Animal Behaviour 231 (2026) 123403

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

A heads-up on danger: a novel avian vigilance call changes subsequent responses to alarm calls

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ARTICLE INFO

Article history:
Received 22 May 2025
Initial acceptance 16 July 2025
Final acceptance 28 August 2025
Available online xxx
MS. number: A25-00331

Keywords:
alarm call
antipredator
decision making
information use
vigilance
vocal sequence

Gaining information about predators is critical when determining an appropriate antipredator response. Many species obtain social information from alarm calls, prompting fleeing or mobbing, but personal vigilance also provides detailed information about the current threat level. The two sources of information on danger may interact in complex ways, but this has rarely been examined. Using a series of field experiments, we first tested the function of an undescribed ‘seet’ vocalization given by superb fairy-wrens, *Malurus cyaneus*, in response to predators and found that it prompted vigilance in conspecific receivers. We then examined whether hearing these calls changed the threshold for response to subsequent aerial alarm calls (warning of airborne predators), either by reducing responsiveness, because individuals had more personal information, or priming individuals to respond more strongly to alarm calls. Fairy-wrens reduced their response to more urgent aerial alarm calls that followed seet calls. There was no difference in immediate response to less urgent aerial alarm calls, but individuals who did not flee were more vigilant if the alarm call followed a seet call. Our work demonstrates contextual variation in response to alarm calls, providing rare evidence that responses to these warning signals can differ based on prior calls from conspecifics, which provides an example of birds integrating social and personal information in an antipredator context.

Predation is a major selective force on small vertebrates, with antipredator defences and information gathering critical for survival. Antipredator defences can involve an animal avoiding detection through the use of morphological or behavioural traits, or recognizing a predator and taking evasive action (Caro, 2005; Seyfarth et al., 1980). Recognizing and then gaining information about potential predators can increase the likelihood that responses are appropriate to the type and urgency of the threat (Caro, 2005). Animals may gain this information through personal vigilance or socially from the behaviour of other individuals of their own or other species (Dall et al., 2005). Personal vigilance can be visual, auditory or even olfactory (Beauchamp, 2015); visual forms of vigilance have been the most widely studied and often involve animals scanning the surroundings for signs of danger (Beauchamp, 2015; Treves, 2000). Vigilance costs both time and attention, so can limit engagement in other activities such as foraging, grooming or sleeping (Isbell & Young, 1993; Mooring & Hart, 1995; Pulliam et al., 1982). Personal vigilance can provide more reliable and detailed information about potential predators than social information, but using information from others, including from their alarm calls, can allow individuals to maximize time spent on other activities (Treves, 2000).

Alarm calls provide social information warning of danger, with some alarm calls being functionally referential and produced in response to a specific predator or class of predators, such as aerial versus terrestrial predators (Macedonia & Evans, 1993; Magrath et al., 2020; Suzuki, 2016; Townsend & Manser, 2013; Zuberbühler, 2009). Referential calls allow receivers to respond appropriately even in the absence of any other cues (Macedonia & Evans, 1993; Smith, 2017). For example, vervet monkeys, *Cercopithecus aethiops*, give different alarm calls to leopards, *Panthera pardus*, snakes and eagles, and receivers respond appropriately to these calls by running into trees for leopard alarm calls, looking down in response to snake calls and looking up in response to eagle alarm calls (Seyfarth et al., 1980). Some alarm calls convey additional information even when given to the same predator, such as its distance (Dutour et al., 2021; Leavesley & Magrath, 2005; Murphy et al., 2013) or behaviour (Cunningham & Magrath, 2017; Griesser, 2008), that can help receivers determine an appropriate response.

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https://doi.org/10.1016/j.anbehav.2025.123403

Responses to alarm calls depend on the perceived trade-off between starvation and predation. This balance can vary depending on contextual factors such as satiation, current visibility of the surroundings, conspicuousness of the receiver and proximity to human settlements (D'Ammando & Bro-Jørgensen, 2023; Kern et al., 2017; McLachlan et al., 2019; McQueen et al., 2017; Ratnayake et al., 2021). For example, dwarf mongooses, *Helogale parvula,* are more likely to respond to alarm calls when they have received supplementary food (Kern et al., 2017), and both topis, *Damaliscus lunatus*, and Thomson's gazelles, *Eudorcas thomsonii*, respond more strongly to conspecific alarm calls in human-impacted areas than in undisturbed areas (D'Ammando & Bro-Jørgensen, 2023). Information from other individuals may affect the perceived risk and so influence responses to subsequent alarm calls. For example, pied babblers, *Turdoides bicolor*, give graded surveillance calls when acting as a sentinel (raised guard) and increase the frequency and call rate when there has been a recent disturbance such as a heterospecific alarm call (Bell et al., 2009). A playback experiment showed that the babblers were more likely to flee to cover to alarm calls that followed surveillance calls given after a disturbance compared to those given when there was no disturbance (Bell et al., 2009). Despite the potential benefits of being primed to respond more quickly during riskier situations, very few studies have examined whether animals use prior social information in this way when responding to alarm calls.

Vigilance is a component of most responses to predators, regardless of type, but can itself vary according to the threat (Campos & Fedigan, 2014; Liley & Creel, 2008; Lima, 1987). Responding to alarm calls by scanning allows the receiver to obtain more personal information without expending excess energy or disrupting another important activity such as foraging to the same extent that fleeing would, but it can be costly to delay fleeing if the threat is urgent. Through vigilance, individuals can obtain information by looking at conspecifics and thus increasing the likelihood of responding in an appropriate way to an alarm call (Hollén & Manser, 2006; Seyfarth & Cheney, 1980). For example, infant vervet monkeys spend more time looking at their mothers when they hear an alarm call and are more likely to respond to alarm calls in a similar way to adults if their mothers are closer (Seyfarth & Cheney, 1980). Vigilance can also be used to look for the predator, and the type of vigilance prompted by an alarm call can reflect the type of threat (Dawson Pell et al., 2018; Suzuki, 2012), allowing individuals to better locate a potential threat. For instance, Japanese great tits, *Parus minor,* orient their head upwards when hearing mobbing calls given in response to jungle crows, *Corvus macrorhynchos*, and downwards when hearing calls given in response to Japanese rat snakes, *Elaphe climacophora* (Suzuki, 2012). Although variation in vigilance to different calls is common, prior information gained from vigilance may affect responses to subsequent alarm calls. However, we are unaware of any studies that have considered this possibility.

