Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls

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Many vertebrates use alarm calls to warn others of the presence of danger, and these calls can contain information about the type of threat, the degree of danger, or both, allowing listeners to choose an appropriate response. Alarm calls are often broadly classified into 'mobbing' alarm calls that attract others to harass terrestrial or stationary predators posing little immediate threat or 'flee' alarm calls that signal immediate danger, such as from a flying hawk, which incite others to freeze or flee to cover (Klump & Shalter 1984; Bradbury & Vehrencamp 1998). Alarm calls can also contain more specific information. For example, vervet monkeys, Cercopithecus aethiops, have different calls for snakes, leopards, and eagles (Seyfarth et al. 1980), whereas meerkat, Suricata suricatta, alarm calls communicate information about both the type and the degree of danger (Manser 2001; Manser et al. 2001, 2002). Similarly, among birds, black-capped chickadee, Poecile atricapilla, mobbing calls communicate information on the size of a perched raptor, and therefore the degree of danger posed (Templeton et al. 2005), and white-browed scrubwren, Sericornis frontalis, flee alarm calls communicate the distance of a predator in flight and therefore the immediacy of threats and the responses necessary (Griesser 2008). As well as heeding conspecific alarm calls, individuals can benefit from eavesdropping on alarms given by other species that are vulnerable to the same threats (Shriner 1998). Recognition of heterospecific alarm calls has been shown among birds (Hurd 1996; Goodale & Kotagama 2008), between mammals (Shriner 1998), and in one reptile responding to a bird (Vitousek et al. 2007). Eavesdropping on other species can provide complementary information to conspecific alarm calls so that the total amount of information available in an interspecific eavesdropping network can be greater than in a group of conspecifics (Goodale & Kotagama 2005, 2008). This is because different species may frequent various parts of the habitat and may have different abilities to discriminate between different threats (Goodale & Kotagama 2005; Magrath et al. 2009a).

Some birds eavesdrop on the alarm calls of other species, but little is known about the specific information obtained. Fleeing in response to nonurgent alarms, such as those given for distant predators, wastes time and energy and so individuals could benefit from decoding information about urgency. White-browed scrubwrens, Sericornis frontalis, and superb fairy-wrens, Malurus cyaneus, flee in response to each other's aerial alarm calls, and scrubwrens communicate urgency by including more elements in their alarms when a threat is closer. We carried out a model-presentation experiment to test whether fairy-wren alarm calls also encode risk-based information, followed by a playback experiment to compare how fairy-wrens and scrubwrens respond to graded information in both their own calls and those of the other species. Fairy-wrens encoded urgency in a way similar to that of scrubwrens, by including more elements when the model predator was closer and by increasing the maximum frequency of elements. Each species was more likely to flee in response to both conspecific and heterospecific alarm calls that included more elements. Fairy-wrens were more likely than scrubwrens to flee regardless of call urgency, particularly when responding to their own species' calls, perhaps because they are more vulnerable to predators or because they use a different scale for decoding risk-based information. Fairy-wrens also spent more time in cover after fleeing multielement conspecific calls with a greater number of elements. Our study reveals that urgency information in the form of graded alarm call variants can be transferred through mutual eavesdropping between bird species.

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various species can therefore allow eavesdropping individuals to become less vigilant than if they were in a group of conspecifics (Dolby & Grubb 2000) or alone (Lea et al. 2008).

Some animals not only recognize which heterospecific calls are alarm calls, but can distinguish between various types of alarm calls and so respond appropriately to different threats. For example, Diana and Campbell’s monkeys (Cercopithecus diana and C. campbelli) respond appropriately to each other’s leopard and eagle alarm calls (Zuberbühler 2000). Similarly, yellow-casqued hornbills, Ceratogymna elata, can distinguish between the leopard and eagle alarm calls of Diana monkeys and respond only to eagle alarm calls, presumably because only eagles pose a threat to the hornbills (Rainey et al. 2004).

