Many vertebrates eavesdrop on alarm calls of other species, which is a remarkable ability, given geographical variation in community composition and call diversity within and among species. We used micro-geographical variation in community composition to test whether individuals recognize heterospecific alarm calls by: (i) responding to acoustic features shared among alarm calls; (ii) having innate responses to particular heterospecific calls; or (iii) learning specific alarm calls. We found that superb fairy-wrens (Malurus cyaneus) fled to cover to playback of noisy miner (Manorina melanocephala) aerial predator alarm calls only in locations where miners were present, suggesting that learning rather than acoustic structure determines response. Sites with and without miners were well within the dispersal distance of fairy-wrens, and philopatric males and dispersing females showed the same pattern, so that local genetic adaptation is extremely unlikely. Furthermore, where miners were present, fairy-wrens responded appropriately to different miner calls, implying eavesdropping on their signalling system rather than fleeing from miners themselves. Learned eavesdropping on alarm calls enables individuals to harvest ecologically relevant information from heterospecifics on an astonishingly fine spatial scale. Such phenotypic plasticity is valuable in a changing world, where individuals can be exposed to new species.

**Keywords:** interspecific communication; eavesdropping; alarm calls; acoustic communication; learning

1. **INTRODUCTION**

Heterospecific interactions—such as competition, mutualism, parasitism or encounters between predators and prey—are important in affecting individual fitness, adaptation and coevolution [1]. Such interactions can be mediated by signals, such as aposematic prey signalling their toxicity to predators and flowers signalling to pollinators, but incidental information flow among species is also pervasive, although often overlooked [2,3]. Individuals can gain fitness-enhancing information about resources or threats by observing the behaviour or location of heterospecifics [4], including eavesdropping on signals evolved to communicate with conspecifics [5,6]. Such eavesdropping is a challenge, however, when there is spatial or temporal variation in community composition, which may select for local genetic adaptation or phenotypic plasticity [7].

A great diversity of vertebrates eavesdrop on and respond appropriately to the alarm calls of other species [8,9], which is a valuable yet astonishing feat given the complexity of any individual’s acoustic world. The community of species varies geographically and temporally, and in any one location there can be many species, each giving a variety of vocalizations, including alarm calls. Despite these challenges, playback experiments have shown that mammals, birds and lizards can gain information about danger by eavesdropping on other species’ alarm calls [10–20]. Some are even known to respond appropriately to heterospecific alarm variants for the type of predator or degree of danger [11,13,21,22]. Eavesdropping on other species can therefore provide detailed information about predators, and so enhance fitness [2,3,19]. But how do individuals recognize heterospecific alarm calls and cope with variation in community composition?

There are three main possibilities, not necessarily mutually exclusive, for heterospecific alarm call recognition. One possibility is that individuals use general rules of alarm call recognition based on acoustic structure. Animals might respond to calls that are similar in detail to conspecific alarm calls [23–25], or recognize general ‘alarm-like’ acoustic properties, regardless of their own alarm call structure [26,27]. Acoustic structure plausibly accounts for widespread eavesdropping because alarm calls given to immediate threats, such as hawks in flight, tend to be of high frequency and narrow frequency range, while mobbing calls, given to predators not posing an immediate threat, tend to be abrupt calls of broad frequency range [23,28,29]. However, alarm call variation among taxa is unlikely to fully explain interspecific eavesdropping. A second possibility is that populations evolve to recognize the alarm calls of particular heterospecifics, comparable to innate recognition of specific predators [33]. Evidence from cross-fostered birds suggests that innate recognition is usually (but not always) confined to conspecific calls [34–36]. A third possibility is that

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individuals learn to recognize heterospecific alarm calls, which would have the advantage of allowing individuals to cope with rapid temporal or small-scale geographical variation in community composition [6,37,38]. Fish can learn to recognize heterospecific chemical cues of danger [39], but comparable learning of acoustic alarms has not been shown for terrestrial species. Overall, local genetic adaptation or learning appear necessary to account fully for the diversity of eavesdropping, and phenotypic plasticity through learning could be a key mechanism allowing populations to track environmental change through time and space [40].