We first examined the function of an undescribed vocalization in superb fairy-wrens, *Malurus cyaneus*, with a focus on its role in prompting vigilance. Alarm communication in superb fairy-wrens has been studied in detail (Colombelli-Négrel et al., 2010; Colombelli-Négrel & Evans, 2017; Fallow et al., 2011; Magrath et al., 2007, 2015; Tegtman & Magrath, 2020), but there is an undescribed tonal call that we casually observed being given when predators were near. Fairy-wrens also gave these tonal calls when a gliding model of a collared sparrowhawk, *Accipiter cirrocephalus*, used to prompt aerial alarm calls, had landed, and in response to a perched model of a southern boobook owl, *Ninox novaeseelandiae,* used to prompt mobbing calls. These undescribed calls have a smooth beginning and ending, are high in frequency and narrowband with no frequency modulation (Fig. 1a). This is similar in structure to 'seet' calls described in many species of birds (Greig & Pruett-Jones, 2008; Klump & Shalter, 1984; Marler, 1955), so we also use this term, although make no assumptions about call meaning or homology. The seet calls of many different species of European and North American birds serve as an aerial or 'hawk' alarm call (Bradbury & Vehrencamp, 2011; Marler, 1957). However, superb fairy-wrens already have an aerial alarm call (Fig. 1b; Magrath et al., 2007), so their seet calls could play a different role. Our first field experiment (experiment 1) tested the response to seet calls compared to aerial alarm calls, and whether, as predicted, they prompt receiver vigilance, rather than being functionally equivalent to aerial alarm calls.

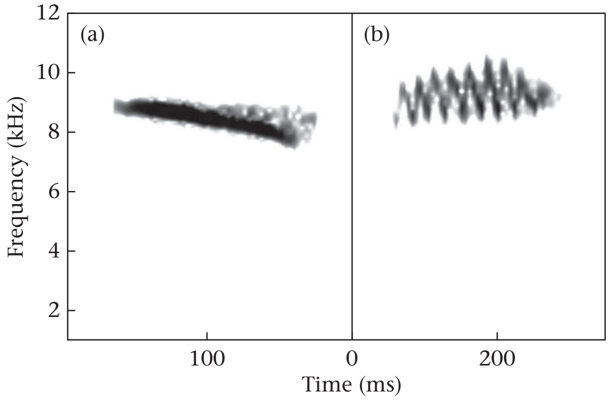

Figure 1. Spectrograms showing examples of single elements from a superb fairy-wren (a) seet call and (b) aerial alarm call. Spectrograms were created using Raven Pro 1.6 with a Hann window function with a 270 sample size, a temporal grid resolution of 2.81 ms with 50% overlap and a frequency grid resolution of 93.8 Hz.

We then used two further field experiments to investigate whether hearing seet calls could impact receiver assessment of risk and thus change the threshold for response to a subsequent aerial alarm call, testing two contrasting hypotheses. Experiment 2 tested the hypothesis that seet calls increase personal information, by assessing whether individuals reduce their response to subsequent alarm calls because they are already aware that no predator is dangerously close. Experiment 3 tested the opposite hypothesis that hearing seet calls increases perceived risk, by assessing whether seet calls 'prime' individuals to respond more strongly to any subsequent signs of danger. While responses to alarm calls are often investigated in isolation, our study allowed us to examine how superb fairy-wrens use prior vocal information when responding to current alarm calls.

METHODS

Study Site and Species

Superb fairy-wrens are small, cooperatively breeding passerines that occur in southeast Australia (Rowley & Russell, 1997). Their diet consists predominantly of insects, which they mostly forage for on the ground (Higgins et al., 2001). We collected data from an individually colour-banded population of fairy-wrens that are part of a long-term study at the Australian National Botanic Gardens in Canberra, Australia (Cockburn et al., 2016). Fairy-wrens at the study site can breed between August and March, when breeding pairs hold territories; some pairs are assisted by up to four subordinate male helpers (Cockburn et al., 2008, 2016). Superb fairy-wren males have been reported to act as sentinels near nests on some occasions (Yasukawa & Cockburn, 2009), but sentinels have only been described in that situation, and we did not study birds in that context.

Superb fairy-wrens give several types of call in the context of danger. They give aerial alarm calls that prompt conspecifics to flee immediately to cover (Fallow & Magrath, 2010). These aerial alarm calls are given in response to flying raptors and large avian omnivores which, at the study site, include collared sparrowhawks, grey butcherbirds, *Cracticus torquatus,* laughing kookaburras, *Dacelo novaeguinea,* and pied currawongs, *Strepera graculina* (Magrath et al., 2009). Signallers increase the number of elements in the call when the predator is closer, and receivers respond more strongly when there are more elements (Fallow & Magrath, 2010). Individuals produce mobbing calls in response to terrestrial threats and perched predatory birds, and these prompt individuals to call, approach and sometimes harass the predator (Colombelli-Négrel et al., 2010). Superb fairy-wrens even produce a whining call in response to cuckoo presence (Langmore et al., 2012) and give distress calls when in great danger (Camerlenghi et al., 2023).

Although seet calls have not been previously described in superb fairy-wrens, both splendid fairy-wrens, *Malurus splendens melanotus* (Greig & Pruett-Jones, 2008, 2009), and variegated fairy-wrens, *Malurus lamberti* (Greig et al., 2010), sometimes give seet calls in response to vocalizations of avian predators. Splendid fairy-wrens give seet calls in an alarm context. They also give 'high chatter' calls, which are similar in structure to superb fairy-wren aerial alarm calls, in response to aerial predators (Greig & Pruett-Jones, 2008). Playbacks of seet calls to splendid fairy-wrens caused individuals to look towards the loudspeaker or flee, but their responses were not compared to other alarm calls (Greig & Pruett-Jones, 2009), so it is unknown whether they have a distinct function.

