ANIMAL BEHAVIOUR, 2007, 74, 1117–1129
doi:10.1016/j.anbehav.2007.01.025

ARTICLES

How to be fed but not eaten: nestling responses to parental food calls and the sound of a predator's footsteps

ROBERT D. MAGRATH, BENJAMIN J. PITCHER & ANASTASIA H. DALZIELL
School of Botany and Zoology, Australian National University

(Received 20 November 2006; initial acceptance 12 January 2007; final acceptance 26 January 2007; published online 24 September 2007; MS. number: 9184)

Nestling birds could minimize the risk of being overheard by predators by becoming silent after parental alarm calls, begging only when parents arrive with food, and independently assessing cues that a predator is nearby. Begging only to parents is challenging because young that respond quickly can be more likely to be fed, so there is a benefit of using subtle cues of parental arrival, potentially leading to erroneous begging. Parents might reduce the risk of error by giving food calls signalling that they have arrived with food, but there have been few studies contrasting begging to food calls compared with other parental vocalizations. Furthermore, it is unknown whether nestlings can use acoustic cues to independently detect predators. White-browed scrubwren, *Sericornis frontalis*, nestlings become silent after parental alarm calls, but it is unknown whether they respond specifically to parental food calls or directly to predator sounds. We conducted a field playback experiment, and found that young begged more vigorously to food calls than other parental vocalizations tested, and nearly as strongly to playback as during real feeding visits by parents. However, nestlings also mistakenly begged to playback of superb fairy-wren, *Malurus cyaneus*, song, possibly because of acoustic similarities to food calls. Finally, nestlings responded with silence to playback of the sound of their major predator (pied currawong, *Strepera graculina*) walking on leaf litter. Scrubwren nestlings can therefore be 'switched on' and 'switched off' by parental vocalizations, are prone to error, and may independently assess risk.

Keywords: acoustic communication; alarm call; begging; error; food call; parent–offspring communication; predation; provisioning call; *Sericornis frontalis*; white-browed scrubwren

Nestling birds often use loud calls to stimulate their parents to provide them with food, but these calls may also be overheard by predators so that young need to balance the benefits of acquiring food with the potential cost of becoming food. Begging more vigorously appears to increase both the rate at which parents provide food to the brood (Kilner et al. 1999; Budden & Wright 2001), and the probability that a particular individual will be fed (Leonard & Horn 2001a), so conflicts between parents and offspring and among siblings may lead to signal exaggeration (reviewed in: Johnstone & Godfray 2002). These exuberant signals are likely to carry both energetic and predation costs, which may explain the reliability of begging calls in signalling nestling need (reviewed in: Wright & Leonard 2002; Searcy & Nowicki 2005). Playback experiments have shown that begging calls can attract predators to artificial nests (Haskell 1994, 1999; Leech & Leonard 1997; Dearborn 1999). On an evolutionary timescale, begging calls may therefore evolve to be less conspicuous in species at greater risk, for example by becoming of higher pitch or lower amplitude (Redondo and Arias de Reyna, 1988; Briskie et al. 1999; Haskell 1999, 2002). In addition to an evolutionary response, or similar facultative adjustment of call properties, young could use three behavioural methods to reduce costs by modulating calling according to current risk by: (1) responding to adult alarm calls; (2) begging selectively when benefits are greatest and costs least; and (3) responding independently of parents to cues that a predator is nearby. We consider each in turn.

Correspondence: R. D. Magrath, School of Botany and Zoology, Australian National University, Canberra 0200, Australia (email: robert.magrath@anu.edu.au).

0003–3472/07/$30.00/0

The first and most-studied possibility is that young respond with silence to adult alarm calls (Platzen & Magrath 2004). Young probably respond to adult alarm calls in many species (O'Connor 1984), but alarm calls could be directed to other adults rather than young, and so it is necessary to test rather than assume that nestlings respond to parental alarms. Playback experiments have confirmed that nestlings become silent after parental alarm calls in several species, including white-browed scrubwrens, *Sericornis frontalis* (Platzen & Magrath 2004), reed warblers, *Acrocephalus scirpaceus*, dunnocks, *Prunella modularis*, robins, *Erithacus rubecula* (Davies et al. 2004), and red-winged blackbirds, *Agelaius phoeniceus* (Madden et al. 2005a). Furthermore, brood parasitic common cuckoos, *Cuculus canorus*, and cowbirds, *Molothurus ater*, can respond to host species' alarm calls (Madden et al. 2005b; Davies et al. 2006). By contrast, alarm calls appear to be directed to other adults in eastern phoebes, *Sayornis phoebe*, in which nestlings do not respond (Madden et al. 2005a).

