Eavesdropping on the neighbours: fledglings learn to respond to heterospecific alarm calls

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Young birds and mammals suffer from a high risk of predation, and should be under strong selection for early response to cues indicating danger, including the alarm calls of other species. Despite this prediction, there has been little investigation of the development of response by young animals to heterospecific alarm calls, and none on fledgling birds. Previous studies have suggested that learning is important in the recognition of heterospecific alarm calls in adult birds, but when learning occurs is unknown. We examined the responses of fledgling white-browed scrubwrens, *Sericornis frontalis*, at three ages to playback of the aerial alarm calls of the sympatric superb fairy-wren, *Malurus cyaneus*, and New Holland honeyeater, *Phylidonyris novaehollandiae*. Fairy-wren and scrubwren alarm calls are acoustically similar, while honeyeater alarm calls are distinct, but adult scrubwrens respond to both. Recently fledged scrubwrens responded strongly to conspecific alarm calls, but weakly to heterospecific alarm calls. By contrast, only 2 weeks after leaving the nest most fledglings responded to fairy-wren and honeyeater alarm calls similarly to conspecific alarm calls. However, fledglings in territories without honeyeaters ignored honeyeater alarm calls. Three weeks later, fledglings on all territories responded to all heterospecific alarm calls, an identical response to that of their parents. These results demonstrate that fledglings can quickly develop appropriate responses to heterospecific alarm calls, and present strong evidence that response is learned over a microgeographical scale.

Adult birds and mammals can gain detailed information about predators from the alarm calls of other species (Zuberbühler 2000b; Caro 2005; Templeton & Greene 2007; Fallow & Magrath 2010; Goodale et al. 2010), yet we know almost nothing about when or how young animals develop appropriate responses to other species' alarm calls (Hollén & Radford 2009). This is surprising, as young are often poor at identifying threats and are more vulnerable to predation than adults (Seyfarth & Cheney 1980; Sih 1982; Lima & Dill 1990; Mateo 1996; Clutton-Brock et al. 1999; Kullberg & Lind 2002; Meri et al. 2008), and so should benefit from responding to heterospecific alarm calls at an early age. If appropriate responses can develop early on, then eavesdropping on heterospecifics by offspring should be widespread.

Evidence from adult animals suggests that response to heterospecific alarm calls can be either innate or learned. For example, acoustic similarity to conspecific alarm calls can facilitate response without prior exposure, particularly in closely related species (Johnson et al. 2003; Russ et al. 2004; Fallow et al. 2011). Innate recognition could enable appropriate response early on, and thus increase the survivorship of even very young animals (Lind & Cresswell 2005). However, animal communities can vary over short periods of time or space, potentially limiting innate responses (Lima & Dill 1990; Griffin 2004; Hollén & Radford 2009; Magrath & Bennett 2012). Indeed, response to heterospecific alarm calls can vary depending on whether or not populations of alarm callers and eavesdroppers are sympatric, suggesting that learning is important in the development of appropriate response. For example, adult bonnet macaques, *Macaca radiata*, respond to the alarm calls of heterospecifics only where their populations frequently overlap (Ramakrishnan & Coss 2000), and superb fairy-wrens, *Malurus cyaneus*, respond to the aerial alarm calls of white-browed scrubwrens, *Sericornis frontalis*, only within species sympatry (Magrath et al. 2009b). Learning is also the most logical explanation for differences in response to heterospecific alarm calls observed over very small spatial scales; for example, within single populations of superb fairy-wren, antipredator responses to the alarm calls of noisy miners, *Manorina melanocephala*, mirror microgeographical structure in species overlap (Magrath & Bennett 2012).

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Thus, learning is probably important in enabling appropriate response to other species' alarm calls, although single snapshots of adults do not examine development, and therefore cannot necessarily rule out fine-scale genetic adaptation to local heterospecific alarm calls.

Young animals typically have both less experience with predators and less exposure to heterospecific alarm calls than adults, and are thus particularly useful for the study of whether responses to other species' alarm calls are likely to be innate or learned. If responses are innate, young animals should respond appropriately without previous exposure, while learned responses require experience (Hollén & Radford 2009). Therefore, pinpointing when animals begin to respond to heterospecific alarm calls will help target periods of behavioural change, and thus potential periods of learning (Lea & Blumstein 2011; Haff & Magrath 2012).

The fledging period in birds is an outstanding time for examining the role of experience in appropriate response to heterospecific alarm calls, and presents an opportunity to examine response development in a very specific life history period. Fledglings emerge from their nests into a 'new' world, one with exposure to new predators and little chance to learn about appropriate response before leaving the nest (Newton & Marquiss 1982; Magrath et al. 2006). In fact, fledglings suffer extremely high predation rates (Sullivan 1989; Naef-Daenzer et al. 2001; Leedman & Magrath 2003), perhaps in part because of their inability to recognize appropriate cues of danger. This life stage is therefore a likely time in which learning about heterospecific alarm calls could occur.