Experimental Overview

We conducted three playback experiments, which we outline here; detailed field methods are given below.

Experiment 1 tested the hypothesis that seet calls function specifically to prompt vigilance by examining how fairy-wrens respond to seet calls alone compared to aerial alarm calls alone, as well as crimson rosella, *Platycercus elegans*, contact 'bell' calls as a control (Supplementary Fig. S1a). We used two-element calls for playback because these are naturally common for both call types, and fairy-wrens almost always flee to two-element aerial alarm calls (Fallow & Magrath, 2010). This facilitates testing the hypothesis that seet calls elicit vigilance rather than fleeing. Because acoustic analysis revealed that the inter-element intervals differed for seet calls and aerial alarm calls (Table 1), both call types were played at the typical interval for aerial alarm calls (50 ms) and at the typical interval for seet calls (500 ms); that is, there were two seet call treatments and two aerial alarm call treatments. In this way we could examine the response according to structural call type, while controlling for interval. Crimson rosella bell calls were chosen as a control as the parrots pose no threat, and these contact calls are commonly heard at the study site and usually ignored by fairy-wrens (Fallow et al., 2013). The five playback treatments were therefore as follows: (1) aerial alarm call with a 50 ms interval between the two elements; (2) aerial alarm call with a 500 ms interval; (3) seet call with a 50 ms interval; (4) seet call with a 500 ms interval; (5) crimson rosella bell contact call. Each of 24 focal adults from 17 groups received all five treatments (Supplementary Fig. S1a) over a minimum of 2 days.

Table 1
Properties of superb fairy-wren natural seet calls and aerial alarm calls

		N territories	Mean ± SD	Median	Range
Amplitude (dB)	***N* elements**				
Seet	101	10	53.4±6.2	54.6	35.2–66.6
Aerial	42	13	54.8±6.1	55.0	42.0–65.6
Interval (ms)	***N* intervals**				
Seet	57	13	577±217	542	113–1142
Aerial	23	6	120±125	47	25–392

Values show mean element amplitude at 10 m, and the duration of intervals between elements within calls. Raven Pro 1.5 was used for acoustic analysis.

Experiment 2 tested whether hearing a seet call would reduce an individual's response to a subsequent aerial alarm call. We presented two playback treatments to 30 focal adults in 18 groups (Supplementary Fig. S1b): (1) a two-element seet call followed by a two-element aerial alarm call and (2) a crimson rosella bell call followed by a two-element aerial alarm call (as a control). We presented fairy-wren calls at natural intervals: 500 ms between seet elements and 50 ms between aerial elements. We included a 5 s interval between the two different call types so that focal individuals would have time to look around and assess risk following the first call. As two-element aerial alarm calls almost always cause fairy-wrens to flee (Fallow & Magrath, 2010), this design allowed a sensitive test for a decline in response. By contrast, this experiment could not test for an increased flight response to aerial alarm calls, as predicted by the risk-priming hypothesis, because the flight response was already at a maximum.

In experiment 3, in contrast to experiment 2, we used less urgent, one-element aerial alarm calls, which only prompt fairy-wrens to flee around 50% of the time (Fallow & Magrath, 2010), to test whether hearing a seet call would increase perceived risk and 'prime' individuals to respond more strongly to a subsequent aerial alarm call. The two playback treatments, a two-element seet call followed by a one-element aerial alarm call, and a crimson rosella contact call followed by a one-element aerial alarm call (Supplementary Fig. S1c), were again presented to 30 focal adults in 18 groups. Intervals between seet elements and between call types were the same as in experiment 2.

Experimental Design

The matched design in each of the three experiments, with each focal individual identified by colour bands and receiving all treatments, controlled for any differences due to such factors as age, sex and status. Those factors were not included in the analyses as that was not our interest in this study and we did not have sufficient power. Some groups had fledglings during experiments 2 and 3, but we excluded groups with young that had fledged less than 3 weeks before, and the presence of fledglings was included in the analyses. Most males during the experimental period had blue breeding plumage; for consistency, we avoided collecting data from those few males with any brown plumage. We used up to three focal individuals from the same territory in a single experiment, and some birds were selected as focal individuals in two or three experiments. In total, 47 birds from 23 territories were used as focal individuals across the three experiments (Supplementary Table S1).

To prepare playback tracks, we recorded calls at the Australian National Botanic Gardens using a Marantz PMD661 recorder sampling wave files at 48 kHz and 24 bits. Aerial alarm calls were recorded in September and October 2017 using a Sennheiser ME66 directional microphone. We used our standard technique (Magrath et al., 2007) to prompt aerial alarm calls ($N = 16$), by throwing a gliding collared sparrowhawk model and recording calls given while the model was in flight. Fairy-wren seet calls were recorded in September and October 2017 and December 2019. We prompted seet calls either by using the gliding sparrowhawk model and recording the calls after the model had landed ($N = 7$ calls, recorded with the directional microphone), or by using a perched, taxidermic model of a Australian boobook, *Ninox boobook* ($N = 9$ calls, recorded using a Sennheiser ME62 omnidirectional microphone placed near the owl). We recorded crimson rosella bell calls ($N = 16$) ad libitum in December 2019 with a Sennheiser ME66 directional microphone.

We used Raven Pro 1.5 (Bioacoustics Research Program, 2014) to create playback tracks. For two-element calls, each aerial alarm call track and seet call track was composed by duplicating a single, unique element. Sixteen unique tracks of each treatment were used in each experiment, with the same calls used across experiments. For experiments 2 and 3, the seet and aerial alarm calls used on a single track were recorded from different individuals. Individual tracks were used a maximum of twice in a single experiment, and between experiments were always broadcast to focal individuals from different territories. We never broadcast calls to individuals from the same group where they were recorded, thus controlling for familiarity and meaning that the caller would not be present. We calibrated playbacks to have an amplitude of 55 dB SPL at 10 m, as acoustic analysis revealed that this amplitude was close to the median and within 1 SD of the mean amplitude for both seet and aerial alarm calls (Table 1), and is the amplitude used previously for playbacks of fairy-wren aerial alarm calls (Fallow et al., 2011; Fallow & Magrath, 2010). The elements themselves were too short to be measured accurately with a sound level meter, so we calibrated calls by comparing the amplitude of broadcast calls to that of pure tones of known amplitude that had been measured using a Brüel & Kjær 2240 sound level meter, then adjusted the calls until they were at the correct amplitude when broadcast (Fallow & Magrath, 2010).