Studies of geographical variation in response to other species’ alarm calls can test hypotheses about the mechanism of heterospecific recognition and spatial scale of behavioural diversity [38]. In the most comprehensive study of mammals, bonnet macaques (Macaca radiata) fled to safety after playback of the alarm calls of only the locally common of two langur species at any one site, showing that their response is not determined by acoustic structure and suggesting that they learn to recognize alarm calls [31]. Similarly, in the only comparable study of birds, superb fairy-wrens fled to cover after playback of alarm calls of white-browed scrubwrens (Sericornis frontalis), where both species occur, but did not flee outside the range of scrubwrens [32]. However, in both these cases, sites were separated by hundreds of kilometres, so that local genetic adaptation rather than learning might explain the geographical patterns. Clearly, we need studies on a small spatial scale, where learning can result in adaptive variation in behaviour on a fine scale [38].

We studied micro-geographical variation in the response of superb fairy-wrens to the aerial alarm calls of noisy miners (Manorina melanocephala). Miners commonly feed in the canopy and could provide early warning of danger to species like fairy-wrens that feed on the ground. Miners form temporally and spatially stable colonies, so we compared the behaviour of fairy-wrens at locations with and without miners on an extremely small spatial scale. We also tested whether fairy-wrens fled in response to miner calls in general, perhaps because they are wary of miners themselves, rather than eavesdropping on miner alarm calls specifically.

2. METHODS

(a) Study species

Superb fairy-wrens (Family: Maluridae) are small (9–10 g), sedentary, cooperatively breeding, insectivorous passerines that feed primarily on the ground [41]. Groups consist of a single breeding female and dominant breeding male, and up to five male helpers, with the sexes differing in plumage and bill colour. Groups defend breeding territories, although during the non-breeding season adjacent groups can form temporary flocks. Fairy-wrens produce high-pitched, multi-element aerial alarm calls in response to predatory birds in flight (figure 1) [19,43], and birds almost always immediately flee to cover after these calls or to playbacks consisting of two or more elements [19,22,32,43]. Furthermore, fairy-wrens also flee to cover after playback of aerial alarm calls of the locally common white-browed scrubwrens or New Holland honeyeaters, Phylidonyris novaehollandiae [19,22,32,43].

Fairy-wrens have extreme sex-biased dispersal, with philopatric males and dispersing females, which means that the sexes could differ in opportunities for learning. In Canberra, where we studied them, 87 per cent of males remain as helpers on their natal territory and 64 per cent eventually gain a mate there [44]. The remaining males disperse up to three territory widths away (240 m [44]). By contrast, all females leave the natal territory, either late in the breeding season in which they were raised or just before the following breeding season, and those located moved a mean of 1.8 territory widths (940 m), and up to 36 territory widths (2.9 km) [44].

Noisy miners are aggressive, medium-sized (approx. 70 g), sedentary honeyeaters (Family: Meliphagidae) that live in breeding colonies that can persist for many years and occupy up to 40 ha [41]. Miners are aggressive to many species, ranging from hawks to small insectivores, probably reflecting both predator defence and interspecific competition for food [45]. However, there are few records of aggression to ground-feeding species like fairy-wrens [45]. Miner abundance and distribution have increased dramatically in Canberra in the last 10 years [46]. Their preferred habitat is woodland, including both trees (often eucalypts) and open areas [47–49].

Noisy miners are conspicuously vocal, and their repertoire includes two acoustically distinct multi-element alarm calls and loud begging calls [41] (figure 1). Aerial alarm calls are given to raptors in flight [50] and mobbing (‘chur’) alarm calls are given to potential predators that are on the ground or perched [51].

(b) Study sites

We studied fairy-wren responses to noisy miner calls at six sites in Canberra, Australia, four of which also contained noisy miner colonies (figure 2). All sites included a mix of open areas, shrubs, and eucalypt and other trees. Before carrying out playback experiments below, we surveyed all areas for miners, and during experiments we noted whether we saw or heard miners within 80 m of each group of fairy-wrens. Miners were found during the course of playbacks in every case in ‘miner present’ sites (n = 46 groups) and
never at the 'miner absent' sites ($n = 45$ groups). Furthermore, miner presence or absence is stable temporally. From January 2000 to October 2009, Canberra Ornithologists Group surveys detected no miners in either ‘miner absent’ site (0/209 surveys in Botanic Garden; 0/29 in Yarramundi), but detected miners in all ‘miner present’ sites that were surveyed (182/233 University; 20/32 Peninsula; 7/13 Weston Park; Blue Gum Point not surveyed; Canberra Ornithologists Group 2011, unpublished data). Furthermore, miner distribution did not change from November 2009 to April–May 2011, when we again surveyed all sites.

