



## Learning to listen? Nestling response to heterospecific alarm calls

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Many nestling birds go silent in response to parental alarm calls, potentially lowering their risk of being overheard by predators. Parents are not always nearby, however, and so offspring could also benefit if they respond to the alarm calls of other species. Response could be innate, particularly if heterospecific alarm calls are acoustically similar to conspecific alarms, or learned through experience or association with parental behaviour. We investigated the responses of both young (5–6 days old) and older (10–11 days old, close to fledging) nestling white-browed scrubwrens, *Sericornis frontalis*, to the mobbing alarm calls of three heterospecifics whose nests are vulnerable to similar predators. Brown thornbills, *Acanthiza pusilla*, produce the most similar alarm calls to scrubwrens, while superb fairy-wren, *Malurus cyaneus*, and New Holland honeyeater, *Phylidonyris novaehollandiae*, produce alarm calls that are distinct. Heterospecific mobbing assays demonstrated that nestlings were likely to overhear the alarm calls of all three species. In support of innate response, even young nestlings suppressed calling after hearing both thornbill and parental alarms. However, young nestlings ignored or increased calling to fairy-wren and honeyeater alarms. Older nestlings continued to suppress calling to thornbill and parental alarm calls, but also suppressed calling to honeyeater and fairy-wren alarms, suggesting that they could have learnt to recognize those calls. This study thus demonstrates that nestlings can respond to the alarm calls of other species, and that these responses are likely to be enabled through both innate mechanisms and learning.

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Information about danger is critical to survival for most animals, and many gather relevant information by eavesdropping on the alarm cues or signals of other species (Goodale et al. 2010). In terrestrial vertebrates eavesdropping on heterospecific alarm calls is widespread (Nuechterlein 1981; Hurd 1996; Shriner 1998; Zuberbühler 2000; Forsman & Monkkonen 2001; Goodale & Kotagama 2005; Magrath et al. 2007b), including examples of birds responding to mammals and mammals to birds (Hauser 1988; Rainey et al. 2004; Randler 2006; Flower 2011), and even lizards eavesdropping on birds (Vitousek et al. 2007; Ito & Mori 2010). Some species can also extract complex messages from heterospecific alarm calls, such as predator size and type, or urgency of response (Zuberbühler 2000; Templeton & Greene 2007; Fallow & Magrath 2010). Given the vulnerability of young animals to predators (Sih 1982; Lima & Dill 1990; Meri et al. 2008), there should also be strong selection on offspring to respond to relevant alarm calls, but we know little about how and when individuals develop appropriate responses to other species' alarm calls.

Young animals might respond appropriately to heterospecific alarm calls through innate recognition, learning or a combination of both. Innate mechanisms benefit young by enabling early response, and minimize the need to learn about predators through trial and error (Hollén & Radford 2009). However, communities of species vary both geographically and temporally, and so even response through fine-scale genetic adaptation to local species' alarm calls is probably not enough to allow response to the full range of relevant alarm calls to which an animal is exposed (Griffin 2004; Magrath & Bennett 2012). Learning could allow individuals to develop appropriate responses to novel alarm calls and thereby to fine-tune their antipredator responses to the local environment (Lima & Dill 1990; Griffin 2004). Furthermore, young could learn to associate social cues such as alarm calls or other parental behaviours with heterospecific alarms, thereby reducing the costs of trial and error learning (Griffin 2004; Hollén & Radford 2009). Response to alarm calls through innate response or learning are not necessarily mutually exclusive, and young that are able to use both mechanisms could be the most successful at escaping predation.

Expression of innate responses to heterospecific calls could be either immediate or delayed. Immediate response would benefit young by allowing them to respond correctly upon first exposure to a threat, and in fact immediate response to conspecific alarm calls is widespread (reviewed in Hollén & Radford 2009; Magrath et al.

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2010). Such responses to conspecific calls could facilitate similar reactions to heterospecific alarm calls that are acoustically similar (Marler 1967; McCracken & Sheldon 1997; de Kort & ten Cate 2001; Johnson et al. 2003; Rendall 2003; Russ et al. 2004; Hollén & Radford 2009; Rendall et al. 2009; Fallow et al. 2011). Yet a delayed or gradual acquisition of adult-like responses to alarm calls does not necessarily preclude innate response. Delayed responses could be the result of physiological maturation, which can constrain how young are able to perceive and thus react to signals of danger (Espmark & Langvatn 1985; Korneeva et al. 2006; Hollén & Radford 2009; Wiedenmayer 2009). For example, many young nestlings are unable to detect high-frequency sounds (Khayutin 1985; Dmitrieva & Gottlieb 1992; Brittan-Powell & Dooling 2004), which may limit their response to high-pitched alarm calls (Magrath et al. 2006; Hollén & Radford 2009). Adaptive timing of appropriate response to age-specific threats could also explain delayed responses of offspring to alarm calls, and adaptive timing of sensory development could provide a mechanism (Magrath et al. 2006).

A gradual acquisition of responses to both conspecific and heterospecific alarm calls by young could be explained by learning, rather than innate mechanisms (Hollén & Radford 2009). Learned responses can develop gradually, particularly when repeated exposure to predators or cues indicating danger is required (Griffin 2004). Learning about heterospecific alarm calls appears to be widespread in adult birds and mammals (Hurd 1996; Shriner 1999; Ramakrishnan & Coss 2000; Forsman & Monkkonen 2001; Griffin 2004; Davies et al. 2006; Magrath et al. 2009a; Magrath & Bennett 2012), and can be important in facilitating appropriate responses by young to conspecific alarm calls (Miller et al. 1990; Mateo & Holmes 1997). Learning probably also enables response by young to heterospecific alarms. For example, young vervet monkeys, *Chlorocebus pygerythrus*, gradually acquire appropriate responses to the aerial alarm calls of superb starlings, *Lamprolornis superbus*, and those on territories with higher starling abundances develop responses more quickly, suggesting that opportunities to learn play a critical role in the timing of development of response by young (Hauser 1988).

