal masking and stop fleeing to alarm calls in the middle of noise if there is simultaneous masking. Furthermore, if temporal masking increases the time needed to process signals, we predicted a greater latency to respond to alarm calls before or after noise compared with alarm calls alone.

METHODS

Study Species and Site

Superb fairy-wrens are small passerines (9–10 g) that primarily forage on the ground (Higgins et al., 2001). They live in territorial groups and cooperate when breeding, typically between September and January. Outside of the breeding season, they often join other groups and move across neighbouring territories (Higgins et al., 2001). Adult males and females can be distinguished by their plumage and bill colour (Higgins et al., 2001). Fairy-wrens produce aerial calls to warn of flying predators, which prompts immediate flight to cover for conspecifics (Magrath et al., 2007). The aerial alarm calls consist of repeated elements that are around 104 ms long with a peak frequency of about 9.1 kHz (Magrath et al., 2007). The number of elements in the aerial alarm call indicates the urgency of danger (Fallow & Magrath, 2010). Single-element alarm calls prompt about half of fairy-wren receivers to flee, while alarm calls with two or more elements result in almost all fairy-wrens fleeing (Fallow & Magrath, 2010). In addition, as the number of elements increases, fairy-wrens stay in cover for a longer time (Fallow & Magrath, 2010).

Our study was conducted on fairy-wrens in Canberra, Australia. The majority of experimental trials (21 out of 24 sites) were conducted in the Australian National Botanic Gardens (35°16′44″S, 149°6′32″E) where fairy-wrens can be found throughout most of the 40 ha of natural woodland, areas planted with native Australian plants and lawn. All the individuals are colour-banded and the population has been under observation for over 30 years. We used another three sites, with unbanded fairy-wrens, in Jerrabomberra Wetland (35°18′54″S, 149°9′43″E). In both study areas, the fairy-wrens are accustomed to human presence and face predation from collared sparrowhawks, *Accipiter cirrhocephalus*, and pied currawongs, *Stepera graculina*, which are locally common.

Experimental Design

To investigate whether fairy-wrens are vulnerable to temporal masking of alarm calls, we broadcast single-element alarm calls before or after 2 s of noise. Birds received five treatments: (1) aerial alarm call alone; (2) noise alone; (3) aerial alarm call mixed together with noise, where the aerial alarm call occurred together with the noise (simultaneous masking); (4) aerial alarm call after the end of noise (forward masking); (5) aerial alarm call before the start of noise (backward masking). We used single-element alarm calls as temporal masking can only affect short signals, and we used 2 s of filtered white noise as the potential masking sound. To provide the strongest test of temporal masking, there was no time gap between the alarm call and noise in the forward and backward masking playbacks.

We used a complete randomized block design at 24 sites, with a unique set of playbacks at each site. We matched by site, rather than specific individual or group, because in the nonbreeding season, groups form larger foraging flocks that move over several territories and because location controls for ecological variables such as local habitat, predator activity and ambient sound (Zhou et al., 2019; 2024a; 2024b). In the Botanic Gardens, all individuals were identified from colour bands during the playbacks. We used three to five individuals at each site except for one where all treatments were conducted on the same individual. In the 21 Garden sites, 77 individuals received 105 playbacks, with three receiving playbacks at two sites but none receiving the same treatment more than once. In Jerrabomberra, to make sure that no individual received the same treatment more than once, the three sites were 150–200 m apart, with focal birds of different sexes used in adjacent sites. The order of the treatments was randomized and balanced as much as possible, with a series of random orders of 1–5 generated by R. The orders were used in the sequence generated, but we rejected an order if it resulted in a treatment occurring more than four times in any order. The outcome was that each order occurred three to four times for each playback type over the 24 sites.