The study sites include both aerial and terrestrial predators. Raptors occur throughout the area [52], including collared sparrowhawks, *Accipiter cirrhocephalus*, which include both focal species in their diet [53], and which prompt both to give aerial alarm calls (R. D. Magrath, personal observation). Dogs occur at all sites except the Botanic Garden, and foxes, cats and snakes are widespread, and all provoke mobbing calls from fairy-wrens and miners [41,51,54].

(c) General protocols for playback experiments
We carried out three playback experiments in November and December 2009, following methods used in previous experiments on fairy-wrens (electronic supplementary material) [19,22,25,32,43]. Sounds were broadcast to adult fairy-wrens from a distance of about 10 m (range 9–11.5 m). Playbacks were carried out when the focal (closest) bird was feeding on the ground at least 1 m from cover, and we categorized its response as: 0, none; 1, scan for a second or more; or 2, flee to cover. We also noted group identity and the sex of the focal bird. We identified groups by colour bands in the Botanic Garden [55], and elsewhere from spatial location. All sounds broadcast were recorded in Canberra using methods given in the electronic supplementary material.

(d) Experiment 1: do fairy-wrens flee miner alarms only when they are familiar?
Experiment 1 tested the hypothesis that fairy-wrens flee to miner aerial alarm calls only in locations where miners are present, and therefore where fairy-wrens have the opportunity to learn to recognize their calls. Fleeing is the almost invariant response to conspecific aerial alarm calls (above), and is therefore the appropriate measure of aerial alarm call recognition. By contrast, fleeing to these calls regardless of miner presence implies an innate response. The experiment was replicated sequentially in different areas, to ensure that any micro-geographical pattern in one area was not due to unique characteristics of a site rather than the presence or absence of miners.

Replicate experiments matched sites where miners were present with nearby sites where miners were absent (figure 2). The area 1 replicate contrasted the response of fairy-wrens on the University campus (miners present) with the Botanic Garden (miners absent), and the closest playbacks at the two sites were separated by only 600 m, which was also the closest place where miners were seen. There was no barrier to dispersal. The area 2 replicate compared three lakeshore sites where miners were present with a lakeshore site (Yarramundi) where miners were absent. The shortest dispersal distance by land between the ‘miner absent’ and ‘miner present’ playback sites along the lakeshore was 1.2 km, and miners occurred as close as 850 m to ‘miner absent’ playback sites.

In each replicate area, we broadcast five- to six-element noisy miner aerial alarm calls, and two control calls in
approximately balanced order to 15 groups at sites where miners were present and 15 groups where miners were absent. A complete set of three playbacks was completed on a group before moving to another, and we alternated between sites with and without miners. Playbacks to a group were separated by a minimum of 5 min (electronic supplementary material). Control calls were four-element aerial alarm calls of fairy-wrens, as a positive control, and the piping contact call of crimson rosellas, *Platycercus elegans*, which are harmless parrots, as a neutral control (figure 1). In each replicate, all 15 groups with miners received unique exemplars of all playbacks, to avoid pseudoreplication, and the same set of 15 playbacks was used at sites without miners, to avoid any playback differences affecting geographical comparisons. Playbacks were carried out only when miners were not currently nearby, so that fairy-wrens could not take cues from miners themselves.

Playback amplitudes were at natural levels. Miner aerial alarms were broadcast at a mean element amplitude of 66 dB at 10 m. Given the natural mean amplitude of 73 dB at 10 m (electronic supplementary material), from the focal bird’s perspective, the amplitude is comparable to the natural context of a miner calling from a nearby tree, about 23 m away. Fairy-wren aerial alarms were broadcast at 54 dB at 10 m and so the amplitude is comparable to a bird calling about 7 m from the focal bird (mean 56.5 dB at 5 m [43]), such as a bird within a foraging group. Rosella contact calls were broadcast at the same amplitude as miner aerial alarms, to control for any effect of amplitude on response.