In addition to recognizing that different alarm calls of other species indicate different types of threats, individuals could benefit from understanding variation within a single heterospecific call type encoding information on the magnitude of danger and therefore the urgency of response required. However, there has been only one example of this behaviour: red-breasted nuthatches, Sitta canadensis, respond appropriately to playback of the mobbing calls of black-capped chickadees representing different degrees of danger (Templet & Greene 2007). The nuthatches show graded responses to these calls that are similar to the graded responses shown by the chickadees to their own calls (Templet & Greene 2007). By contrast, banded mongooses, Mungos mungo, respond to the alarm calls of crowned plovers, Vanellus coronatus, with anti-predator behaviour but seem unable to interpret the risk-based information encoded (Müller & Manser 2008). We are unaware of any study showing mutual understanding of urgency encoded by variation in a single type of alarm call. Furthermore, it remains to be shown whether individuals can interpret risk-based information encoded in other species’ flee alarms. An understanding of urgency in heterospecific flee alarms may be critical because urgent variants can signal immediate threats, yet there may be less opportunity to learn to interpret detailed information in these calls because they are given to transient danger (Magrath et al. 2009b).

This study investigated whether two bird species could interpret risk-based information in variants of each others’ aerial alarms, a type of flee alarm call given for predators in flight. White-browed scrubwrens encode urgency information in their aerial alarm calls by repeating the same type of call element, producing graded calls with more elements in response to closer threats, to which conspecifics respond appropriately (Leavesley & Magrath 2005). Superb fairy-wrens, Malurus cyaneus, are ecologically similar to scrubwrens and both species respond to playback of the other’s multielement aerial alarms (Magrath et al. 2007). However, it was unknown whether fairy-wrens communicated urgency in their aerial alarms or if either species could interpret graded risk-based information encoded by the other. We presented a model predator at various distances to determine whether superb fairy-wrens encode urgency in aerial alarm calls and then used a playback experiment to test how fairy-wrens and scrubwrens respond to risk-based information in conspecific and heterospecific calls.

METHODS

Study Area and Species

We studied superb fairy-wrens and white-browed scrubwrens in the Australian National Botanic Gardens (35°16′S, 149°6′E) in Canberra, Australia, where both species have been the subject of long-term study (Magrath 2001; Cockburn et al. 2008a). The Botanic Gardens comprises a variety of natural and managed habitats consisting of native vegetation ranging from arid plants to rainforest, as well as garden beds and open lawn. Fairy-wrens and scrubwrens are cooperatively breeding passerines that forage primarily on the ground and are of similar size, weighing about 9–12 and 13–14 g, respectively (Higgins et al. 2001; Higgins & Peter 2002). Fairy-wren groups in the Gardens have a mean size of 2.9 (Higgins et al. 2001), with each group consisting of a breeding female, a dominant male, and up to four subordinate males that are often unrelated to the female (Cockburn et al. 2008b). Fairy-wren groups are territorial during the breeding season but will combine with birds from other territories to form larger groups during the rest of the year. Scrubwren groups have a mean size of 2.7 and consist of a breeding pair that may be accompanied by up to four subordinate males that defend their territory year round (Magrath & Whittingham 1997). Fairy-wren and scrubwren territories overlap, and in the nonbreeding season these species can gather together in temporary mixed-species flocks (Magrath et al. 2009b). In our study site, all fairy-wrens and around 70% of scrubwrens wore coloured leg bands, allowing us to identify groups by the inclusion of at least one banded individual.

