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Parental alarm calls suppress nestling vocalization

Dirk Platzen* **and Robert D. Magrath**

School of Botany and Zoology, Australian National University, 0200 Canberra, Australia

Evolutionary models suggest that the cost of a signal can ensure its honesty. Empirical studies of nestling begging imply that predator attraction can impose such a cost. However, parents might reduce or abolish this cost by warning young of the presence of danger. We tested, in a controlled field playback experiment, whether alarm calls cause 5-, 8- and 11-day-old nestlings of the white-browed scrubwren, *Sericornis frontalis*, to suppress vocalization. In this species, nestlings vocalize when parents visit the nest ('begging') and when they are absent ('non-begging'), so we measured effects on both types of vocalization. Playback of parental alarm calls suppressed non-begging vocalization almost completely but only slightly reduced begging calls during a playback of parental feeding calls that followed. The reaction of nestlings was largely independent of age. Our results suggest two reasons why experiments ignoring the role of parents probably overestimate the real cost of nestling vocalizations. Parents can warn young from a distance about the presence of danger and so suppress non-begging vocalizations that might otherwise be overheard, and a parent's presence at the nest presumably indicates when it is safe to beg.

Keywords: cost of begging; alarm calls; nestling vocalization; nest predation; vocal communication; non-begging vocalization

1. INTRODUCTION

Begging by nestling birds has been used to test evolutionary models of signalling that suggest that the honesty of communication depends on dishonesty being costly (Johnstone & Godfray 2002). Nestlings beg using vocal signals, colourful mouths and postural displays to transfer information about hunger state, size and health (Budden & Wright 2001*a*). Conflicts of interest between parents and offspring, and among siblings, about the amount and distribution of food might lead to dishonest exaggeration unless it is reigned in by costs (Godfray 1995; Rodriguez-Gironés 1999). The two probable costs of exaggeration are increased energy expenditure and risk of predation (Chappell & Bachman 2002; Haskell 2002). The evidence so far suggests that energetic costs are minimal (Chappell & Bachman 2002), although it is possible that they are best measured by growth rather than metabolic rate (Kilner 2001; but see Leonard *et al.* 2003). We focus on the potential costs of predation.

Predation is potentially a major cost, but it has proved difficult to gain realistic estimates of the cost (Haskell 2002). Across-species comparisons showed that species with high predation rates have begging calls that are probably more difficult to overhear or locate (Redondo & De Reyna 1988; Popp & Ficken 1991; Briskie *et al.* 1999). It is difficult to interpret these results, as there is no necessary connection between predation rates and the cost of begging vocalizations. The predation costs of begging are represented only by the share of total nest predation that is directly caused by begging noise, rendering across-species comparisons problematic as nest predators and nesting ecology are highly variable (Haskell 2002). Experimental studies avoid these problems and have found that playback of begging calls can attract predators (Haskell 1994, 1999; Leech & Leonard 1997; Dearborn 1999). However, although these results show that predators can hear and respond to begging calls, they do not estimate the actual risks (Haskell 2002). In addition to being performed at artificial nests or sites, these experiments did not take into account the behaviour of parents. This is an important limitation.

Parents potentially warn young of danger so that they do not vocalize when predators are near. If parents do indeed warn nestlings to keep quiet, it means that playbacks of begging cannot estimate the real risk that predators will overhear nestlings. So far, the evidence that parents can suppress nestling vocalizations is suggestive but incomplete. Early playback studies were performed by Ryden (1978) and Greig-Smith (1980) who showed that great tit (*Parus major*) and stonechat (*Saxicola torquata*) nestlings, respectively, suppressed begging after hearing playbacks of alarm call. In a third study, Knight & Temple (1986) observed that nestling American goldfinches (*Carduelis tristis*) crouch into the nest upon hearing alarm call playbacks in the field, but did not analyse nestling vocalization. These studies are suggestive, but incomplete because they suffer from pseudoreplication of playback stimuli. Halupka (1998) found that nestlings became silent when a human walked near the nest, and suggested that the parents' alarm calls were responsible. However, it is possible that parents warned the nestlings in other ways, or that nestlings detected the human independently of the behaviour of the parent. A study by Kleindorfer *et al.* (1996) had similar limitations. One laboratory experiment on white-browed scrubwrens, *Sericornis frontalis*, showed that adult alarm calls did not suppress nestling vocalizations; in fact, nestlings responded to alarm calls with increased vocalizations (Maurer *et al.* 2003). However, that experiment was possibly constrained by the laboratory environment and requires testing on nestlings in the field. Overall, there is no strong evidence that parental alarm calls suppress nestling vocalizations, despite the

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* Author for correspondence (d.platzen@anu.edu.au).