(e) Experiment 2: do fairy-wrens flee simply because miners are nearby?
In experiment 2, we tested whether fairy-wrens fled to miner aerial alarm calls because they recognized them as alarm calls, or because the calls were a cue that a miner was near. Fairy-wrens might flee simply because miners are aggressive towards other species. Methods were the same as for experiment 1, except that we restricted playback to sites where miners were present and used a set of three different miner calls, all broadcast at an amplitude of 66 dB at 10 m: (i) five- to six-element aerial alarm calls; (ii) four-element mobbing (‘chur’) calls; and (iii) 6–12 element begging calls of young given when an adult arrives with food [56] (figure 1). If fairy-wrens recognize the meaning of these miner signals, they should be more likely to flee to aerial alarm calls signalling immediate danger, than to mobbing calls, signalling potential danger, and should not flee to begging calls, which do not signal anything about predators. By contrast, if fairy-wrens flee simply because miners are near, they should flee to all three playbacks. In this experiment, we also quantified scanning, as increased vigilance might be an appropriate response to mobbing calls.

(f) Experiment 3: do fairy-wrens respond differently to miner calls regardless of experience?
Experiment 3 tested if any differences in fairy-wren response to different miner calls revealed in experiment 2 could be due to their different acoustic properties and not solely because fairy-wrens had learnt to recognize their meaning. We therefore played back the same set of miner calls to fairy-wrens at sites where miners were absent. If the differential response of fairy-wrens to these calls does not depend on experience, then fairy-wrens should respond in a similar way to those in experiment 2.

(g) Statistical analyses
All experiments entailed presenting three different playbacks to each group of fairy-wrens, so where appropriate we used analyses taking into account group identity. In experiment 1, however, birds had almost invariant responses to both control playbacks, and the key prediction was about variation among groups in response to miner aerial alarm calls, so we used generalized linear models (GLM; family binomial with logit link) and Fisher’s exact tests for independent comparisons, or McNemar tests with exact binomial probabilities for specific matched comparisons [57,58]. For analysis of experiments 2 and 3, we used generalized linear mixed models (GLMM; family binomial with logit link), with group as the random term [59]. Model selection entailed fitting full models followed by simplification based on dropping individual terms and assessing change in deviance, which follows a χ²-distribution [59]. All analyses were carried out in R 2.7.0 [60], in which we used the glmmML and lme4 packages for GLMM analyses [61,62].

3. RESULTS

(a) Experiment 1: micro-geographical variation in response to miner aerial alarm calls
Fairy-wrens behaved as expected by fleeing to cover after conspecific aerial alarm calls and never to rosella contact calls, regardless of whether the sites had miners (figure 3). The almost invariant response of fairy-wrens to these control sounds allowed us to restrict analyses to miner aerial alarms.

Fairy-wrens usually fled to cover after playback of noisy miner aerial alarm calls at sites where miners were present, but rarely did so at sites where miners were absent (figure 3; for each replicate area, Fisher’s exact test *p* < 0.001). Analysis including both replicate areas revealed a strong effect of miner presence on response (GLM, miner presence: χ² = 40.8, *p* < 0.001), but no difference between replicate areas (area: χ² = 1.5, *p* = 0.2); interaction of area and miner presence: χ² = 0.75, *p* = 0.4). Overall, 83 per cent of fairy-wrens fled to miner alarm calls in sites where miners were present, but only 7 per cent fled at sites where they were absent.

At sites where miners were present, fairy-wrens responded similarly to miner and conspecific aerial alarms (McNemar tests: area 1, *p* = 0.13; area 2, *p* = 1.0; areas combined, *p* = 0.06). Overall, 25/30 birds fled to both conspecific and miner alarms, and 5/30 fled to conspecific alarms but not miner alarms. By contrast, fairy-wrens were much less likely to flee to miner than conspecific alarms at sites where miners were absent (McNemar tests: *p* < 0.001 for each area and areas combined). Only 25/30 fled to both species’ alarms, whereas 27/30 birds fled to conspecific but not miner alarms, and one fled to neither species’s alarm.