Sound Stimuli

We prepared 24 unique single-element alarm calls for playback (Fig. 1a). Each alarm call was recorded from a different individual, prompted using gliding models of collared sparrowhawks (as in Magrath et al., 2007; Zhou et al., 2019, 2024a, 2024b). The alarm calls had a mean ± SD duration of 96.7 ± 27.3 ms, with an overall minimum frequency of 8.6 kHz and maximum frequency of 10.2 kHz. The low and high frequency were measured as the frequencies containing 5% and 95% of the energy, respectively, in the spectrogram slices of the alarm calls in Raven Pro 1.5 (https://ravensoundsoftware.com/software/raven-pro/). To calibrate the calls to 52 dBA sound-pressure level (SPL) at 10 m (mean amplitude of individual elements, Magrath et al., 2007), we re-recorded call playbacks at 10 m using a Sennheiser ME66 directional microphone mounted on a tripod and a Marantz PMD670 recorder sampling at 44.1 kHz and 16 bits, along with a calibration tone that had its amplitude measured with a Brüel & Kjær 2240 sound-level meter. The calibration recordings were done in an open area of lawn with no nearby buildings or similar reflective surfaces. Then, the alarm calls were iteratively adjusted and compared to the tone to ensure a 52 dBA SPL playback amplitude at 10 m using the Average Power measurement in Raven Pro 1.5 (the same method as in Zhou et al., 2019).

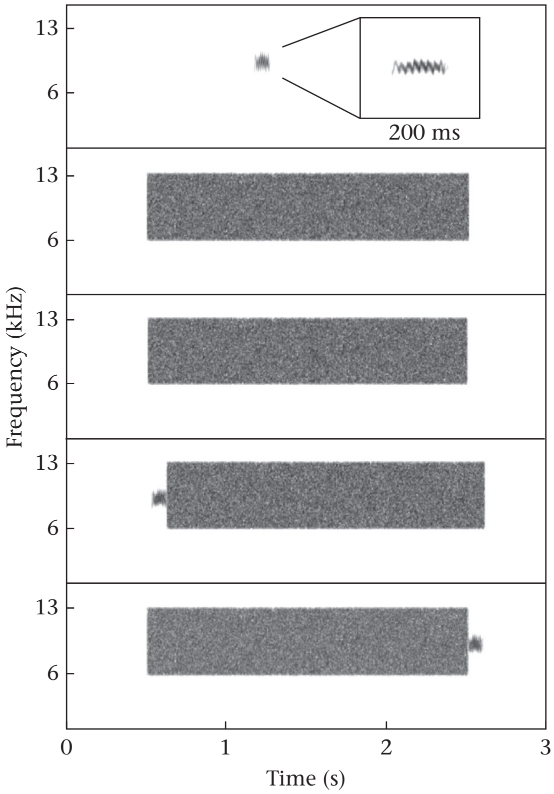

Figure 1. Spectrogram of the playback treatments: (a) single-element alarm call alone, with a zoomed-in spectrogram of the alarm call on the right; (b) filtered white noise (6–13 kHz) alone; (c) filtered white noise (6–13 kHz) with single-element alarm call 1 s after the start of noise; (d) filtered white noise (6–13 kHz) followed by single-element alarm call; (e) single-element alarm call followed by filtered white noise (6–13 kHz).

We generated 24 clips of 2 s white noise in Adobe Audition 2022 (https://www.adobe.com/) (Fig. 1b). The clips were then filtered to a range of 6–13 kHz using the bandpass function in Raven Pro1.5 so that the frequency of noise fully covered that of alarm calls. To avoid a 'pop' sound from the loudspeaker when there was a sudden loud sound, all noises had 10 ms of fade in and out at the beginning and the end. We calibrated the noise clips to 58 dBA at 10 m using the same method as for alarm calls. We chose 58 dBA SPL of noise because it was the lowest amplitude that prevented birds from responding to alarm calls of 52 dBA SPL during simultaneous masking in our previous study (Zhou et al., 2019).

In each site, we broadcast a unique set of playback sounds composed of one of the recorded alarm calls and one of the generated noise clips to avoid pseudoreplication (Kroodsma et al., 2001). For simultaneous masking playbacks, we mixed the alarm call in the middle of the noise clip. The alarm call was positioned in the track 0.8, 1 or 1.2 s from the onset of noise to ensure birds were responding to alarm calls and not just a specific time (Fig. 1c); the position was randomly picked via Excel. For both forward masking (Fig. 1d) and backward masking (Fig. 1e) playbacks, we created tracks with no time between the noise and the alarm call using the 'mixdown session to new file' function in Adobe Audition CC 2022, to be broadcast from one loudspeaker. Using a single loudspeaker avoided any effect of masking release if an alarm call and the noise came from different directions ('spatial release of masking'; Brumm, 2013).