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plausibility that they do so and the potential for parents to thereby modulate the costs of begging (Haskell 2002).

We report the results of a field playback experiment that tested whether parental alarm calls suppress nestling vocalizations. We performed playbacks to white-browed scrubwren nestlings at three ages. Scrubwren nestlings vocalize not only during feeding visits ('begging'), but also when no adult is near the nest ('non-begging'). We therefore assessed the effect of parental alarm calls on each type of vocalization. Nestlings were tested for their response to parental 'buzz' alarm calls directly, without any other sign of an adult, and subsequently during a playback of adult feeding calls that imitated the arrival of an adult at the nest with food. We predicted that nestlings would reduce begging as well as non-begging vocalizations after hearing parental alarm calls.

2. MATERIAL AND METHODS

(a) *Study species*

The white-browed scrubwren is a small passerine in the family Acanthizidae (Schodde & Mason 1999) which builds well-hidden domed nests on or near the ground. The mean brood size in scrubwrens is three nestlings, and young fledge at *ca.* 15 days (Magrath *et al.* 2000). Scrubwrens can breed in pairs or trios, consisting of a dominant pair and subordinate male (Magrath 2001), but we confined our experiments to birds breeding in pairs. The birds were studied in the Australian National Botanic Gardens, Canberra (35°16′ S, 149°06′ N), and all were colour marked to allow individual recognition.

Depredation of nest contents increases from a consistent 1% per day on eggs to 5% per day within 4 days of hatching (R. D. Magrath, unpublished data), suggesting that the nestlings, or adults feeding them, betray the nest location. Pied currawongs, *Strepera graculina*, large omnivorous birds, are the major predator of scrubwren nestlings at the study site (Prawiradilaga 1996) and presumably hunt by sight and sound.

Nestlings have two different types of vocalization (Maurer *et al.* 2003). When begging during a feeding visit they give long and loud 'whine' calls with a broad frequency range. Between feeding visits, when parents are absent, they vocalize with a short and soft high-pitched 'peep' call. Peeps also often follow whines in the later stages of a feeding visit. Vocalization during the absence of the parents is common and the call rate of a brood can vary from 0 to 200 calls per minute in the field (D. Platzen, unpublished data).

Parents give 'buzz' alarm calls, which are short and of a broad frequency range, when a predator is perched or on the ground close to the nest (Higgins & Peter 2002). This call is normally repeated in rapid succession and a call sequence can last up to several minutes depending on how long the danger is present (D. Platzen, unpublished data). When arriving at the nest with food, parents give short 'chip' calls; just before feeding, they give long, modulated 'provisioning' calls (Higgins & Peter 2002).

(b) *Playback experiment*

The experiment was designed to test whether a playback of alarm calls suppressed 'non-begging' vocalizations (peeps), and whether 'begging' vocalizations (whines or peeps) were also suppressed during a playback of chip and provisioning calls shortly after the alarm call playback. The playback sequence consisted of 10 s of alarm calls, 15 s of silence and a 3.5 s long series of the parental feeding calls. Although adults can alarm call for longer than 10 s in the wild, we chose this time to avoid interference by parents that might overhear the playback. The period of silence was used to record the 'non-begging' vocalizations, and it was designed to be short enough to ensure that any effect of the preceding playbacks was still present at the beginning of the chip and provisioning call playback. The parental feeding vocalizations consisted of four chip calls followed by a provisioning call, which is a common pattern of adult vocalizations given on arrival at the nest with food. The begging response of the nestlings was recorded for 15 s after the first chip call. In the control playbacks, we substituted the alarm calls with 10 s of background noise taken from the same recording as the adults' calls, and filtered and amplified in the same way. This control tests whether our experimental procedure, or background sounds recorded with the adults' vocalizations affected the nestlings. It is the appropriate control given the question of whether nestlings change their behaviour after hearing their parents' alarm calls, compared with their parents being absent or remaining silent. We did not address the separate issue of what acoustic features of alarms are important.