Second, young may reduce costs by begging selectively only when adults are at the nest. In this circumstance the benefit of begging is greatest and the cost minimal, as parents are unlikely to visit the nest when predators are nearby (Platzen & Magrath 2004; Madden et al. 2005a). Selective begging only when parents are present with food is harder than it might seem because the first nestling to start begging is often the most likely to be fed and so there is a premium on a rapid response to any cues of parental arrival (e.g. Roulin 2001; Porkert & Spinka 2006). As a result, young can beg to subtle cues such as vibration of the nest substrate as the adult approaches the nest, making selective begging difficult and prone to error (Leonard et al. 2005). Theoretically, young cannot maximize both the probability of begging to a parent's arrival and minimize mistaken begging, since lowering the threshold for response will increase mistaken begging (Wiley 1994; Leonard et al. 2005; Dor et al. 2007). In many species parents appear to help young detect their arrival, and perhaps therefore minimize error, by giving a 'food call' as they arrive to feed (Bengtsson & Rydén 1981; Khayutin 1985; Sieber 1985; Buitron & Nuechterlein 1993; Clemmons 1995a; Lessells et al. 1995; Leonard et al. 1997; Madden et al. 2005a). Such food calls are more likely to be given when the nestlings are young or are not begging when the parent arrives at the nest, and appear to prompt young to beg (Clemmons 1995a; Leonard et al. 1997; Grieco 2001). However, there are few species in which replicated playback experiments have shown that food calls prompt begging independently of the other cues of parental arrival (Clemmons 1995b; Buitron & Nuechterlein 1993; Leonard et al. 1997; Madden et al. 2005a).

Madden et al. (2005a) contrast these two methods of modulating begging according to risk and reward as a 'switch off' strategy compared with a 'switch on' strategy. In the first, young beg to many stimuli that might signal parental arrival, but switch off calling after parental alarm calls. By contrast, other species may remain quiet unless switched on by a parent's food call. In the switch on species, young are quiet unless a parent arrives at the nest, so there is little need to have an ability to respond to parental alarm calls. Species might therefore rely primarily on one strategy or the other. Madden et al. (2005a) further suggested that the strategy may depend on the nest site. In species that nest in vegetation, approaching adults will cause vibration of the nest that can, therefore, be used as a cue of arrival, making food calls redundant, whereas those nesting in cavities or hard substrates may have few cues of parental approach, and so young may focus on food calls by parents. These ideas were prompted by the contrasting behaviour and nesting site of eastern phoebes, which nest on solid substrates, and red-winged blackbirds, which nest in vegetation. Phoebe parents give food calls to which young beg, but direct alarm calls to their mate rather than nestlings, which ignore alarm call playback. Furthermore, nestlings begged little to manual stimulation. By contrast, red-winged blackbird nestlings stopped begging after parental alarm calls, showed little response to food calls, and begged vigorously to gentle tapping on their bills. Overall, phoebes were switched on by food calls, but reacted little to alarm calls, whereas blackbirds begged to the merest vibration or tapping, but switched off after parental alarms.

The third way nestlings might reduce risk, and one that has been largely ignored, is that young might regulate begging using independent assessment of risk. Older nestlings of many species crouch in the nest at the approach of an observer or other stimuli, even in the absence of parents (Schaller & Emlen 1961; O'Connor 1984; Kleindorfer et al. 1996), suggesting that at least older nestlings assess risk independently of parents. In some cases visual cues appear to alert nestlings to danger, such as during a response to model presentation (Schaller & Emlen 1961; Kleindorfer et al. 1996), but acoustic cues might be more useful in species in enclosed nests or in visually occluded environments, and are available before vision develops (Khayutin 1985). Independent assessment of danger could have a large effect on nestling survival, and might also affect a parent's decision to give an alarm call (Kleindorfer et al. 1996). Giving an alarm call may warn nestlings but also alert a predator that nestlings are nearby (Krama & Krams 2005), so parents may remain silent if their young can themselves detect the predator at a safe distance. Understanding how nestlings detect predators is therefore important itself and may give insight into parental behaviour, because parents may benefit from assessing the probability that their young have detected a predator (Kleindorfer et al. 1996).

White-browed scrubwren young 'switch off' calling after playback of parental alarm calls signalling danger. Nests are usually on or near the ground, and nestlings fall silent after playback of 'buzz' alarm calls, which are given to predators on the ground or perched near a nest (Platzen & Magrath 2004, 2005). Falling silent is related specifically to risk, rather than being a general response to parental calls, because nestlings do not fall silent to playback of aerial alarm calls which are given to predatory birds in flight (Platzen & Magrath 2005; Magrath et al. 2006). While predators on or near the ground are a risk to nestlings, nests are enclosed and hidden, and so are not visible to a predator flying overhead. By contrast, young are vulnerable to aerial attack as soon as they leave the nest, and young fledglings do respond with silence to aerial alarms (Magrath et al. 2006).