Birds might flee to the noise playback alone, so birds were repeatedly exposed to noise playbacks before proceeding with the experimental treatments. We made a unique 5 min sound file for each site, which consisted of five repeats of the 2 s noise subsequently used in playback treatments. In each minute, one noise segment occurred at a random time. After habituation, we found no bird fled to noise itself during the treatment playbacks. In addition to receiving the complete 5 min sound file, we had a second predetermined criterion for habituation. Habituation was deemed complete if the focal bird was in the open and showed no response to two successive noise playbacks, but in practice this applied to only one bird, while many birds were not in the open when receiving playbacks.

Playback Procedure

The playback procedure followed the same protocol used in our previous studies (Zhou et al., 2019; 2024a). In brief, we followed a group of fairy-wrens from 5–10 m for at least 5 min to ensure that there were no predators or heterospecifics nearby and that there had been no detectable alarm calls in the area. During this period, the 5 min habituation sound file was played to the fairy-wrens, regardless of whether they were in the open or in vegetation. The treatments were then played within 30 min of the habituation track ending. We carried out a new round of habituation if the interval exceeded 30 min.

Before playback, we identified the focal bird by its colour bands, if in the Botanic Gardens, or its sex and location, if in Jerrabomberra Wetland. We avoided carrying out playbacks to males in blue breeding plumage because they are more likely to respond to alarm calls than brown males or females (McQueen et al., 2017). Playbacks were initiated only when the focal bird was the closest individual to the observer and between 0.5 m and 10 m from cover. The number of other fairy-wrens present during the playbacks and the distance of the focal bird to the closest vegetation were recorded. We played the treatments using a Peerless 810921 tweeter loudspeaker (frequency response 2–11 kHz), connected to a custom amplifier and a Roland Edirol R-05 HR digital recorder as the playback device. We recorded the focal bird's response using a Panasonic HC-V770M video camera (50 frames/s, where 1 frame = 20 ms, resolution 1920 × 1080p) mounted on the observer's shoulder. If there was a disturbance during playback, such as the approach of predators or audible alarm calls, the trial was stopped and repeated after 5 min. To reduce the risk of habituation to treatments, there was a maximum of three playbacks per site per day, with a minimum of 5 min between the first and second playbacks and a minimum of 1 h between the second and third, during which the bird received a 5 min noise habituation playback.

To control for the effect of natural background noise, we avoided conducting playbacks in windy or noisy conditions and measured background sound levels. The background noise was recorded for 30 s after each playback, from the position of the focal bird, using a Sennheiser ME64 omnidirectional microphone connected to a Marantz PMD670 recorder sampling at 44.1 kHz and 16 bits. We later measured the amplitude of the background noise using the Average Power function in Raven Pro1.5 and calibrated it against a prerecorded 1 kHz tone of known amplitude. The tone was recorded and the amplitude of the tone was measured by a Brüel & Kjær 2240 sound-level meter at the same time in an open area of lawn with no nearby buildings or similar reflective surfaces. Overall, the background noise level during playbacks was 35.3 ± 9.1 dBA SPL (mean ± SD), ranging from 25.3 to 49.3 dBA SPL.

Response Measurement

We scored the responses to playback blindly via video, as far as possible, but where the bird fled to was scored in the field, as potential cover was usually out of the camera's field of view. Videos were scored blind, frame by frame, by Y.Z., after the names of video files were reassigned by others and the sound was muted. The exact time of the start of an alarm call in playbacks with alarm calls (alone, alarm in the middle of noise, alarm after noise and alarm before noise), as well as the end of 2 s noise in noise-alone playbacks, was noted before anonymizing the videos so that the analyst knew the potential start time of alarm calls for each muted anonymous video. We categorized the focal bird's response to playbacks as follows: 0 = no response, the bird continued moving or feeding as before the playback; 1 = look, the bird raised its head and looked around or towards the loudspeaker; 2 = flinch, the bird crouched or jumped up; 3 = flee but not to cover, the bird flew away but landed outside cover; 4 = flee to cover, the bird flew into the cover of vegetation. Blind scoring enabled scoring into no response (0), look (1), flinch (2) and flee, but only occasionally was it possible to see where birds fled (out of cover (3), or into cover (4)). We therefore used field data to separate flee responses into flee but not into cover (3) and flee to cover (4).

