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Species specificity of grey warbler begging solicitation and alarm calls revealed by nestling responses to playbacks

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Vocal communication between parents and offspring, including feeding solicitations by parents and begging calls of young, can increase the risk of predation by attracting predators. Parents can use a 'switch-off' signal (alarm call) to suppress progeny vocalizations or movement, making chicks less detectable to predators. Alternatively, a 'switch-on' signal (feeding or solicitation call) may be used to initiate a begging display in young by parents. The presence and species specificity of either or both of these signals have rarely been tested, as acoustically similar cues may have evolved amongst avian species. We examined the behavioural and acoustic responses of individual grey warbler, *Gerygone igata*, nestlings to both feeding and alarm calls at 12 and 16 days of age (nestling period: 17 days) in a sound-isolation chamber. Overall, nestlings consistently reduced the amplitude of begging calls in response to alarm calls, regardless of the developmental stage. Nestlings responded by gaping only to conspecific, and not heterospecific, begging solicitation calls or other acoustic stimuli. After alarm calls, nestlings did not cease begging, but altered the structure of the begging call. Differences in several begging call acoustic structures were also detected between age groups. These patterns are consistent with a trade-off in chicks' signal-specific responses to parental calls, which optimizes the probability of being fed during parental nest visits whilst also reducing predator detection.
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Vocalizations of nestling birds can be used to solicit food from provisioning parents by signalling the chicks' need (Kilner et al. 1999), but can also be given when parents are absent (Budden & Wright 2001; Leonard & Horn 2001a; Dor et al. 2007). Nestlings raise their begging rate and amplitude to communicate greater hunger levels to increase provisioning by parents (Leonard & Horn 2001b; Hauber & Ramsey 2003) or to compete more successfully with siblings (Dearborn 1998; Lichtenstein & Sealy 1998; Leonard et al. 2000; Roulin et al. 2000; Hauber et al. 2001; Leonard & Horn 2001a; Roulin 2002). However, these signals can be exploited by predators that eavesdrop on begging sounds to locate nests, with nests containing louder, more conspicuous nestlings suffering a greater risk of predation (Haskell 1994; Leech & Leonard 1997; Briskie et al. 1999; Dearborn 1999).

These two selection pressures, signals of need and predators that eavesdrop, can act in opposing directions. A behavioural strategy to increase the chicks' own fitness requires discrimination by nestlings between cues given by parents arriving at the nest (i.e. nest movement, shadows cast by arriving parent) and false cues (i.e. wind, clouds; called false alarms by Dor et al. 2007). In many species of birds, the parents utter calls as they arrive at the nest or when feeding nestlings (Clemmons 1995a; Leonard et al. 1997a; Madden et al. 2005a; Magrath et al. 2007; Raihani & Ridley 2007). These feeding calls, or begging solicitation calls, may be a cue that young nestlings can perceive, as they are typically given just after hatching and then used less frequently as nestlings develop (Bengtsson & Ryden 1981; Clemmons 1995a). Begging solicitation calls also have the added benefit of reducing inappropriate begging due to false cues, as begging can be energetically costly (Leech & Leonard 1996; Kilner 2001; Rodriguez-Girones et al. 2001; Chappell & Bachman 2002).

Begging solicitation calls may also act as a strategy to reduce detection by predators, by indicating that it is safe to beg, effectively acting as a 'switch-on' cue (Madden et al. 2005a). By responding only to begging solicitation calls, nestlings are able to reduce greatly the chance of predation, as parents are unlikely to arrive at the nest when predators are present (Platzen & Magrath 2004, 2005; Madden et al. 2005a). However, several factors can act to decrease the threshold of chick responsiveness to external cues

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or to release chicks from remaining silent. Nestlings in broods of more than one also face the selection pressure of benefiting from being the first in the nest to respond when parents arrive, as being first increases the chance of being fed at that particular visit (Roulin 2001a; Porkert & Pinka 2006). In addition, as an individual's hunger levels increase, the benefit of being fed over siblings increases (Dickens & Hartley 2007). Finally, lower relatedness of chicks in broods with high extrapair parentage reduces the kin-selected benefits of ensuring the safety of the whole brood at some cost to the individual chick who begs less, implying increased begging intensity and reduced threshold to external cues for the onset of begging in species with lower within-brood relatedness (Briskie et al. 1994; Hauber 2003; Boncoraglio & Saino 2008).

A second parental strategy that can be used to reduce nest predation by acoustically oriented predators is the use of alarm calls. Alarm calls are an effective means for parents to elicit from a distance an appropriate response (silence, crouching in the nest) in nestlings of several species (Platzen & Magrath 2004; Davies et al. 2004; Madden et al. 2005a). Alarm calls differ from the switch-on strategy in that nestlings vocalize while the parents are not at the nest, allowing them to negotiate and compete with siblings (Roulin et al. 2000; Roulin 2001a), while also maintaining readiness for when the parents return and maximizing their chance of being fed (Dor et al. 2007).