Altricial nestlings provide a good system for studying how young develop appropriate responses to heterospecific alarms (Rydén 1978; Davies et al. 2004; Hollén & Radford 2009; Anderson et al. 2010). In many species, vocalizing nestlings are both vulnerable to eavesdropping predators and responsive to parental alarm calls (Halupka 1998; Davies et al. 2004; Platzen & Magrath 2004; Madden et al. 2005a). However, young could also benefit from responding to the calls of heterospecifics vulnerable to similar predators, as parents are not always present to warn of danger (Roulin et al. 2000; Leonard & Horn 2001; Dor et al. 2007; Bulmer et al. 2008; Haff & Magrath 2010; Magrath et al. 2010).

Surprisingly, few studies have examined the response of nestlings to heterospecific alarm calls, and none has tested how nestling response changes over time. Common cuckoos, *Cuculus canorus*, are innately pretuned to the alarm calls of reed warbler, *Acrocephalus scirpaceus*, hosts, but require exposure to respond appropriately (Madden et al. 2005b; Davies et al. 2006), while brown-headed cowbirds, *Molothrus ater*, respond innately to the alarm calls of one closely related species (Madden et al. 2005b). Similar responses outside brood parasites are generally unknown (but see Anderson et al. 2010 for an example of grey warbler, *Gerygone ignata*, nestlings ignoring both conspecific and heterospecific alarm calls). Cross-fostering experiments have not revealed learning about heterospecific alarm calls (Davies et al. 2004), yet if young learn through association with parental behaviour then cross-fostering may not provide appropriate learning opportunities. Furthermore, the general ability of nestlings to learn is well documented (Kedar et al. 2000; Grodzinski et al. 2008; Raihani &

Ridley 2008), suggesting that learning to recognize heterospecific alarms is also plausible. For example, very young cuckoo nestlings in both Europe and Australia learn through experience to mimic host species' begging calls accurately (Madden & Davies 2006; Langmore et al. 2008).

We studied the response of nestling white-browed scrubwrens, *Sericornis frontalis*, to the mobbing alarm calls of three species that overlap with scrubwrens in habitat use, predator vulnerability and geographical range: brown thornbill, *Acanthiza pusilla*, New Holland honeyeater, *Phylidonyris novaehollandiae*, and superb fairy-wren, *Malurus cyaneus*. Nestling scrubwrens can detect and respond to sounds near the nest, and go silent to parental mobbing alarm calls indicating nearby predators (Platzen & Magrath 2004; Haff & Magrath 2011). Adults respond to aerial alarm calls, which are produced in response to predators in flight, of both fairy-wrens and honeyeaters (Magrath et al. 2007b, 2009b), and probably also thornbills (Fallow et al. 2011), but the response of young scrubwrens to heterospecific alarm calls of any type is unknown. We examined nestling response to heterospecific alarm calls using call playback when nestlings were several days old, and again when they were closer to fledging, to test whether nonparasitic offspring respond to the alarms of other bird species, and if so, how those responses change over time.

## METHODS

### Study Site and Species

We conducted experiments in the Australian National Botanic Gardens in Canberra (35°16'S, 149°06'E) between September and December 2010. The 40 ha gardens consist of both planted (27 ha) and natural (13 ha) vegetation, and are adjacent to Black Mountain Nature Reserve, a 9 km<sup>2</sup> area of natural vegetation. All experiments were conducted under permits from the Environment ACT, the Australian Bird and Bat Banding Scheme, the Australian National Botanic Gardens, and the Australian National University Ethics Committee.

Scrubwrens are small (14 g), facultatively cooperative breeding songbirds that build well-concealed domed nests on or near the ground (Higgins & Peter 2002). Females lay and incubate an average of three eggs, and young are attended by the female, the dominant male and up to three male helpers, who are often offspring from previous years (Magrath & Wittingham 1997). Nests are vulnerable to predation, and failure caused by predation in the Gardens is common. During the nestling stage the mortality rate is approximately 5% per day, primarily caused by predation by omnivorous birds (see below; Magrath & Yezerinac 1997; Platzen & Magrath 2004; Haff & Magrath 2011). Nestlings fledge at about 15 days old, and are dependent upon adults for approximately 6–7 weeks (Magrath et al. 2000).

Both nestlings and adult scrubwrens use a range of calls at or near nests. Nestlings give begging calls or 'whines' when parents arrive at the nest with food (200–800 ms, with sidebands and harmonics), as well as repeat calls ('peeps') in the absence of parents (Fig. 1; 50–150 ms, often without sidebands; Maurer et al. 2003). The rate and amplitude of both whines and peeps increase as nestlings become hungrier (Maurer et al. 2003). Adults give 'buzz' mobbing alarm calls (Fig. 2; 120–180 ms in duration, 3–12 kHz) when predators are on the ground or perched near the nest, and vocalizing nestlings respond to these calls with silence (Platzen & Magrath 2004, 2005; Haff & Magrath 2011), even when very young (3 days old; Platzen & Magrath 2004). Adults also use a variable set of provisioning calls (5–665 ms in duration, 4.6–6.6 kHz) when arriving at the nest with food (Platzen 2004).

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