For the cases where the focal bird fled, we used two measures of the latency to respond. The latency to initial response was measured as the time from onset of alarm call playback to onset of the bird's initial response; that is, the point when the bird started to raise its head or move its body. The latency to flee was measured as the time from onset of alarm call playback to the point when the bird's feet left the ground while fleeing. In both cases, time was measured by as number of video frames (1 frame = 20 ms). In addition, there were eight out of 57 cases where the focal birds were in the air, in a foraging hop, at the start of the alarm call. In these cases, if the birds fled, they might not show a noticeable response until after they landed, causing a longer time latency compared to birds standing on the ground at the start of playback. Therefore, whether the focal bird was in the air when alarm call started was also scored during video analysis and included in statistical analysis.

Statistical Analysis

We conducted all statistical analyses in R version 4.2.0 (R Core Team, 2022). We used cumulative link mixed models (CLMMs) to analyse the categorical responses of fairy-wrens to each treatment. The response was ranked into five ordered levels: 0 = no response, 1 = look, 2 = flinch, 3 = flee, but not to cover, 4 = flee to cover. CLMMs are appropriate for analysing the ordinal responses in this study, which arranges the response strength without implying quantitatively equal intervals between categories (Agresti, 2007, pp. 173–203). The fixed factors were the treatment type (alarm call alone, noise alone, alarm and noise together, alarm after noise, alarm before noise) and natural background noise level (a continuous variable), and random factors were treatment order and site. The number of other fairy-wrens present during the playback was dropped from the model because it had no significant effect on model performance (likelihood ratio: $\chi^2_1 = 0.039$, $P = 0.843$). CLMMs were conducted using the ‘clmm()’ function of the ‘ordinal’ package (Christensen, 2019), with a probit link function and an equidistant threshold.

We used linear mixed models (LMMs) to analyse the time latency to initial response and latency to flee. We included only cases where birds fled, including to cover and not to cover, which were all to the alarm alone, alarm after or alarm before noise treatments. Both measurements were logarithmically transformed to improve fit for the models. The fixed factors were treatment type (alarm alone, alarm after noise, alarm before noise), natural background noise level (a continuous variable) and whether the focal bird was in the air when alarm call started (yes, no), and random factors were treatment order and site. The number of other fairy-wrens present during the playback was dropped from the models as it again showed no significant effect (time latency to initial response: $\chi^2_1 = 0.40$, $P = 0.526$; time latency to flee: $\chi^2_1 = 0.104$, $P = 0.747$). LMMs were conducted using the ‘lmer()’ function of the ‘lme4’ package (Bates et al., 2014). We used the ‘emmeans()’ function of the ‘emmeans’ package (Lenth, 2018) to compare within the fixed factors and ‘Anova()’ function of the ‘car’ package (Fox & Weisberg, 2019) to test the significance of each fixed factor.

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. No bird responded to playbacks of noise alone after noise habituation. To mitigate the potential impact of alarm call playbacks, each site had a maximum of three playbacks per day. Birds quickly resumed foraging after the playbacks.

RESULTS

Analysis of categorical responses revealed complete simultaneous masking yet no effect of temporal masking. Noise completely masked simultaneous alarm calls but had no significant effect on response to alarm calls that occurred immediately after or before noise (CLMM: likelihood ratio = $\chi^2_4 = 121.07$, $P < 0.001$; Table 1, Fig. 2). Birds responded similarly to noise alone and alarm calls in the middle of noise, with no birds fleeing (parameter estimate (noise − alarm and noise together) ± SE = -0.01 ± 0.019; *z* ratio = -0.41, $P = 0.994$). By contrast, most of the birds fled to alarm calls played alone (17/24 fled), to alarm calls after noise (19/24 fled) and

Table 1
Comparison of categorical responses to the playback treatments using CLMM, shown in Fig. 2