Our experimental design controlled for treatment order. For experiment 1, each playback treatment occupied each order position six times, thus controlling for order and carryover effects. This was achieved by initially choosing the four fairy-wren treatments with random order, but rejecting a random order that led to a treatment occupying an order position more than six times. The control call was presented to equal numbers of focal individuals either before or after all fairy-wren playbacks on ‘day 1’ or ‘day 2’, although sometimes experiments took place over more than 2 days. In these cases, we still used the planned ordering. The two playback treatments in experiments 2 and 3 were presented in a counterbalanced order.

Field Methods

We conducted all three experiments in and around the Australian National Botanic Gardens between August 2020 and February 2021. Treatments were broadcast from a Peerless 810921 tweeter loudspeaker (mean ± SD frequency response: 2–11 ± 2 kHz) connected to a custom amplifier and Roland R-05 Studio WAVE/MP3 recorder. We mounted the loudspeaker on the observer's waist using our standard mobile playback protocol (Magrath et al., 2007). We filmed playbacks using a Panasonic HC V-800 video camera attached to a Wizmount CU2 Pack so that the camera was mounted over the observer's shoulder. Videos were filmed at 50 frames/s at 1920 × 1080 pixels. We observed focal individuals for at least 5 min before any playback, and carried out playbacks only if there had been at least 5 min without any naturally occurring aerial alarm calls, seet calls or mobbing bouts. Playbacks were started when the focal individual was about 10 m away from the observer and foraging 0.5–5 m from cover, either foraging alone or in the presence of conspecifics from the same group. Playbacks to the same focal individual on the same day were spaced a minimum of 15 min apart, and a maximum of two fairy-wren playbacks and one control playback were presented to a focal individual on a single day. Playbacks to different focal individuals from the same territory were always on different days.

In experiments 2 and 3, trials were abandoned if a focal individual fled to cover or moved greater than 15 m away from the observer following broadcast of the seet or rosella call and were repeated after at least 1 h had passed. This was done to ensure that the focal individual was close enough to hear the second call, and so all calls were presented within 15 m of the focal individual. We measured the distance of the focal individual from the loudspeaker when each call was played using a Bushnell 1300 ARC rangefinder.

Behavioural Responses

We initially scored behavioural responses to playbacks in the field as flee to cover, flee to perch, flee other (focal individual fled to another position on the ground), vigilance (i.e. scan the surroundings) or none. This system graded the urgency of response. Birds that fled to cover showed an immediate response based on social information without seeking further personal information. Birds that fled to a perch would be able to gather more personal information, potentially from a safer place or a position that allowed for a better view of their surroundings (Radford et al., 2009). Birds that scanned were able to gather more personal information from their original position. Finally, birds that did not respond had no increase in visual information gathering. Scoring these responses in the field was designed to back up video scoring when necessary (see below).

We scored all videos using Adobe Premier Pro (Adobe Systems Incorporated, San Jose, CA, U.S.A.; version 14.0). To enable blind scoring, the frame when the playback started was noted and then the video names were changed by a second individual. Moreover, video watching was done with the sound turned off, so the scorer knew when the playback occurred, but not which treatment. Where possible, we recorded the immediate response to the playback, time to respond to each call, time to flee (if applicable) and vigilance in the 5 s following the playback from the videos. Focal individuals were scored as vigilant when they were stationary and looking around (Magrath et al., 2015). The immediate response to playbacks was scored as in the field, except that we divided vigilance into scan (focal individual looked around for longer than 1 s) and glance (focal individual looked around for 0.5–1 s), as used in previous studies (Potvin et al., 2018). For 16 out of 120 playbacks (trials) in experiment 1 and three out of 60 playbacks in experiment 2, it was not clear from the videos whether a focal individual fled to cover or to a perch. In these 19 cases, the response scored in the field was used. When scans and glances, as defined in the video analyses, were combined into ‘vigilance’, the field and blind-scored responses were the same in 96.3% of playbacks (213/221) across the three experiments, so using field scores for 19 cases is unlikely to change any results. The proportion of time scanning in the 5 s following playback was included only if at least 2.5 s could be scored.

Statistical Analyses

We carried out all analyses in R version 3.6.2 (R Core Team, 2019); transformations were performed if necessary to meet the assumptions of parametric testing. Cumulative link mixed models (CLMMs) were performed using the package ‘ordinal’ (Christensen, 2015) and linear mixed models (LMMs) were performed using the package ‘lmerTest’ (Kuznetsova et al., 2017).

For experiment 1, we initially coded the immediate response to playbacks as any response or no response. Exact McNemar tests from the exact 2 × 2 package (Fay, 2010) were used to compare the response to the rosella control with responses to the four fairy-wren treatments. Focal individuals never fled in response to rosella playbacks and were much less likely to respond to the rosella playbacks than any of the fairy-wren playbacks (see Results), so the rosella treatment was dropped from further analyses. We then used a CLMM to examine the full suite of responses to fairy-wren playbacks: flee to cover, flee to perch, scan, glance or none. The call type (aerial or seet) and interval length (50 or 500) were included in the model as fixed effects and focal individual identity nested in territory identity was included as a random effect. We used LMMs with the same fixed and random effects to examine the time to respond (square-root-transformed) and the time to flee (log-transformed) to playbacks. All three models were initially run with the interaction between call type and interval length included, but likelihood ratio tests revealed no significant difference between the models with and without the interaction (see Results) and so the interaction was dropped from further analysis.