Despite the obligate natal dispersal of female fairy-wrens, compared with philopatry of male fairy-wrens, females did not show a weaker micro-geographical pattern of response to miner alarm calls (GLM, replicate areas 1 and 2 combined: χ² = 3.2, *p* = 0.07). The trend, in fact, was the opposite: females fled to none of 11 playbacks at sites where miners were absent and 12 of 13 (92%) at sites where miners were present, while males fled to two of 19 (11%) at sites where miners
Figure 3. The probability of superb fairy-wrens fleeing to cover in response to playbacks of noisy miner and superb fairy-wren aerial alarm calls, and crimson rosella contact calls in experiment 1 (a) area 1 and (b) area 2; n = 15 for each bar. Black bars, miner alarm; white bars, wren alarm; grey bars, rosella control.

were absent, and 13 of 17 (76%) at sites where miners were present.

(b) Experiments 2 and 3 response to different noisy miner calls

In experiment 2, which was conducted at sites where miners were present, fairy-wrens were most likely to flee after playback of miner aerial alarm calls compared with mobbing alarm or begging calls (figure 4a; GLMM: flee to cover, $\chi^2 = 17.2$, $p < 0.001$). Treating playback type as an ordered term, there was a strong linear decline in the probability of fleeing from aerial to mobbing to begging calls (linear term: $z = 2.55$, $p = 0.01$), but no nonlinear pattern among playbacks (quadratic term, flee: $z = 0.50$, $p = 0.6$). This ordered pattern is that predicted if fairy-wrens recognize the magnitude of threat signalled by the different miner calls, rather than merely fleeing from miners themselves. The pattern was similar for the probability of any response, including both fleeing and scanning (figure 4a; difference among playbacks, $\chi^2 = 13.9$, $p < 0.001$; linear decline, $z = 2.22$, $p = 0.03$; quadratic term, $z = 0.94$, $p = 0.3$).

Experiment 3, which was conducted at sites where miners were absent, revealed a lower probability of fleeing to cover overall and only a weak effect of miner playback type on fleeing (figure 4b; GLMM: flee, $\chi^2 = 7.25$, $p = 0.03$), with no linear decline from aerial to mobbing to begging (linear term in ordered model: $z = 0.68$, $p = 0.5$). Fairy-wrens fled to only one of 15 (7%) miner aerial alarm calls, which was identical to the response in experiment 1 (2/30). Instead, they fled most frequently to miner mobbing calls rather than aerial calls, so there was a weak nonlinear pattern (quadratic term: flee, $z = 2.11$, $p = 0.04$). The pattern was similar but weaker still for any response (figure 4b; difference among playbacks, $\chi^2 = 6.1$, $p = 0.05$; linear term, $z = 1.82$, $p = 0.07$, with a trend for an increase; quadratic term, $z = 1.54$, $p = 0.12$). There was a significantly different pattern of response to the three playbacks between experiments 2 and 3 (GLMM, unordered interaction of playback type and experiment: flee, $\chi^2 = 12.8$, $p = 0.002$; any response, $\chi^2 = 14.4$, $p < 0.001$).

Consistent with the results of experiment 1, the focal bird's sex did not affect its probability of fleeing to playback (GLMM: sex alone and all interactions involving sex, experiment and playback type, $p \geq 0.2$). Specifically regarding aerial alarms, when miners were present (experiment 2), six of seven females and seven of nine males fled to cover after playback, whereas when miners were absent (experiment 3) only one of five females and none of 10 males fled to playback (GLM: interaction of sex and experiment: $\chi^2 = 1.3$, $p = 0.3$).

4. DISCUSSION

Fairy-wrens fled to cover after playback of miner aerial alarm calls only at sites where miners were locally present, strongly suggesting that individuals learn to recognize the alarm calls of other species. This result was replicated in two areas, strengthening the conclusion that micro-geographical variation in anti-predator behaviour reflects learning opportunities. Furthermore, at sites where miners were present, fairy-wrens responded as if they recognized the meaning of different types of miner calls, which provides one of few examples of vertebrates
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