Fixed effects	Estimate ± SE	Likelihood ratio	*df*	*z* ratio	*P*
Background noise level (dBA)	0.034±0.039		1	0.859	0.390
Treatment		121.07	4		**<0.001**
Treatment (noise − alarm)	-0.897±0.060		1	-14.955	**<0.001**
Treatment (noise − alarm + noise together)	-0.008±0.019		1	-0.412	0.994
Treatment (noise − alarm after noise)	-0.941±0.041		1	-22.961	**<0.001**
Treatment (noise − alarm before noise)	-0.959±0.032		1	-29.743	**<0.001**
Treatment (alarm − alarm + noise together)	0.889±0.061		1	14.503	**<0.001**
Treatment (alarm − alarm after noise)	-0.043±0.054		1	-0.806	0.929
Treatment (alarm − alarm before noise)	-0.062±0.052		1	-1.193	0.755
Treatment (alarm + noise together − alarm after noise)	-0.933±0.044		1	-21.444	**<0.001**
Treatment (alarm + noise together − alarm before noise)	-0.952±0.036		1	-26.753	**<0.001**
Treatment (alarm after noise − alarm before noise)	-0.019±0.034		1	-0.553	0.982

Responses are categorized as no response, look, startle/flinch, flee but not to cover, flee to cover. Background noise level was recorded immediately after playback of each treatment. Significant outcomes are shown in bold.

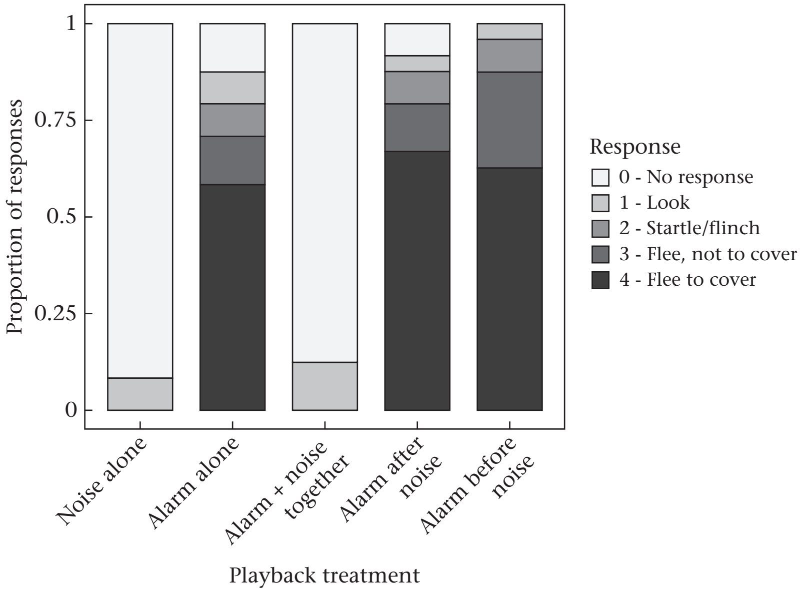

Figure 2. The proportion of fairy-wrens responding to noise and alarm calls alone, as well as alarm calls together with, after or before noise. The results of statistical analyses are presented in Table 1; *N* = 120 playbacks in 24 sites.

to alarm calls before noise (21/24 fled; parameter estimates ± SE: alarm alone − alarm after noise: -0.04 ± 0.054; *z* ratio = -0.81, *P* = 0.929; alarm alone − alarm before noise: -0.06 ± 0.052; *z* ratio = -1.19, *P* = 0.755).

Temporal masking had a small effect on the latency to initial response when the noise occurred before the alarm call (forward masking) but no significant effect on the latency to flee. Birds significantly increased the latency to initial response to alarm calls after noise, but the latency to alarm calls before noise were not affected (LMM: alarm alone − alarm after noise: *t* = -2.60, *P* = 0.036; alarm alone − alarm before noise: *t* = -1.16, *P* = 0.487; Table 2, Fig. 3). However, the difference in latency to initial response was small (a delay of ca. 20 ms) and did not differ significantly according to whether alarm calls were broadcast after or before noise (*t* = 1.51, *P* = 0.299). Furthermore, there was no significant effect of noise before or after an alarm call on the latency to flee

Table 2
Comparison of latency to initiate responding to an alarm call alone, or after or before noise, shown in Fig. 3

Fixed effects	Estimate ± SE	χ^2	*df*	*t* ratio	*P*
Background noise level (dBA)	0.002±0.010	0.034	1		0.8543
In the air when alarm call starts (Yes − No)	0.341±0.133	6.626	1		**0.0101**
Treatment		7.104	2		**0.0287**
Treatment (alarm − alarm after noise)	0.286±0.108		1	-2.598	**0.0364**
Treatment (alarm − alarm before noise)	0.129±0.108		1	-1.156	0.4897
Treatment (alarm after noise −alarm before noise)	-0.157±0.102		1	1.512	0.2986

Cases where the focal bird fled to cover and not to cover were included, where *N* = 17 for alarm alone, *N* = 19 for alarm after noise and *N* = 21 for alarm before noise. Latency was measured as the number of video frames from the start of the alarm call to when the focal bird initiated the response, including first head or body movement (1 frame = 20 ms). Latency is logarithmically transformed. Background noise level was recorded immediately after playback of each treatment. Significant outcomes are shown in bold.