For experiments 2 and 3, we analysed the response to the aerial alarm calls using CLMMs. Responses were coded as flee to cover, flee to perch, flee other, scan, glance or none. LMMs were used to analyse the proportion of time spent vigilant in the 5 s following the seet or rosella call and the time taken to respond to the aerial alarm calls (experiment 2: square-root-transformed; experiment 3: log-transformed). For experiment 2, we also used an LMM to analyse the time taken to flee in response to aerial alarm calls (log-transformed); this was not done for experiment 3 because individuals only fled in response to aerial alarm calls in 9 of the 60 playbacks. For the remaining 51 playbacks from experiment 3 where focal individuals did not flee, LMMs were used to examine the proportion of time spent vigilant in the 5 s following the aerial alarm call. Rather than seet calls changing the response to aerial calls, the differences between treatments could be because individuals were already vigilant in response to seet calls, so increased vigilance could be due to the seet calls rather than to the aerial alarm call. To address this, and test whether the combination of calls caused the increase in vigilance, we also examined the proportion of time spent vigilant in the 5 s following the aerial alarm call in the subset of ‘nonflees’ where focal individuals had returned to nonvigilance before the aerial alarm call (N = 23 rosella aerial playbacks, 14 seet aerial playbacks). Treatment and fledgling presence were included as fixed effects and focal individual identity nested in territory identity was included as a random effect for all models used for experiments 2 and 3.

Ethical Note

The study was approved by the Australian National University Ethics Committee (protocol A2015/67). Alarm and seet calls were prompted by model predators that posed no danger to birds. Experiments used a matched design, where individuals acted as their own controls, reducing required sample sizes. Individuals were only exposed to two short (<10 s) alarm call playbacks on a given day and always returned to normal behaviour following the playbacks.

RESULTS

Experiment 1: Response to Seet Calls versus Aerial Alarm Calls

Fairy-wrens responded to all aerial alarm call and seet call playbacks, typically flying to a perch or cover, but showed no or weak responses to the rosella control (Fig. 2; no response versus any response: McNemar exact test: $P < 0.001$ for all pairwise comparisons of rosella calls with other treatments). The rosella control therefore had little or no effect on behaviour, as anticipated from previous work on this species (Fallow & Magrath, 2010), and so was dropped from subsequent analyses.

Fairy-wrens had a reduced categorical response and took longer to respond to seet calls compared to aerial alarm calls, but the interval between call elements had little effect. Fairy-wrens had a weaker immediate categorical response to seet calls than to aerial alarm calls (CLMM: $\beta = -2.29$, SE = 0.49, $P < 0.001$; Fig. 2, Supplementary Table S2) and tended to respond less strongly to calls with a 500 ms interval between them compared to those separated by 50 ms, but this was not significant ($\beta = -0.79$, SE = 0.43, $P = 0.07$). Similarly, focal individuals took longer to respond (mean ± SD = 132.92 ± 85.60 ms, range 20–380, $N = 48$; LMM: $t_{70.91} = 2.93$, $P = 0.005$) and flee (236.00 ± 196.41 ms, range 40–980, $N = 30$; $t_{60.75} = 3.44$, $P = 0.001$; Supplementary Table S3) to seet calls compared to aerial alarm calls (time to respond: mean ± SD = 91.25 ± 42.86 ms, range 20–280, $N = 48$; time to flee: 149.77 ± 152.15, 60–680, $N = 43$), but did not differ significantly in their response time to calls with a 50 ms or 500 ms interval (response: $t_{70.91} = 0.99$, $P = 0.327$; flee: $t_{52.45} = 0.67$, $P = 0.508$).

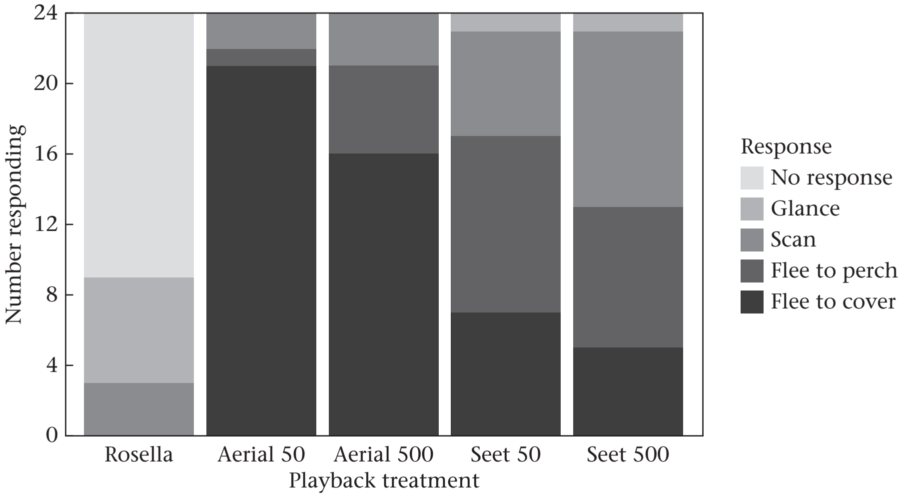

Figure 2. The immediate categorical response to playbacks in experiment 1. Each fairy-wren aerial alarm call and seet call consisted of two elements that were presented with an interval of 50 or 500 ms, as indicated. N = 24 individuals receiving all treatments including rosella control. Statistical analysis is shown in Supplementary Table S2.