Fairy-wrens and scrubwrens are vulnerable to the same predators and produce aerial alarm calls in response to sighting predators in flight (Magrath et al. 2009a). Within the Botanic Gardens these include pied currawongs, Strepera graculina; grey butcherbirds, Cracticus torquatus; laughing kookaburras, Dacelo novaeguineae; and collared sparrowhawks, Accipiter cirrocephalus (Magrath et al. 2009a). Fairy-wrens and scrubwrens both produce high-frequency aerial alarm calls that are rapidly frequency modulated about a constant carrier frequency, but scrubwrens calls are lower in frequency, have a slightly larger frequency range (peak frequency: 7.1 kHz; range: 6–11 kHz; compared with peak frequency: 9.1 kHz; range: 8–11 kHz in fairy-wrens), and consist of a double rather than a single band (Magrath et al. 2007; Fig. 1). Scrubwrens encode urgency in aerial alarms by producing calls with a greater number of elements and a higher minimum frequency for threats that are closer and typically produce only a single element when sighting a currawong flying by at a distance of 10–20 m away, but a median of four elements when one flies within 10 m (Leavesley & Magrath 2005). Scrubwrens respond

Figure 1. Spectrograms of aerial alarm call elements produced by (a) superb fairy-wrens and (b) white-browed scrubwrens. Spectrograms were produced in Raven Pro 1.2 using settings as described under Methods for Acoustic Analyses.
appropriately to playback by being more likely to flee when a call contains more elements, with four-element calls usually prompting immediate flight to cover (Leavesley & Magrath 2005).

Recording Fairy-wren Calls

To determine whether fairy-wrens encode urgency in their aerial alarm calls, we provoked alarm calls using a gliding life-sized model of the pied currawong (see Magrath et al. 2007 for model specifications). The model was thrown by hand so that it glided 2–3 m above the ground, parallel to the birds at either a short distance (3–8 m) or a long distance (12–19 m). We used a currawong as our model predator and these distance categories to be similar to a study of urgency encoding in scrubwrens, in which live currawongs were used to prompt aerial alarm calls (Leavesley & Magrath 2005).

We recorded fairy-wren aerial alarm calls on dry days with low wind over a period of 7 weeks during May and June 2008. While one person launched the model, another recorded calls from a distance of 2–6 m from the group using a Sennheiser ME66 directional microphone and a Marantz PMD670 digital recorder, sampling wave files at 44.1 kHz and 16 bits. Prior to each throw we observed the behaviour of the group for 5 min and waited for most group members to be on the ground and out of cover before throwing. We did not attempt throws if any member of the group gave alarm calls during observation or if any potentially threatening species were seen nearby. At this time of year territorial groups of fairy-wrens combine to form larger wintering groups, so we prevented resampling the same birds by recording groups in different areas. We made 43 recordings across 40 groups, with three groups recorded once at each distance category.

Acoustic Analyses

Recordings were downloaded to a computer and then cropped using Cool Edit Pro version 1.2a software (Syntrillium Software, Phoenix, AZ, U.S.A.) to isolate alarm calls, leaving several seconds of background noise prior to the model’s release and after its landing. We used Raven Pro 1.3 software (Charif et al. 2008) to generate spectrograms using a Blackman window function, a temporal grid resolution of 0.295 ms with 94.9% overlap, and a frequency grid resolution of 86.1 Hz.

From the spectrograms we measured both the acoustic properties and the number of elements in calls prompted by the model at short and long distances. In cases in which more than one bird called when a model was presented we analysed only the first call per recording to ensure samples were independent, and this left us with 19 calls prompted by the model at short distances and 24 calls prompted at long distances. We measured the number of elements per call and considered elements to be part of the same call when they were of similar frequency and signal strength and separated by intervals of less than 200 ms. To analyse the acoustic properties of calls we chose only those 14 at each distance category with a high signal-to-noise ratio, minimal reverberation, and no overlapping background sounds and then randomly selected one element from each of these calls. We then measured element duration (ms), lowest frequency (kHz), highest frequency (kHz), peak frequency (the frequency at greatest amplitude, kHz), frequency range (kHz), and rate of frequency modulation (Hz).