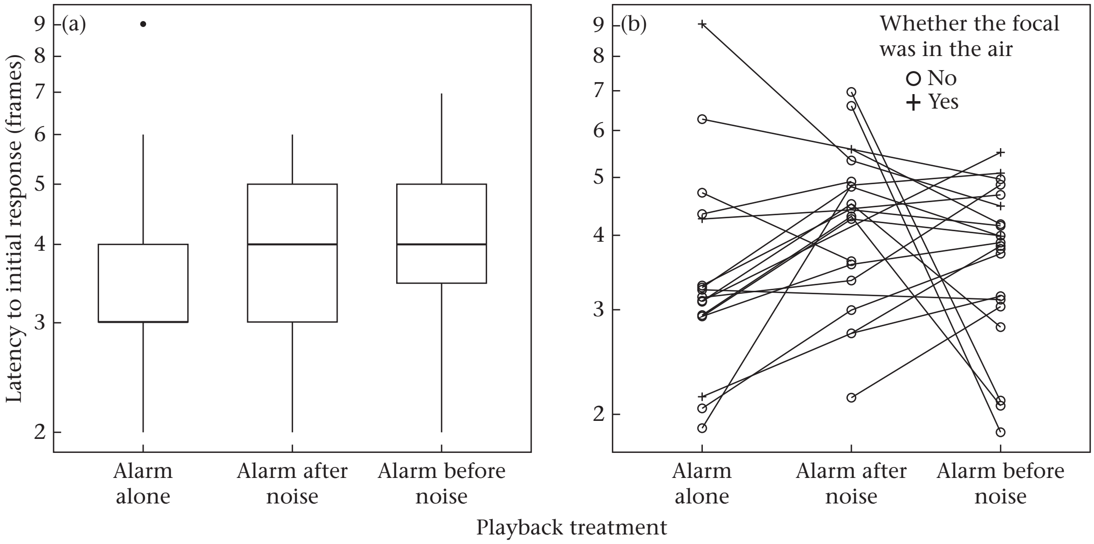

Figure 3. Latency to initial response to an alarm call alone, or after or before noise: (a) latency according to playback type, not matched by site; (b) raw data from each site, with values from the same site joined by a line, with symbols indicating whether the focal bird was in the air at the beginning of the alarm call (which on average slows the response). Latency was measured as the number of video frames from the start of the alarm call to the start of the response (1 frame = 20 ms). Note that the *Y* axis is on a log scale. The results of statistical analysis are shown in Table 2; cases where the focal bird fled to cover and not to cover were included, where *N* = 17 for alarm alone, *N* = 19 for alarm after noise and *N* = 21 for alarm before noise.

($\chi^2_2 = 1.69$, $P = 0.429$; Table 3, Fig. 4). These analyses included whether a bird was in the air when the alarm call started. Focal birds that were in the air when the alarm call started (*N* = 9) had a slower initial response compared to focal birds that were on the ground ($\chi^2_1 = 6.63$, $P = 0.010$; Table 2) with a similar but nonsignificant tendency for the latency to flee ($\chi^2_1 = 3.46$, $P = 0.063$; Table 3).

DISCUSSION

Noise temporal masking did not affect the likelihood that superb fairy-wrens fled to alarm calls, but forward masking might have caused a slight delay in the initial response to alarm calls. Most of the fairy-wrens fled to alarm calls alone, as well as alarm calls after and before the noise. By contrast, fairy-wrens did not respond to alarm calls during noise; a case of simultaneous masking in line with our previous work (Zhou et al., 2019; 2024a). Fairy-wrens initiated their response slightly more slowly to alarm calls after noise, compared to alarm calls alone, but the effect was small and the time latency for the birds to take off from the ground was similar among these treatments. Therefore, temporal masking had little to no effect on signal reception compared with simultaneous masking.