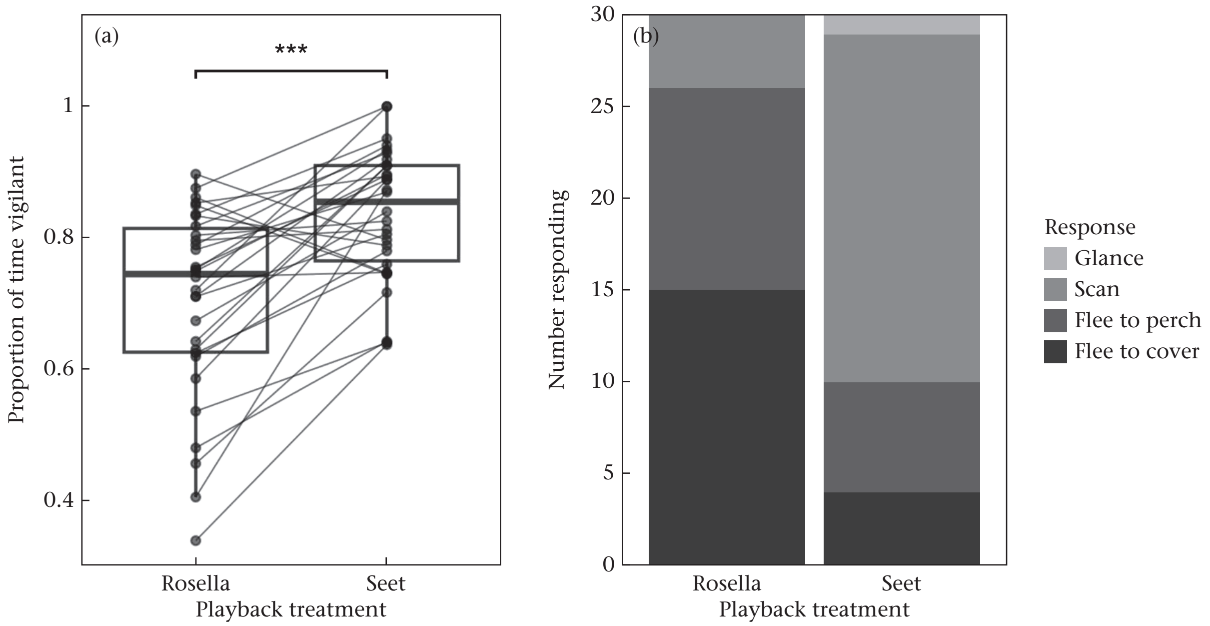

Figure 3. The effect of seet calls on the focal bird's (a) vigilance and (b) subsequent response to two-element aerial alarm calls in experiment 2. (a) Box plots of the proportion of time vigilant between playback of the first call and the aerial alarm call, showing the median, quartiles and whiskers to points within 1.5 times the interquartile range. Lines connect raw data points from the same focal individual. ****P* < 0.001. (b) Number of individuals showing immediate categorical response to the aerial alarm call according to the call type played previously. Rosella contact calls were the controls. *N* = 30 focal individuals received playbacks. Statistical analysis is shown in Supplementary Tables S5–S6.

Including the interaction between call type and interval did not significantly improve model fit when looking at categorical response ($\chi^2_1 = 0.585$, $P = 0.444$), time to respond ($\chi^2_1 = 1.243$, $P = 0.265$) or time to flee ($\chi^2_1 = 0.061$, $P = 0.805$; Supplementary Table S4).

Experiment 2: Do Seet Calls Decrease the Response to Subsequent Urgent Aerial Alarm Calls?

Fairy-wrens spent a greater proportion of time vigilant following seet calls than following rosella controls, and responded less strongly to two-element aerial alarm calls that followed seet calls than those that followed rosella controls. Focal individuals spent more time vigilant following seet calls than following rosella calls (LMM: $t_{29.00} = 5.42$, $P < 0.001$; Fig. 3a, Supplementary Table S5). Individuals subsequently had a weaker immediate categorical response to two-element aerial alarm calls that followed seet calls than to those that followed rosella calls (CLMM: $\beta = -2.46$, SE = 0.67, $P < 0.001$; Fig. 3b, Supplementary Table S6). Despite the strong effect on categorical responses, fairy-wrens did not differ significantly in the time to respond or flee to aerial alarm calls that followed seet calls and the rosella control (LMM: respond: $t_{28.30} = 0.71$, $P = 0.48$; flee: $t_{33.00} = 0.49$, $P = 0.63$; Supplementary Table S5).

Experiment 3: Do Seet Calls Increase the Response to Subsequent Less Urgent Aerial Alarm Calls?

Unlike experiment 2, most individuals in experiment 3 responded in the same way to one-element calls that followed rosella calls and seet calls. As in experiment 2, focal individuals were more vigilant following seet call playbacks than following rosella call playbacks (LMM: $t_{40.58} = 3.30$, $P = 0.002$; Fig. 4a, Supplementary Table S7). Far fewer individuals fled to the one-element aerial alarm calls in experiment 3 (9/60) compared to the two-element alarm calls in experiment 2 (36/60), as expected. As found in experiment 2, fewer focal individuals fled in response to one-element aerial alarm calls that followed seet calls than to one-element aerial alarm calls that followed rosella control calls (2/30 versus 7/30), but the difference was not statistically significant (CLMM: $\beta = -0.06$, SE = 0.53, $P = 0.912$; Fig. 4b, Supplementary Table S8), perhaps because of the small number of individuals fleeing. Consistent with experiment 2, there was no significant difference in the time it took individuals to respond to alarm calls following the two treatments (LMM: $t_{28.67} = 0.53$, $P = 0.603$; Supplementary Table S7).

When focal individuals did not flee, they spent a higher proportion of time vigilant in the 5 s following the aerial alarm call when it was preceded by a seet call rather than a rosella call (LMM: $t_{36.52} = 4.07$, $P < 0.001$; Fig. 4c, Supplementary Table S7), after controlling for a lower proportion of time vigilant when there were fledglings present ($t_{14.95} = -4.20$, $P < 0.001$). Focal individuals were still more vigilant following aerial alarm calls that were preceded by seet calls even when the focal individual had returned to foraging prior to the aerial alarm call playback ($t_{20.23} = 2.45$, $P = 0.024$; Fig. 4d, Supplementary Table S7), after controlling for less time vigilant when fledglings were present ($t_{13.72} = -3.48$, $P = 0.004$).