Playback Experiment

The playback experiment aimed to test how fairy-wrens and scrubwrens respond to graded conspecific and heterospecific aerial alarm calls. Both scrubwrens (Leavesley & Magrath 2005) and fairy-wrens (Results) encode a higher degree of danger through a greater number of elements in a call, so we constructed alarm calls that varied in the number of elements. Each set of playbacks presented to a group included nine treatments: one-, two-, three-, and four-element fairy-wren calls; one-, two-, three-, and four-element scrubwren calls; and a control sound. Multielement calls were constructed by repeating a single unique element at an interval of 45 ms, a natural timing for both species. We used a unique element to compose calls for each species in each set of playbacks to avoid pseudoreplication. Alarm playbacks were composed from high-quality aerial alarms provoked by gliding models of a pied currawong or collared sparrowhawk (model specifications in Magrath et al. 2007). As far as we can tell, alarm calls prompted by models are acoustically indistinguishable from those prompted by real predators (Magrath et al. 2007), the structure of alarm call elements does not differ between calls prompted by these types of model (Magrath et al. 2007), and birds respond to playback of calls prompted by models in the same way as to playback of calls prompted by natural predators (Leavesley & Magrath 2005; Magrath et al. 2007). During the playback experiments, calls were matched across playback species within a set according to the type of model that prompted the call to ensure that no undiscovered differences between model types affected the results. As a control we used unique examples of the piping or ‘bell’ call (Higgins 1999; Magrath et al. 2007) of crimson rosellas, Platycercus elegans, parrots that are common at the study site and do not threaten either focal species. We filtered out all sound below 4 kHz in fairy-wren and scrubwren calls and all sound below 1.5 kHz in the rosella calls.

Once composed, playback tracks were downloaded as uncompressed wave files and broadcast from a Roland Edirol R-09 HR solid-state playback and recording device via an amplifier and a Response Dome Tweeter speaker. The playback equipment was mounted around the observer’s waist. Playbacks were broadcast at an element amplitude of around 61 dB at 5 m, which is above but within 1 SD of the mean amplitude of alarm elements of both scrubwrens and fairy-wrens (Magrath et al. 2007). This amplitude was chosen as it is easily audible but well within the natural range for each species.

We conducted playbacks to 15 groups of fairy-wrens and 15 groups of scrubwrens over a period of 7 weeks during September and October 2008, completing each group before any chicks fledged. Each group received playbacks of calls from birds living at least three territories away from their own to prevent any effect of familiarity. Playbacks within a set were conducted in a random order with no more than one call per species presented on a single day so that all playbacks to a group took at least 4 days to complete. Prior to each playback, the group was observed for 5 min to ensure that the birds were not agitated and that no threatening species or individuals of the other focal species were present (<10 m). If no territorial disputes or alarm calling occurred during this period, the playback was presented to a randomly chosen focal bird when it was foraging on the ground at least 50 cm from cover. We presented playbacks from a distance of 6–10 m (mean ± SD = 8.17 ± 0.98) from the focal bird and recorded one of the following immediate responses (from least to most urgent): 0, no response; 1, scan (raise head and look around); 2, scan, then flee; 3, flee to cover or away from the area. For comparison with a study of urgency in scrubwren calls (Leavesley & Magrath 2005), these were sorted into binomial responses: 0, nonflee (0, 1, 2), and 1, flee (3). If the focal bird fled to cover, the duration of time spent inside cover (s) was recorded if possible and capped at 20 s. Playbacks presented to birds from the same group on the same day were carried out a minimum of 10 min apart.

The methods we used to provoke alarm calls and present playbacks were designed to minimize stress caused to the birds.
Currawongs are abundant in the Botanic Gardens and we collected alarm calls from different groups spread over a large area. Both scrubwrens and fairy-wrens call frequently and birds typically emerged from cover within 20 s of fleeing in response to playbacks. This study was carried out with approval from the Australian National University Ethics Committee and under permits from the Australian National Botanic Gardens, Environment ACT, and the Australian Bird and Bat Banding Scheme.