The categorical responses to alarm calls revealed a strong effect of simultaneous masking but no effect of temporal masking. Fairy-wrens stopped responding to alarm calls when broadcast simultaneously with noise, which is consistent with previous research on fairy-wrens (Zhou et al., 2019; 2024a) and other animals (Damsky & Gall, 2016; Kern & Radford, 2016; Templeton et al., 2016). However, noise broadcast before or after alarm calls did not lead to a change in responses compared to alarm calls broadcast alone. In these cases, birds responded mostly by fleeing, suggesting that fairy-wrens were able to recognize alarm calls broadcast before or after noise. Furthermore, the proportion of birds fleeing to alarm calls before or after noise tended to be higher than to alarm calls alone, contrary to our hypothesis of temporal masking. It is possible that birds follow the rule of 'better safe than sorry' and in noisy conditions overestimate the current danger indicated by alarm calls that are audible but not distinctly clear (Crane et al., 2024; Feyten et al., 2019; Johnson et al., 2013). We suggest further investigation on the issue of risk assessment in conditions of imperfect or ambiguous information.

Noise immediately before alarms calls appeared to reduce the speed of signal detection, but there was only a slight increase in the latency to first response. Initial responses of fairy-wrens were delayed by only 20 ms by noise before the alarm call, which was at the limit of resolution from our video analysis (i.e. a single frame). This small effect, together with the lack of a significant difference compared to backwards masking, and no effect of noise on the latency to flee, make this an inconclusive finding. Future studies, using higher temporal resolution, are therefore necessary to clarify whether there is any effect of temporal masking on the latency of behavioural responses.

Table 3
Comparison of latency to flee to an alarm call alone, or after or before noise, shown in Fig. 4

Fixed effects	Estimate ± SE	χ^2	*df*	*t* ratio	*P*
Background noise level (dBA)	0.007±0.007	1.243	1		0.2649
In the air when alarm call starts (Yes − No)	-0.170±0.092	3.458	1		0.0630
Treatment		1.694	2		0.4287
Treatment (alarm − alarm after noise)	0.286±0.108		1	1.270	0.4218
Treatment (alarm − alarm before noise)	0.129±0.108		1	0.772	0.7223
Treatment (alarm after noise − alarm before noise)	-0.157±0.102		1	0.522	0.8610

Cases where the focal bird fled to cover and not to cover were included, where *N* = 17 for alarm alone, *N* = 19 for alarm after noise and *N* = 21 for alarm before noise. 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 playback of each treatment.