DISCUSSION

Seet calls appear to play a unique role in fairy-wren communication as well as affecting responses to subsequent alarm calls. Playback of seet calls prompted superb fairy-wrens to increase vigilance and reduced their subsequent response to aerial alarm calls. Seet calls therefore act as ‘vigilance alarm calls’, which prompt individuals to scan for danger, and so differ from superb fairy-wren aerial alarm calls that prompt immediate flight to cover (Fallow & Magrath, 2010). Seet calls also reduced rather than increased the categorical response to subsequent aerial alarm calls, implying that the heightened vigilance increased personal information and so reduced reliance on social information from

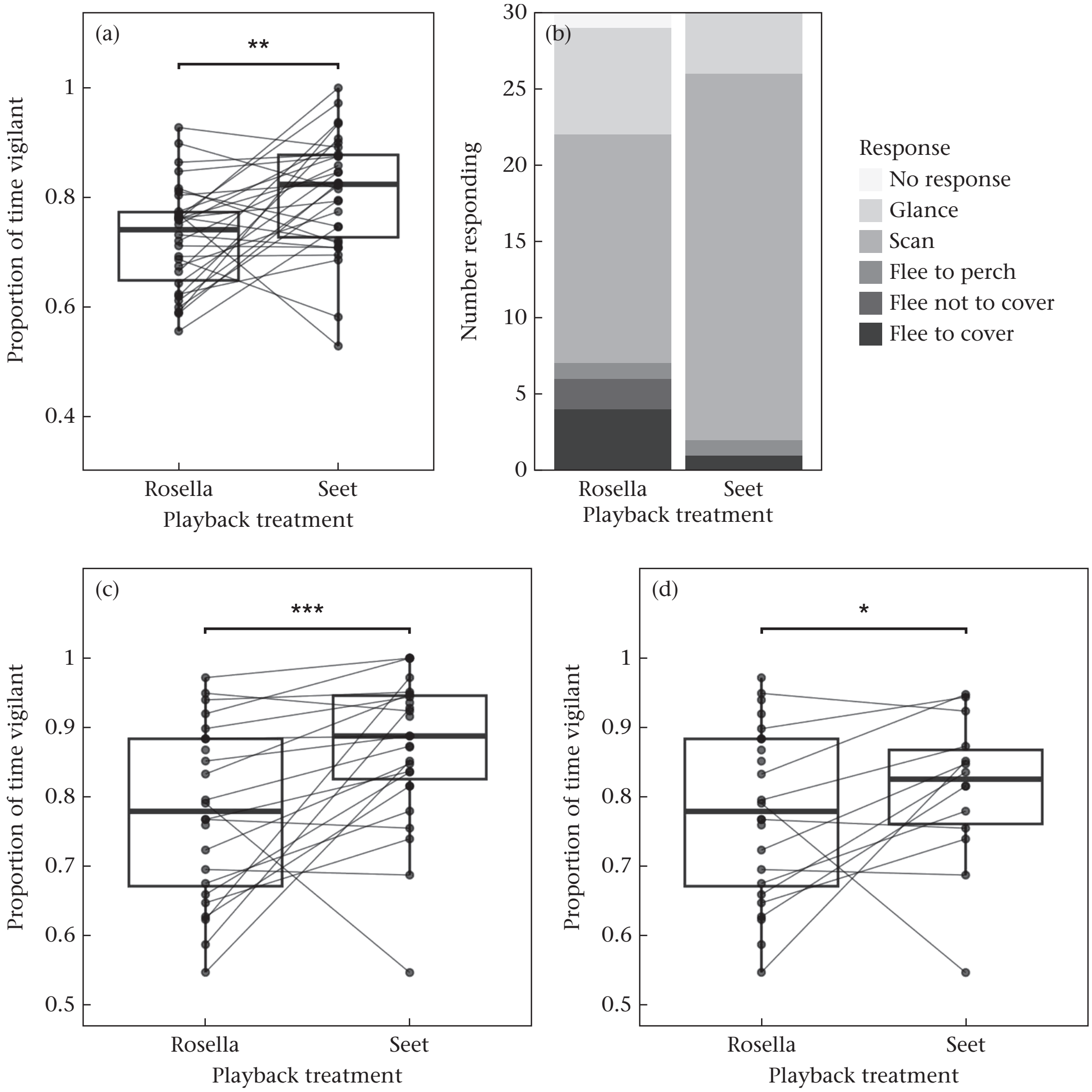

Figure 4. The effect of seet calls on vigilance and subsequent response to one-element aerial alarm calls during experiment 3. (a) Box plots of the proportion of time vigilant between playback of the first call and the aerial alarm call. (b) Number of individuals showing immediate categorical response to the aerial alarm call according to the call type played previously. For playbacks where the focal individual did not flee to the aerial alarm call, box plots show the proportion of time spent vigilant in the 5 s following the aerial alarm call in (c) all playbacks and (d) playbacks where the focal individual had returned to nonvigilant behaviour prior to the aerial alarm call. Boxes in (a), (c) and (d) show the median and quartiles, and whiskers show points within 1.5 times the interquartile range. Lines connect raw data points from the same focal individual where data are matched. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. Rosella contact calls were the controls. (a, b) $N = 30$ focal individuals received playbacks; (c) $N = 23$ rosella, 27 seet playbacks; (d) $N = 23$ rosella, 14 seet playbacks. Statistical analysis is shown in Supplementary Tables S7–S8.

alarm calls. This illustrates that the birds use a combination of personal and social information when determining an antipredator response and that they vary their response to alarm calls based on social information from prior calls.

Fairy-wrens fled to aerial alarm calls, as found in previous experiments, but primarily increased vigilance in response to seet calls. Focal individuals almost always fled immediately to cover after playbacks of two-element aerial alarm calls. This is consistent with previous results looking at responses to multi-element calls in fairy-wrens (Fallow & Magrath, 2010; Magrath et al., 2007, 2009). By contrast, focal individuals typically scanned in place or flew to an exposed perch, presumably to gain a better view of their surroundings, in response to two-element seet calls. These differences in responses show that seet calls are functionally discrete. Increasing vigilance could be the most appropriate response in some antipredator contexts because fleeing to cover costs both energy and time (Ydenberg & Dill, 1986). It can also allow the individual to gain additional personal information about the threat, which might be more difficult to do if it flees to cover (Beauchamp, 2015). For example, when pied babbler sentinels are in a higher position, foragers are less vigilant likely due to the sentinel having a greater chance of spotting any predators (Radford et al., 2009). Our study provides the first examination of seet calls in superb fairy-wrens and the first comparison of seet calls with aerial alarm calls for any fairy-wren species. Further work is needed to understand better the context of production of these calls, which would allow assessment of whether they are referential to a specific predator type or behaviour.