The playback tapes were prepared with calls from each brood's own parents, and therefore avoided any effects of pseudoreplication (Kroodsma 1998) or parent–offspring recognition (Medvin *et al.* 1992). Alarm calls were obtained when nestlings were 3 or 4 days old by placing a mounted currawong close to the nest on the ground while the parents were foraging. Adults gave buzz alarm calls on their return and these were recorded onto a Sony TCD-D100 DAT recorder at 44.1 kHz sampling frequency with an Audio Technica ATM15a condenser lapel microphone attached close to the nest. The recordings were edited and amplified to achieve standardized call rates (six calls per second) and amplitudes. The adults' chip and provisioning calls were recorded with the same equipment during natural feeding visits, with the microphone 16 cm from the nest entrance. Recordings were digitally transferred onto a Macintosh computer, filtered to remove sound below 2 kHz, and edited for playback (below) using CANARY 1.2.4. (Charif *et al.* 1995).

Experiments were conducted between October and December 2001 at 11 different nests when nestlings were 5, 8 and 11 days old. All experimental broods had three nestlings. We placed an ATM15a microphone 16 cm from the nest entrance, connected by a 15 m cable to a DAT recorder, and a Sony SRS-A60 active speaker 1 m from the nest, connected to another DAT recorder. After 30–45 min acclimatization, we waited for the adults to be out of our hearing range ($\geqslant$ 20 m) to avoid the behaviour of the nestlings being influenced by any parental calls or activities, or adults overhearing our alarm call playbacks. We then played either an alarm call or a control from the speaker while simultaneously recording the nestlings. The second playback series followed at least one natural feeding visit (5–20 min). The order of alarm and control playbacks was changed from nest to nest but remained the same for one nest on all three tested ages. Habituation or learning effects are extremely unlikely as all calls used in our playbacks occur frequently in the auditory environment of the nestlings. Calls were played back to the nestlings at natural sound levels: buzz calls 45–55 dB (mean ± s.e.m. of field recordings: 54.3 ± 4.0 dB); chip calls 60–70 dB (71.4 ± 4.8 dB); and provisioning calls 45–55 dB (53.2 ± 7.5 dB). Background playback was 35–40 dB (39.4 ± 3.2 dB) after editing and amplification of alarm calls. Decibel values are re 1 pW m^{-2}. Recordings were calibrated in CANARY using a reference file of known sound pressure level, measured with a Bruel & Kjaer type 2205 sound level meter.

We digitally transferred the recordings of broods to Canary and measured non-begging vocalizations, in the 15 s after alarm playback, and begging vocalizations, in the 15 s after the simulated parental visit, using a filter bandwidth of 699.4 Hz, and a grid resolution of 43.07 Hz with 50% overlap. We counted the number of non-begging vocalizations and measured the start time, duration, average amplitude, and minimum, maximum and peak frequency, for every begging vocalization, to test for changes in call structure in reaction to our playbacks. We measured overlapping vocalizations when more than one nestling called at a time, but excluded these calls from the amplitude and peak frequency analysis.

(c) *Statistical analysis*

Despite the experimental design, the data were not fully balanced because two broods were depredated before day 11 ($n = 9$ on day 11) and technical difficulties at one nest (day 8) as well as adult interference at four nests (twice on day 5, once on day 8 and day 11, respectively) led to only partial data sampling for some but not all variables. Furthermore, variables relating to the attributes of begging calls were missing if broods were silent (day 5 = 1, day 8 = 2, day 11 = 1), so that the sample size varies with analyses.

We analysed non-begging and begging vocalizations separately.