**Statistical Analyses**

To compare the number of elements contained in fairy-wren calls elicited by the model predator at short and long distances we conducted a chi-square test using the Monte Carlo simulation with an estimate of significance based on a 99% confidence level and 10,000 samples. We used a stepwise discriminant analysis to determine whether elements contained in calls made for a threat at various distances could be classified by the following acoustic measures: element duration (ms), lowest frequency (kHz), highest frequency (kHz), peak frequency (kHz), frequency range (kHz), and rate of frequency modulation (Hz; Tabachnick & Fidell 2007). Analyses were performed using SPSS (version 17.0; SPSS, Inc., Chicago, IL, U.S.A.) with significance levels set at $P < 0.05$.

To analyse the binary responses observed during the playback experiment we used a generalized linear mixed model (GLMM) with binomial error. We started with a full model with playback set as the random term and the number of elements, playback species, response species, and interaction terms as fixed effects and then sequentially removed the highest order nonsignificant interactions followed by nonsignificant terms until only significant effects remained. We used playback set as the random term as it accounts for group variation within each species as well as acoustic variation between the natural elements used to generate calls for each set ($\sigma^2 = 0.925$). Wald statistics were used to test for fixed effects. We fitted linear, quadratic, and cubic models to test which best explained the data.

We analysed the time spent in cover by fairy-wren groups that fled after playback of all multielement conspecific alarm calls ($N = 12$) using an analysis of variance (ANOVA) with bird group as a block. Too few scrubwrens spent time in cover to allow comparable analyses on that species. The GLMM and ANOVA were performed using GenStat Software version 11 (VSN International Ltd.) with significance levels set at $P < 0.05$.

**RESULTS**

**Encoding Urgency in Fairy-wren Calls**

Fairy-wrens included more elements in their aerial alarm calls when the model predator was closer ($\chi^2 = 14.54, P = 0.002$; Table 1), while also increasing the maximum frequency of the call elements. They included a mean of 2.6 ± 1.3 elements when the model was close and 1.4 ± 0.9 when it was far (mean ± SD; $N = 19$ close and 24 far). When the model was presented at short distances 79% of calls contained more than one element, whereas at long distances only 25% did so ($\chi^2 = 12.35, P = 0.001$). Elements had a greater maximum frequency when the model was closer (short distance: mean ± SD = 10.7 ± 0.3 kHz, $N = 14$; long distance: 10.3 ± 0.3 kHz, $N = 14$; $F_{1,23} = 12.25, P = 0.002$) and maximum frequency correctly classified 67.9% of calls. No other acoustic property encoded proximity ($P > 0.05$).

**Responses to Conspecific and Heterospecific Calls**

Both fairy-wrens and scrubwrens showed graded responses to their own calls and to the calls of the other species, with the probability of fleeing increasing with an increasing number of elements ($\chi^2 = 22.59, P < 0.001$, Fig. 2). There was an increase in the probability of each species fleeing in response to both conspecific and heterospecific calls with a greater number of elements, although the response of fairy-wrens to conspecific calls was more categorical; they fled to eight of 15 single-element conspecific calls, but to all 45 calls containing two or more elements. Nonlinear models did not provide a significantly better fit than the linear model (coefficient of slope from linear model: 2.30, $P = 0.925$).

![Figure 2](image_url)  
**Figure 2.** The response of fairy-wrens and scrubwrens to playback of fairy-wren and scrubwren aerial alarm calls containing one to four elements. Responses to playback were recorded from a randomly selected focal bird from each group. Observed proportions fleeing are shown as columns and were calculated using all 240 responses to the eight alarm treatments presented to 15 groups of each species ($N = 15$ for each column). Probabilities of fleeing are represented by lines and were predicted from the GLMM. Playbacks of the rosella control call did not elicit any responses and so are not represented here.