Yet, another strategy that nestlings may use to avoid detection by predators is to assess the risk of predation independently. This requires nestlings to be able to respond appropriately to cues that may be given by predators when near the nest. Magrath et al. (2007) were the first to test experimentally the response of nestlings to cues given by known predators. Accordingly, white-browed scrubwren, *Sericornis frontalis*, nestlings are not only able to use switch-on and switch-off cues given by parents, but are also able to recognize the sound of their predators' footsteps and respond appropriately with silence. It is adaptive for nestlings to possess the ability to assess potential risk independently, as parents are not always near the nest to warn nestlings of predation. It is likely that this strategy is used by many other species, with the prevalence and accuracy being mediated by the habitat-specific variation in predation pressure and the reliability of the perception of the predators' cues.

In our study, we used a playback experiment to test the response of grey warbler, *Gerygone igata*, nestlings to parental vocalizations, to test whether a switch-on and/or a switch-off mechanism is used and if chicks respond specifically to the cues given by their own species. The playback experiment was designed to test the response of nestlings to various classes of acoustic stimuli. This was to quantify several aspects of nestling begging behaviour to determine whether (1) chicks gave a begging response only to begging solicitation calls and not other stimuli, (2) nestling vocalizations were altered after hearing parental alarm calls, and (3) there was an ontogenetic shift in nestling responses. To do this we used a sound chamber setup, in which nestlings were transported from the nest and tested individually, removing any other potential cues that may stimulate a begging response (e.g. light, siblings). We then tested the response of nestlings to conspecific begging solicitation calls and several other acoustic stimuli (heterospecific begging solicitation calls and heterospecific songs) as controls. Finally, we evaluated the potential patterns of ontogenetic change in nestlings' responses to parental calls, by comparing various chicks' behavioural categories at two ages prior to fledgling. We predicted that conspecific solicitation calls should cause chicks to gape and alter the begging rate and acoustic properties of the begging call more so than heterospecific controls. For the separate test of the switch-off signal, we monitored the responses of individual grey warblers that were solicited to beg using a begging solicitation call but which were then played a parental alarm call. To assess species specificity, we also played heterospecific alarm calls and controls after grey warbler begging solicitation calls. We predicted that chicks should cease begging after the alarm call or, alternatively, give a scream response (Roulin 2001b; Benedict 2007).

METHODS

Study Species and Site

The grey warbler is an endemic New Zealand passerine in the family Acanthizidae (Heather & Robertson 1997). Grey warblers build enclosed, pensile nests at heights of 1–10 m, with an average of 3.5 m (Gill 1982). Pairs are formed prior to the breeding season and are highly territorial, with some territories being maintained year round. During the breeding season, pairs usually have one or two clutches of three or four eggs (Gill 1982; M.G.A., unpublished data). The nestling period is 17–18 days, at which time offspring fledge and remain dependent on the parents for a further 28–35 days (Gill 1982). This research was conducted at Tawharanui Regional Park (36°22′S, 174°50′N), located 52 km north of Auckland.

Grey warbler nestlings have two types of vocalizations: (1) a short, nonbegging vocalization when parents are absent from the nest and (2) a longer begging vocalization that is given when parents feed the nestlings. Both vocalizations are high pitched (7.5–9 kHz) and vary with age (McLean & Waas 1987; M.G.A., unpublished data). The rate at which nonbegging calls are given varies with age, but can be as often as five calls per second for a brood of chicks during the final stages of the nestling period (M.G.A., unpublished data). Nestlings start to vocalize at about 4 days of age, but are difficult to elicit a begging response from out of the nest until 8–10 days (M.G.A., unpublished data). Nestlings of 12 and 16 days from different broods were used for this experiment, to test for developmental differences in responses to stimuli. These ages were most suitable for carrying out the experiments, as this is when the chicks are most vocal and display vigorously, which are relevant to our questions about conspecific versus heterospecific call recognition.

Parents give two types of calls that are of apparent importance for nestlings. Alarm calls (Fig. 1a) are given when potential predators (e.g. shining cuckoo, *Chrysococcyx lucidus*: Briskie 2007; morepork, *Ninox novaeseelandiae*; pukeko, *Porphyrio porphyrio*; and humans) are detected in the vicinity of the nest. These calls tend to be a series of repeated trill calls. Parents also give parental feeding calls, or begging solicitation calls (Fig. 1b), when arriving at the nest with food for nestlings. These calls tend to be a series of short 'chip' calls that can be given during the entire feeding event and can be given either before or after arrival at the nest (M.G.A., unpublished data).

Collection of Acoustic Stimuli

Five types of acoustic stimuli used for the playback experiments were recorded prior to these experiments at the study location. Grey warbler begging solicitation calls and alarm calls were recorded during the early nestling stages before the nestlings are able to vocalize (1–4 days after hatching; $N = 11$ nests; one call of each type was used from each nest). Only the calls of the nestlings' own parents were used in the playback sequences to avoid any possible problems of either pseudoreplication (Kroodsma 1989) or parent–offspring recognition (Leonard et al. 1997b; Rowley 1980). We chose heterospecific stimuli to serve as biological controls to test if nestlings showed a begging response to any acoustic stimuli. These were the vocalizations of sympatric oscines: the grey fantail,

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