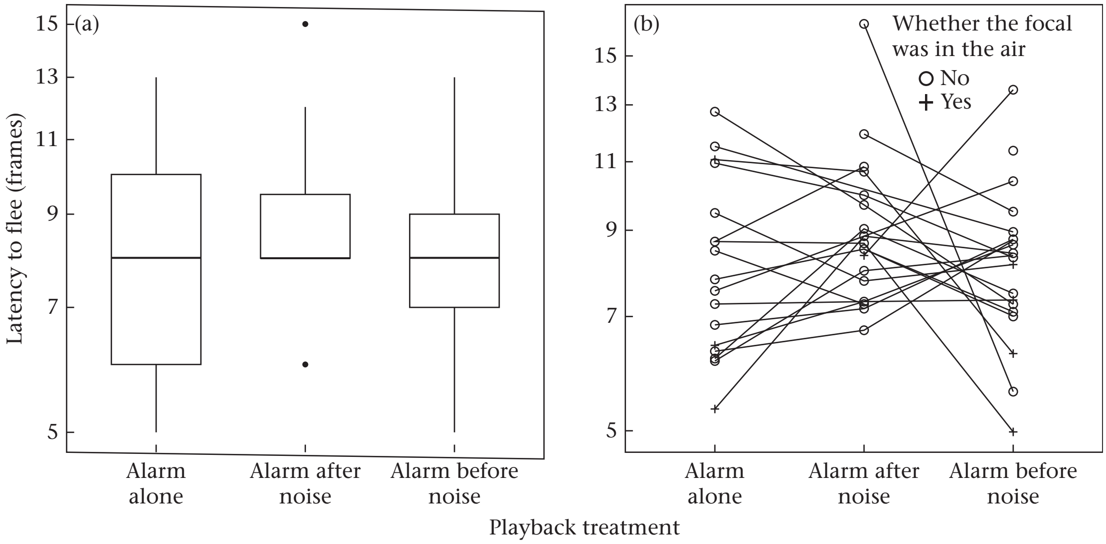

Figure 4. Latency to flee to an alarm call alone, or after or before noise: (a) latency according to playback type, not matched by site; (b) raw data from each site, with values from the same site joined by a line, with symbols indicating whether the focal bird was in the air at the beginning of the alarm call. 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). Note that the *Y* axis is on a log scale. The results of statistical analysis are shown in Table 3; cases where the focal bird fled to cover and not to cover were included, where *N* = 17 for alarm alone, *N* = 19 for alarm after noise and *N* = 21 for alarm before noise.

We suggest three reasons for minimal to no temporal masking on fairy-wren responses to alarm calls. First, the alarm calls used in this study were longer (mean 96.7 ms) compared to previous studies that found temporal masking (5–55 ms for humans and budgerigars, 0.033–2 ms for echolocation studies). The characteristics of both masking sounds and signals, such as frequency, amplitude and duration, are closely related to the degree of masking (Moore, 2012) and so shorter calls than the ones we used, such as aerial alarm calls from New Holland honeyeaters, *Phylidonyris novaehollandiae* (mean duration 47.9 ms; Magrath et al., 2009), and snake alarm calls from oriental tits, *Parus minor* (median duration 75 ms; Ha et al., 2020), might be more vulnerable to noise temporal masking. Second, birds, including fairy-wrens, might be better at dealing with temporal masking than humans (Dooling & Searcy, 1980), who have been the subject of most studies of temporal masking. Birds have better auditory temporal resolution than some mammals (Henry et al., 2011), which is likely also to make them less vulnerable to temporal masking. Third, the possibly slower initial response to alarm calls following noise might indicate an incomplete reception of alarm calls. With noise before or after, the alarm call might have been partially masked, preventing the birds from hearing the details of the calls and thus delaying their responses. In the case of fairy-wrens, the key feature of their aerial alarm calls that is crucial for call recognition is the peak frequency; other details are not necessary (Fallow et al., 2013). Therefore, fairy-wrens might still be able to respond by fleeing, even with a partially masked alarm call, but it might nevertheless require a longer time to process the information.

Although temporal masking did not affect fairy-wrens' fleeing to aerial alarm calls, temporal masking might be important in other situations, especially when information is encoded in the details of animal calls. A possible example is the ‘precedence effect’, in which females prefer a male that leads advertisement calls when there were two males calling in succession (Dent & Dooling, 2004; Greenfield et al., 2016; Marshall & Gerhardt, 2010; Party et al., 2014; Reichert et al., 2016; Siegert et al., 2011; Yue et al., 2017). The precedence effect could be explained by the directional hearing of the females, where the leading call determines the location of the sound source, making it unlikely that females would be able to locate the second male (Reichert et al., 2016). However, masking, especially forward masking, might lead to the second call being at least partially masked by the call before, and from a female's perspective, any details missing may indicate a male with poorer quality. As mechanisms of precedence effects, masking and directional hearing are not mutually exclusive, yet masking, especially temporal masking, has surprisingly drawn less attention in terms of mate choice via acoustic signals.

Our study addresses the ecological importance of noise temporal masking. To our knowledge, it is the first to investigate the effect of temporal masking on wild animals. Using alarm calls and noise as signals and as the masking sound, we simulated scenarios mirroring natural conditions where alarm calls are given just before, during or after noise. Alarm calls, as warning signals of predation risk, are likely to be produced in response to predators regardless of noise. Although temporal masking did not affect whether fairy-wrens fled to aerial alarm calls, we found a hint of forward masking increasing latency to response, which might increase the chance of predation. We suggest the that it would be valuable to conduct studies that quantify temporal masking according to signal and noise characteristics, and in different species, to understand the extent of temporal masking in animals. Only then will we know whether temporal masking is of general significance in compromising animal communication.

Author Contributions

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

Data Availability

The raw data for this study are available in the Mendeley Data repository (https://doi.org/10.17632/5jy9wj5myz.1).

Declaration of Interest

The authors declare that they have no conflicts of interest.

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