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**Table 1** The number of elements in fairy-wren aerial alarm calls prompted by a model predator at various distances.

<table>
<thead>
<tr>
<th>No. of elements</th>
<th>Close</th>
<th>Far</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4</td>
<td>18</td>
<td>22</td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>3</td>
<td>6</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>5</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>19</td>
<td>24</td>
<td>43</td>
</tr>
</tbody>
</table>

Count of alarm calls containing various numbers of elements. Calls were prompted by a model currawong presented at two distance categories, simulating situations of high (close: 3–8 m) and low (far: 12–19 m) danger.
Fairy-wrens were more likely to flee in response to playbacks than were scrubwrens (χ² = 19.33, P < 0.001), and each species was more likely to flee in response to conspecific calls than to heterospecific calls (interaction of focal species and playback species: χ² = 14.55, P < 0.001). The increased response to conspecific calls was primarily due to fairy-wrens, whereas scrubwrens had only a slightly higher probability of fleeing in response to their own calls (Table 2).

For both species, the lower probability of fleeing in response to calls with fewer elements, or to those of heterospecifics, was not simply due to the birds not hearing calls with fewer elements. Individuals of both species responded at least with vigilance to all but one alarm playback, the exception being one scrubwren that showed no response to a two-element fairy-wren call. By contrast, the control sound of a rosella call broadcast at the same amplitude never elicited even a vigilance response from either species.

Because all fairy-wrens fled to cover after all multielement fairy-wren calls, it was unclear whether more elements signalled greater danger or whether extra elements were redundant and did not provide additional information about danger. However, fairy-wrens spent more time in cover when there were more elements in the call, showing that even within multielement calls, a greater number of elements increased the strength of response (coefficient of slope: 3.33, P = 0.006; Fig. 3). Some birds spent more than 20 s in cover, and if actual values had been recorded this would probably have increased the slope.

**DISCUSSION**

Superb fairy-wrens and white-browed scrubwrens shared a mutual understanding of the graded risk-based information in their alarm calls. Fairy-wrens encoded urgency in their aerial alarm calls in a way similar to that of scrubwrens, primarily by producing calls containing more elements for closer threats. Each species responded appropriately to both conspecific and heterospecific calls by being more likely to flee for cover as the number of elements increased. However, fairy-wrens were generally more responsive to alarm calls than scrubwrens, especially to their own calls. Fairy-wrens also increased the amount of time spent in cover after fleeing conspecific calls containing more elements. Our results show the mutual transfer of graded information between species through variation within a single type of call, revealing that the understanding of heterospecific flee alarms can extend beyond recognition.

Fairy-wrens encoded greater urgency in their aerial alarm calls by producing calls that contained more elements and with a greater maximum frequency. They usually produced only single-element calls when the model predator was greater than 10 m away but produced at least two elements when the model was closer.

Table 2

<table>
<thead>
<tr>
<th>Response species</th>
<th>Playback species</th>
<th>Probability of fleeing</th>
<th>LSI (P &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fairy-wren</td>
<td>Fairy-wren</td>
<td>0.933</td>
<td>0.876 0.965</td>
</tr>
<tr>
<td>Fairy-wren</td>
<td>Scrubwren</td>
<td>0.592</td>
<td>0.490 0.691</td>
</tr>
<tr>
<td>Scrubwren</td>
<td>Fairy-wren</td>
<td>0.330</td>
<td>0.238 0.437</td>
</tr>
<tr>
<td>Scrubwren</td>
<td>Scrubwren</td>
<td>0.447</td>
<td>0.344 0.554</td>
</tr>
</tbody>
</table>

Estimated mean values of response strength were predicted by a GLMM on a logit scale and then back-transformed to obtain the predicted probability of birds fleeing in each situation. LSI, least significant interval.