We examined the ontogeny of response by fledgling white-browed scrubwrens to heterospecific aerial alarm calls, which are given to predators in flight and signal the need to freeze or flee to cover immediately (Caro 2005; Bradbury & Vehrencamp 2011). New Holland honeyeater, *Phylidonyris novaehollandiae*, and superb fairy-wren are sympatric with scrubwrens in many locations, and all three species are vulnerable to similar predators. Adult scrubwrens in sympatry respond equally strongly to the aerial alarm calls of conspecifics, honeyeaters and fairy-wrens by fleeing to cover (Magrath et al. 2009a). Young just out of the nest respond to conspecific alarm calls (Magrath et al. 2006), but when response to heterospecifics develops is unknown. Fledglings have an extended dependency period of 6–8 weeks (Magrath et al. 2000), during which they may have time to learn to recognize honeyeater and fairy-wren aerial alarm calls. We tested whether newly fledged young responded to the alarm calls of these heterospecifics and how fledgling response changed over time, using call playback experiments at three different ages that spanned the period of fledgling dependency.

METHODS

Study Site and Species

We conducted experiments on a colour-banded population of white-browed scrubwrens in the Australian National Botanic Gardens in Canberra (35°160′S, 149°060′E) between August and December 2011. The Gardens consist of 40 ha of natural (13 ha) and planted (27 ha) Australian native vegetation adjacent to the Black Mountain Nature Reserve, a 9 km² tract of natural vegetation. All experiments were conducted under permits from the Australian Capital Territory government, 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 cooperatively breeding songbirds that build well-concealed domed nests on or near the ground (Magrath & Wittingham 1997; Higgins & Peter 2002).

Females lay and incubate an average of three eggs per clutch, and nestlings fledge at about 15 days old (Higgins & Peter 2002).

We found nests primarily in the building and incubation period, and monitored nests daily when they were close to transitions such as laying, hatching and fledging. We colour-banded nestlings 9 days after hatching. Parent scrubwrens were tolerant of us visiting nests, and resumed normal feeding or incubation activities within several minutes after nest visits during regular nest checks and after banding nestlings. To minimize any impact of us visiting nests on nest survival we placed mesh cages over nests. Cages excluded mid-sized predators including larger birds, but allowed adult scrubwrens and small predators such as snakes free access to and from nests. Cages were successful in protecting nests, and caged nests in this study had higher fledging rates than observed in previous years at uncaged nests in the Gardens (84% of nests produced at least one fledgling at caged nests in this study versus 29.3% at unmanipulated nests; Magrath & Yezerinac 1997). Adults never abandoned nests because of caging, and typically resumed normal behaviour immediately after the cages were in place. Fledgling mortality in this study was similar to that of fledglings from unmanipulated nests in the Gardens studied in previous years (this study: 23.72% mortality during the first week after fledging and 40.7% by week 5, $N = 59$ fledglings; 1992–1998: 29.9% mortality during the first week and 38.2% by 4 weeks after fledging, $N = 638$ fledglings; Leedman & Magrath 2003).

The behaviour of fledglings changes markedly as they age. Newly fledged young remain in dense bushes for approximately 1–2 weeks, with occasional flights between places of cover (Higgins & Peter 2002; Magrath et al. 2006). During this period fledglings often give 'peep' repeat calls (50–150 ms duration; 7 kHz mean peak frequency; call rate of about 1/s per individual) when parents are not present (Magrath et al. 2006). Within the first 2 weeks of fledging most groups undergo brood division, and individual young are subsequently fed primarily by a single adult (Leedman & Magrath 2003). Fledglings begin to leave cover and cease giving peep calls after about 12–16 days, and start to spend some time foraging independently (Higgins & Peter 2002; Leedman & Magrath 2003). Over the following 3–4 weeks fledglings slowly gain independence, and by the time they are 30–40 days old young spend much of their time foraging on their own (Magrath et al. 2000). Overall, fledglings suffer from a daily mortality rate of approximately 5.1% in the first week after leaving the nest, with avian predators responsible for most losses (Leedman & Magrath 2003). Daily mortality decreases dramatically after the first week of fledging (Leedman & Magrath 2003).

Adults give aerial alarm calls when predators fly over. Scrubwren aerial alarm calls consist of a series of similar elements that are repeated in rapid succession. The alarm calls are high-frequency, modulated calls with two bands of sound (102 ± 58 ms duration; 7.1 kHz mean peak frequency; 6.4–10.6 kHz frequency range; 90 ± 6 Hz modulation), which cause other adults to flee to cover (Fig. 1; Leavesley & Magrath 2005; Magrath et al. 2007b). Nestlings pay little attention to parental aerial alarm calls, but recently fledged young respond to the calls with silence, indicating that they use conspecific aerial alarm calls as a signal of danger (Platzen & Magrath 2005; Magrath et al. 2006).

Two songbird species common in the Gardens that regularly give alarm calls to aerial threats are New Holland honeyeater and superb fairy-wren. Like scrubwren aerial alarm calls, both fairy-wren and honeyeater aerial alarm calls consist of a single element type that is rapidly repeated (Magrath et al. 2009a). Fairy-wren aerial alarm calls are structurally similar to scrubwren aerial alarm calls, but have only a single sound band (Fig. 1; 104 ± 32 ms duration; 9.1 kHz mean peak frequency; 8.2–10.6 kHz; 98 ± 6.3 Hz modulation; Magrath et al. 2007b). New Holland honeyeater aerial