(i) *Non-begging vocalizations*: in 24 out of 31 experiments the reaction to alarm calls was silence (day 5, 8 and 11 = 8) so we modelled the probability of vocalizing using a generalized linear mixed model with restricted maximum-likelihood estimation (REML) in Genstat 5 (release 4.2, Genstat-Committee 2000). Fixed effects were type of playback (alarm or control), age of nestlings, daytime and an interaction term of age and type of playback. Brood identification was used as a random factor. We used Wald statistics to assess the significance of fixed effects when the effect of interest was last in the model (Genstat-Committee 2000).

(ii) *Begging vocalizations*: We used a linear mixed model with REML estimation with the same random and fixed effects as in the 'non-begging' analysis. To assess significance, we calculated the change in deviance caused by dropping the fixed effect of interest with the sub-model routine implemented in Genstat (Genstat-Committee 2000). As well as the call features already described we used the time from the start of the playback to the beginning of the first nestling call as a measure of response latency. We transformed this variable with a natural logarithm to normalize the residuals. The residuals of all other models did not deviate from normality.

3. RESULTS

(a) *Reaction to alarm calls*

Broods went completely silent after playback of alarm calls, but not control sounds, in almost all experiments (alarm versus control: $\chi^2_1 = 21.5, p < 0.001$; figure 1*a*). No other variable had a significant influence on nestling vocalization (age: $\chi^2_2 = 0.1, p = 0.93$, daytime: $\chi^2_2 = 0.3, p = 0.77$, age × playback: $\chi^2_2 = 0.5, p = 0.61$). Furthermore, even in the 7 out of 31 experiments in which the brood did not go silent, the average number of calls was lower after the alarm playback compared with the control (two-tailed exact test: $p = 0.047$; figure 1*b*). In only one of these experiments was the number of calls after the alarm calls higher than after the control (four calls compared with one).

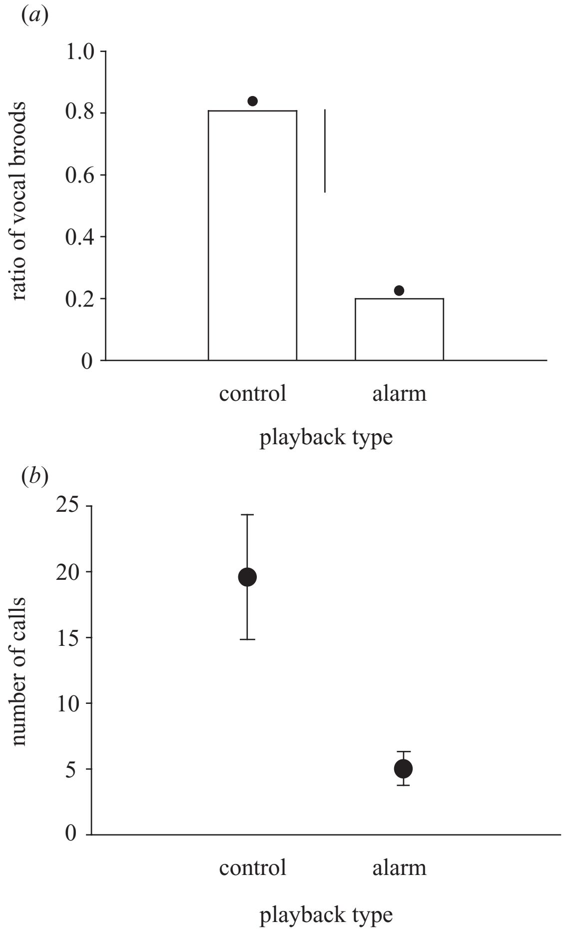

Figure 1. Reaction to alarm calls. (*a*) Ratio of broods that kept vocalizing during the 15 s interval after the experimental playbacks. Bars show means estimated from a mixed model, the line between the bars represents the least significant difference, and the black dots represent means of the observed data. (*b*) Number of calls that were given by the seven broods in which nestlings kept vocalizing after control as well as alarm call playbacks. Means and standard errors are depicted.