Element structure was similar at both distances, except that the maximum frequency was slightly greater when the model was closer. The playback experiment showed that fairy-wrens responded appropriately to the degree of danger represented, by being more likely to flee to cover after playback of multielement calls than after single-element calls. This encoding scheme was similar to that used by scrubwrens, which also typically give single-element aerial alarm calls when a currawong flies by at a distance greater than 10 m, but multielement calls when it is closer (Leavesley & Magrath 2005). Furthermore, all measures of scrubwren element frequency tended to increase when a currawong was closer, significantly so for minimum frequency.

Birds and mammals use various methods for encoding urgency in their alarm calls (Klump & Curio 1983; Ficken 1990; Manser 2001; Müller & Manser 2008), but signalling greater danger with a greater number of elements per call or unit time seems to be common (Haftorn 1993; Leavesley & Magrath 2005; Templeton et al. 2005; Müller & Manser 2008). For example, black-capped chickadees signal a greater threat by including more ‘D notes’ in their mobbing calls (Templeton et al. 2005). Encoding greater danger with a greater rather than fewer number of elements is likely to be adaptive because signalling greater urgency with fewer elements could lead to false alarms, as multielement calls must start with a single element (Leavesley & Magrath 2005). Furthermore, it is important that more urgent signals are heard by conspecifics, and repetition is likely to increase the possibility of detection, leading to selection for increased repetition as a general method of encoding greater urgency (Bradbury & Vehrencamp 1998). For similar reasons, greater urgency may also be signalled by a greater rate of element delivery, particularly for flee alarms that can require immediate action. We suspect, therefore, that birds often signal greater danger with a greater number of elements in their alarm calls, which might select for an innate predisposition to flee in response to alarm calls that contain repetition and include more elements.

Fairy-wrens responded to conspecific calls in a graded manner, consistent with the greater number of elements given when
a predator is closer, showing that they are like scrubwrens in communicating about the urgency of danger (Leavesley & Magrath 2005). Fairy-wrens fled about half the time in response to single-element calls but always did so to multielement calls. Furthermore, although they always fled after multielement calls, they spent more time in cover with a greater number of elements. Fairy-wrens therefore appeared to interpret a greater number of elements as an indication of greater danger, leading to more caution in re-emerging from cover. This suggests that, as in scrubwrens, a greater number of elements communicates urgency rather than merely increasing the probability that the signal will be detected.

Scrubwrens and fairy-wrens treated heterospecific calls in a way broadly similar to that for conspecific calls and were more likely to flee after playback of calls containing more elements. These results have parallels in the greater response of red-breasted nuthatches to black-capped chickadee mobbing calls indicating different degrees of risk (Templeton & Greene 2007), but we are aware of no previous demonstration of graded responses to heterospecific flea alarms. Scrubwrens showed the same linear increase in the probability of fleeing to a greater number of elements in both conspecific and fairy-wren calls. Fairy-wrens likewise were more likely to flee in response to scrubwren calls containing more elements, although this contrasted with their response to conspecific calls, to which there was uniform flight after multielement calls but with gradeness revealed in the time spent in cover (above). Overall, each species responded more urgently to heterospecific calls encoding greater danger.

Although both species responded with greater urgency to calls with more elements, fairy-wrens were more responsive than scrubwrens regardless of the number of elements, especially when reacting to their own calls. We suggest that the greater responsiveness might be because fairy-wrens are more vulnerable to aerial attack. Fairy-wrens commonly venture into open areas, whereas scrubwrens usually stay under or near cover (personal observation). Furthermore, whereas scrubwrens are brown, male fairy-wrens have conspicuous blue breeding plumage, and plumage brightness can increase predation risk among bird species consumed by sparrows (Huhta et al. 2003). During the breeding season male fairy-wrens spend more time in cover than females (Mulder 1987), perhaps because they are at greater risk of predation. Finally, although there have been no studies of flight performance, fairy-wrens appear to be weak fliers (Rowley & Russell 1997) and so may be less able to evade a sudden aerial attack. For any of these reasons fairy-wrens may have been more likely to flee in response to aerial alarms than the less vulnerable scrubwrens.