Superb fairy-wrens were less likely to flee when a two-element aerial alarm call was preceded by a seet call rather than by a rosella control call in experiment 2, which differs from work on babblers where individuals were primed to flee to alarm calls by surveillance calls given after a disturbance (Bell et al., 2009). Fairy-wrens were likely prioritizing personal information gained through scanning after the seet call over social information gained from the aerial alarm call. Personal information is more reliable and detailed than social information (Treves, 2000), so when individuals already have that information available to them, it could be beneficial to prioritize that information rather than waste energy fleeing when they have not seen a threat. For example, New Holland honeyeaters, *Phylidonyris novaehollandiae*, prioritize personal information when determining whether to flee to alarm calls, with birds foraging with a restricted view of their environments being more likely to flee than birds perched in the open (McLachlan et al., 2019).

Superb fairy-wrens did not respond more strongly or more quickly to one-element aerial alarm calls that were preceded by seet calls versus rosella calls in experiment 3. That is, there was no evidence that seet calls prime an increased responsiveness to more ambiguous alarm calls given in a less urgent situation. Contrary to the possibility of priming, fewer birds fled to one-element aerial alarm calls that were preceded by seet calls than to those preceded by control calls, a similar pattern to what was found with two-element aerial calls, but few birds fled to any one-element call and the difference was not statistically significant. There was also no difference in the time to respond to alarm calls that followed seet calls in either experiment 2 or 3, implying that seet calls did not prime birds' responses to alarm calls. While some studies have found that cues indicating predator presence increased responsiveness to alarm calls (Bell et al., 2009), others have found no difference (Kern et al., 2017). For example, dwarf mongooses were no more likely to flee in response to an alarm call after interacting with predator urine versus a control (Kern et al., 2017). However, mongooses were more vigilant following predator urine presentation than following a control cue, and the authors suggest that they might be prioritizing personal over social information when responding to the alarm calls, as is also suggested by our study.

Despite the prioritization of personal information when determining an immediate response, hearing a seet call did seem to alter the fairy-wrens' assessment of risk. In experiment 3, if individuals did not flee, they spent a greater proportion of time vigilant in the 5 s following a one-element aerial call if it followed a seet call instead of a rosella control. Using social information in this way might be adaptive for fairy-wrens as hearing two different calls indicating danger may mean it is more likely that a threat is present even if they have not spotted it for themselves and therefore it is probably not close. Spending the additional time vigilant could allow them to obtain more personal information about the current level of danger without expending extra energy by fleeing, as they already know from previous vigilance that a predator is not close. Similarly, Australian magpies, *Gymnorhina tibicen*, adjust their response to alarm calls when given additional social information, by responding more strongly to two callers than to one caller of the same heterospecific species (Igic et al., 2019).

Our study reveals a discreet vigilance call in superb fairy-wrens, in addition to their aerial and mobbing calls. Many bird species are described as having two main alarm calls: an aerial alarm call for flying predators and a terrestrial alarm call or mobbing call for terrestrial or perched predators (Cunningham & Magrath, 2017; Evans et al., 1993; Grieves et al., 2014), with vigilance usually being just one of a suite of behaviours that can be prompted by these terrestrial or mobbing calls (Dubreuil et al., 2023; Salis et al., 2021). However, communication about predators can be more complex, with some species using a range of alarm calls (Blumstein & Armitage, 1997; Collier et al., 2017; Seyfarth et al., 1980). For example, dwarf mongooses have up to 11 different alarm call types given to nine different stimulus categories, although the function of each of these calls has not been tested (Collier et al., 2017). Having a specific vigilance call could be important as there are limits to the information conveyed through a referential alarm call. There are currently no studies showing that acoustic signals can indicate specific directions (Liao et al., 2024). For example, a call could indicate that a predator is flying or on the ground, but it may not be able to indicate that it is on the left or right. Vigilance could allow individuals to spot the predator for themselves or look to the calling individual to obtain additional information, which may be the best option when the predator does not pose an immediate danger. Seeking extra information can allow individuals to optimize their response if danger is not immediate (Dubreuil et al., 2023; Lima & Dill, 1990). In many cases, individuals might be expected to integrate social and personal information when deciding on a response, as the fairy-wrens did in this study. Further work could seek to examine whether specific vigilance calls exist in other species and aim to understand better the range of alarm calls that can be used in antipredator contexts.

Our study also provides an example of vocal sequences affecting how alarm calls are perceived. Fairy-wrens were less likely to flee in response to two-element aerial alarm calls that were proceeded by a seet call, likely due to the prioritization of personal over social information. Animals live in complex worlds and integrating different types of information when determining an antipredator response could increase an individual's chance of survival while reducing the costs associated with antipredator responses. Our study adds to a growing body of work showing that context can change individuals' responses to alarm calls (D'Ammando & Bro-Jørgensen, 2023; Kern et al., 2017; McQueen et al., 2017) and is one of few studies that have illustrated that responses to alarm calls can also change based on prior calls from conspecifics (see also Bell et al., 2009). Many species use different types of vocalizations, including alarm calls, and future work could investigate how vocal sequences of information can impact responses to alarm calls in other species.

Author Contributions

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

Data Availability

Data are available as Supplementary Material.

Declaration of Interest

None.

Acknowledgments

We thank A. Cockburn and H. Osmond for allowing work on the fairy-wren population and the Australian National Botanic Gardens for permission to conduct research. The research was funded by an Australian Research Council grant to R.D.M., A.N.R. and E. Fernández-Juricic (DP150102632).

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123403.

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