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

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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.

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 urgency of the response required (Leavesley & Magrath 2005). Furthermore, Siberian jays, *Perisoreus infaustus*, give different calls depending on the behaviour of raptors, therefore signalling 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), between birds and mammals (Rainey et al. 2004; Randler 2006), 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). The additional information provided by alarms of

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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 (Templeton & 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 (Templeton & Greene 2007). By contrast, banded mongooses, *Mungos mungo*, respond to the alarm calls of crowned plovers, *Vanellus coronatus*, with antipredator 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 predatory birds 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

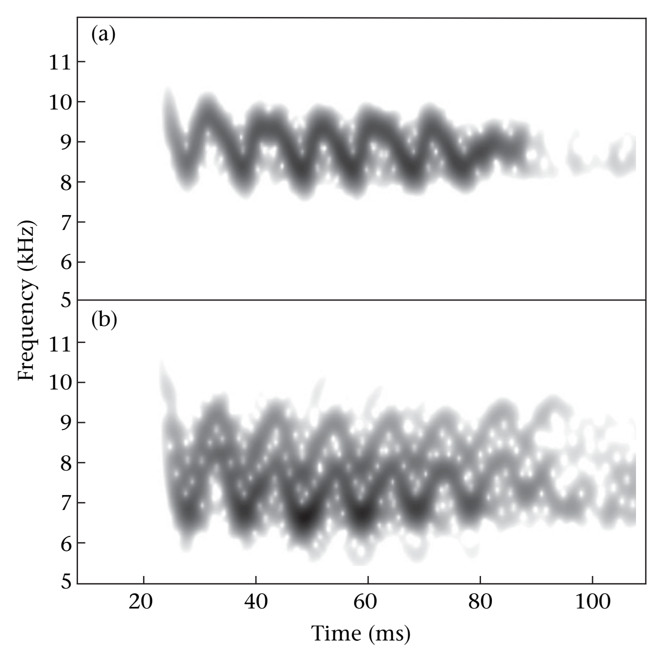

Figure 1. Spectrograms of aerial alarm call elements produced by (a) superb fairy-wrens and (b) white-browed scrubwrens. Spectrograms were produced in Raven Pro 1.3 using settings as described under Methods for Acoustic Analyses.