(b) *Reaction to chip and provisioning calls*

Nestlings begged less vigorously to simulated parental visits after hearing alarm calls than after hearing the control playback. The latency of the response increased ($\chi^2_1 = 9.0, p = 0.003$; figure 2*a*) and the total duration of all calls decreased after the alarm call playback ($\chi^2_1 = 5.2, p = 0.022$; figure 2*b*). The frequencies of the calls given by nestlings did not change significantly although there was a trend towards an increase in low frequencies after alarm calls (low frequency: $\chi^2_1 = 3.5, p = 0.06$; high frequency: $\chi^2_1 = 0.3, p = 0.8$; peak frequency: $\chi^2_1 = 1.0, p = 0.33$). Young nestlings did not change the amplitude of their calls according to playback type, but 11-day-old nestlings begged more quietly after the alarm than control playback (playback × age: $\chi^2_2 = 6.3, p = 0.043$; figure 3).

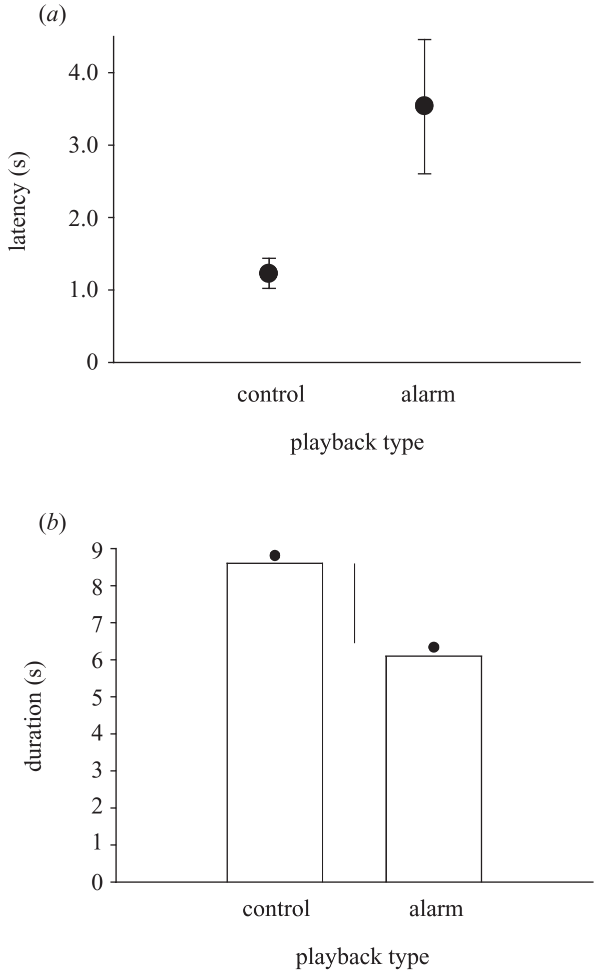

Figure 2. Begging response to the chip and provisioning calls. (*a*) Latency until nestlings start to call (mean ± s.e.m.). (*b*) Total duration of all calls. Bars show means estimated from a mixed model, the line between the bars represents the least significant difference, and the black dots represent means of the observed data.

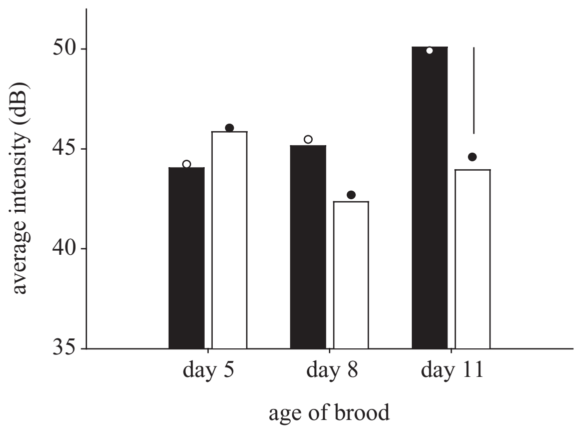

Figure 3. Amplitude of the begging response. Bars show means for control (filled bars) and alarm (open bars) playbacks estimated from a mixed model over the three age classes, the line between the two last bars represents the least significant difference, and the black and white dots represent means of the observed data.