We do not know why fairy-wrens are particularly responsive to their own calls, and so flee in response to all multielement alarms, because fairy-wren alarm calls are not a more reliable indication of danger than scrubwren alarms (Magrath et al. 2009a). Perhaps fairy-wren alarm calls are relatively difficult to hear because they are slightly softer and have a higher peak frequency than scrubwren calls (Magrath et al. 2007). Listeners might therefore be able only to estimate the minimum number of elements in a fairy-wren call rather than having complete information. Birds might then use a rule of thumb of fleeing to cover after detecting two or more elements and in some circumstances even fleeing after hearing a single element. However, it is unclear why a problem with audibility would affect fairy-wrens and not scrubwrens. Another possibility is that there is a different scaling of element number compared to urgency within fairy-wren and scrubwren calls, although our methods used only two predator distance classes and so cannot resolve if there are such differences between species.

Our results raise questions about how each species develops appropriate responses to the alarm calls of the other. Fairy-wrens, at least, seem to have to learn to recognize which scrubwren calls are alarm calls: they respond to four-element scrubwren alarms when living in sympathy with scrubwrens, but not in an allopatric population, implying experience is necessary for call recognition (Magrath et al. 2009b). We suggest three possibilities for the development of understanding graded levels of urgency in heterospecific calls, assuming that birds initially have to learn to recognize which calls are alarm calls. First, birds have to learn the encoding scheme used by the other species; second, they innately respond more strongly to greater element repetition; third, they interpret information in heterospecific calls by generalizing from their own urgency-encoding scheme. First, a requirement for learning is possible given that fairy-wrens and other species need to learn to recognize that heterospecific alarm calls and predator calls are signs of danger (Ramakrishnan & Coss 2000; Kindermann et al. 2009; Magrath et al. 2009b). Second, an innate predisposition to respond more strongly to the repetition of elements might result from alarm calls often signifying greater urgency with more elements (above). Third, animals often generalize responses from familiar to novel stimuli (Ghirlanda & Enquist 2003), so it is conceivable that they generalize from conspecific to heterospecific signals. In this case, fairy-wrens and scrubwrens may respond appropriately to each other because they both encode greater danger with a greater number of elements. Generalization or an innate response may be particularly useful for interpreting aerial alarms, which are brief calls given in dangerous circumstances and may be relatively difficult to learn (Magrath et al. 2009a). Species may differ in how they develop responses to heterospecific calls. For example, scrubwrens responded in a very similar way to conspecific and fairy-wren calls, with a linear increase in the probability of flight with an increasing number of elements, so they may use a similar innate rule in responding to both or may generalize from their own graded system of risk to fairy-wren calls. On the other hand, fairy-wrens fled in response to all multielement conspecific calls but showed a linear increase in flight response to scrubwren calls. This suggests that they may not generalize from their own signalling system, but either learn to decode urgency in scrubwren calls or use an innate or broad recognition system used by birds as a general rule for interpreting risk-based information. Each of the three possible systems for developing an understanding of urgency in heterospecific alarm calls could allow for plasticity in interpreting alarms, enabling individuals to gain information from different species in different locations.

The ability of fairy-wrens and scrubwrens to understand risk-based information contained within each other’s aerial alarm calls and to respond accordingly highlights the value of subtle acoustic information from other species. The high degree of mutual understanding between these species suggests that each benefits from being near the other, even if only through mutual eavesdropping (Magrath et al. 2009a). The existence of complex interspecific eavesdropping networks suggests that important relationships can exist between species that do not appear to interact directly and in which the benefits of association are not obvious. Further studies of information transfer between species may reveal the limits to interspecific understanding and how far such interspecific eavesdropping networks can extend.

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