4. DISCUSSION

Parental alarm calls almost completely suppressed non-begging nestling calls and reduced begging calls during a simulated feeding visit. This is the first robust evidence, to our knowledge, that adult alarm calls can transfer information about the presence of danger to nestlings. Given that parental alarms can suppress nestling vocalization, it follows that playback experiments that use artificial nests are likely to exaggerate the true likelihood of predation and therefore cost of vocalizing.

Although alarm calls almost completely suppressed non-begging vocalization, they caused only a 30% reduction in the duration of begging vocalization compared with the control playbacks. Furthermore, we found no effect of preceding alarm calls on call frequencies and no uniform reduction of amplitude (below). We suggest that the much greater effect on non-begging vocalization is adaptive because the arrival of a parent at the nest is an ‘all clear’ signal indicating that danger has passed. Adults appear cautious when approaching the nest with food, and so seem unlikely to overlook predators within earshot of the brood. Furthermore, it is even less likely that they would feed young in the presence of a predator that has already prompted alarm calls or overlook another predator in these circumstances. Our results imply that the cost of begging due to predation risk is likely to be small, and that evolutionary models that assume low costs of begging activity may be relevant. These could either be cost-free honest signalling models (Maynard Smith 1994; Bergstrom & Lachmann 1998), different theoretical approaches that focus on begging as a consequence of sibling competition or signalling of information other than nestling need (e.g. health; Saino *et al.* 2000). Our results suggest that costly signalling in the white-browed scrubwren occurs in the absence of parents rather than in their presence.

If begging calls are usually given only after the ‘all clear’ signals of an arriving parent, then predators may have little opportunity to overhear these calls, and it is more relevant to examine the likelihood of predators overhearing vocalizations emitted when parents are not at the nest. There has been relatively little study of vocalizations in the absence of parents (Greig-Smith 1980; Wright & Cuthill 1990; Budden & Wright 2001*b*; Leonard & Horn 2001*b*; Roulin 2002). In some species, at least, the calls resemble those given when parents are present, and so could be ‘mistaken’ begging in response to other stimuli, in which case such calls could be considered a ‘cost of begging’ (Leonard & Horn 2001*b*). In the scrubwren, however, these non-begging vocalizations (peeps) are quite different from begging calls (whines), suggesting that they are not mistakes and that any costs to peeps could be independent of the cost of begging. The adaptive significance of these signals remains to be tested. The acoustic structure of scrubwren peeps, which are narrow-band, short calls, compared with whines, implies that they may have evolved to be difficult for predators to overhear or locate (Klump 2000). Nonetheless, as they are given over a long period, they might still be overheard by a predator that approaches close enough to the nest. By contrast, the broad-band, long nature of whine calls suggests that begging vocalizations have been subject to little selection from predation, consistent with parental arrival acting as an 'all clear' signal.

Our results contrast with a previous laboratory study on scrubwrens by Maurer *et al.* (2003), who found that playback of adult alarm calls increased nestling calls and did not affect begging vocalizations during simulated parental visits. Possible causes of the contrasting results are: (i) that we used the parent's own vocalizations during playbacks, whereas Maurer *et al.* (2003) were constrained to use calls from strangers; and (ii) that we used the responses of whole broods in their natural nests, whereas Maurer *et al.* (2003) isolated individual nestlings. Other studies of isolated nestlings imply natural behaviour (Greig-Smith 1980; Leonard & Horn 2001*a*), although we know of no explicit tests of the effects of isolation. Maurer *et al.* (2003) suggested that the paradoxical behaviour of nestlings may have been the result of developmental constraints, and studies of other species have reported an increase in responsiveness to alarm calls in later ages (Khayutin 1985; Kleindorfer *et al.* 1996). However, we found only minor age effects, despite testing nestlings up to 11 days old, only 4 days before the mean fledging age.

We conclude that parent–offspring communication about predators must be included in evolutionary models of begging and taken into account in further empirical studies. We also urge study of the function and costs of non-begging vocalization, which seem more likely to suffer the cost of increased predation despite being more difficult to overhear. By contrast, most studies have focused almost exclusively on begging in the presence of parents, which could be almost exempt from such costs.

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