To call or not to call: parents assess the vulnerability of their young before warning them about predators

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Communication about predators can reveal the effects of both conspecific and heterospecific audiences on signalling strategy, providing insight into signal function and animal cognition. In species that alarm call to their young, parents face a fundamental dilemma: calling can silence noisy offspring and so make them less likely to be overheard, but can also alert predators that young are nearby. Parents could resolve this dilemma by being sensitive to the current vulnerability of offspring, and calling only when young are most at risk. Testing whether offspring vulnerability affects parental strategy has proved difficult, however, because more vulnerable broods are often also more valuable. We tested experimentally whether parent white-browed scrubwren, Sericornis frontalis, assessed brood noisiness when alarm calling near nests. When a model predator was nearby, parents gave more alarm calls when playbacks simulated noisy broods, yet brood noisiness did not affect adult calling when only a control model was present. Parents were therefore sensitive to the tradeoff between silencing young and alerting predators to the presence of nests. Our study demonstrates that receiver vulnerability can affect signalling decisions in species other than primates.

1. Introduction

An animal’s audience can affect the way it communicates [1], revealing costs and benefits of signalling. Audience effects occur in a range of contexts, but may be particularly strong in alarm communication [2]. This is because signals can be variably costly to produce [3], and the benefit to the caller will vary depending on the receiver’s value to the caller and vulnerability to the predator. Previous studies have shown that the value of intended audiences, such as mating potential or degree of relatedness, can affect alarm signalling [4,5]. Audience vulnerability to predation could also affect alarm calling by influencing the benefits of signalling, but surprisingly this has seldom been tested [6–8].

Parent–offspring communication provides an excellent model for studying the influence of audience vulnerability on alarm signalling. In birds, for example, the intensity of nestling begging affects their conspicuousness to predators [9], and parents of many species reduce risk by silencing young with alarm calls [10]. However, separating the influences of offspring vulnerability and value on parental behaviour has proved difficult, because both brood conspicuousness to predators and value to parents increase as offspring age [11]. It is critical, therefore, to isolate the effect of offspring vulnerability independently of brood value.

Parental flexibility in response to nestling conspicuousness in broods of constant value would show that brood vulnerability affects parental signalling. Parents face the tradeoff that alarm calls can silence young, the intended audience, but also alert predators that a nest is nearby [12,13]. Parents could minimize risk to young by giving alarm calls only if young are likely to be overheard by a nearby predator. Parents should remain quiet when young are silent,
but give alarm calls if nestlings are calling loudly, because begging calls can lead predators to nests [14]. Such assessment of audience vulnerability could be a powerful parental tactic to reduce nest predation.

We examined whether nestling vulnerability to predators affected parental alarm calling independent of brood value using white-browed scrubwrens, Sericornis frontalis, a species in which nestling calling attracts predators [9], and parental alarm calls silence young [15]. We combined playback of nestling vocalizations with presentation of model predators to test whether parental alarm calling varied in response to brood conspicuousness. Matched experiments within broods ensured that we manipulated parents’ perception of brood conspicuousness and predation risk while holding brood value constant.

2. Material and methods

We studied a colour-banded population of scrubwrens in the Australian National Botanic Gardens in 2009 (see electronic supplementary material). Scrubwrens are small passerines that build domed nests on or near the ground [16]. The primary predator is the pied currawong, Strepera graculina [17], which can use nestling calling to locate nests [9], see electronic supplementary material).

Both adults and nestlings vocalize around nests. Nestlings call during adult feeding visits (begging calls or ‘whines’: 200–800 ms; figure 1a), as well as between parental visits (repeat calls or ‘peeps’: 50–150 ms; figure 1b; [18]). Parent-absent peeping often continues for tens of minutes or longer, and both peeps and whines can be audible 2 m or more from the nest [9]. The rate and amplitude of nestling calls increase with hunger [18]. Adults give contact calls, which stimulate nestling peeping, when approaching nests (‘chips’: 20–30 ms, 6–8 kHz; figure 1c; [19]). Adults often alarm call when predators are near nests (‘buzz’ alarms: 120–180 ms, 3–12 kHz; figure 1d), and nestlings typically respond with silence [15].

We combined nestling call playback with model predator presentation at nests to test whether adults were more likely to alarm call in response to a predator when nestlings were noisy. We predicted that adults would give proportionally more buzz alarms, but not chip contact calls, in response to playback simulating noisy compared to quiet offspring when a model predator was near the nest, but not when a control model was nearby. To test these predictions, we conducted a two-stage experiment at 20 nests containing broods of three 7–10-day-old nestlings.

In stage 1, we manipulated parents’ perception of brood noisiness using playbacks of nestlings. Playbacks mimicked a hungry brood of three and comprised about three peep calls per second played continuously when adults were not directly at the nest, and 12 s of nestling begging (the average length of nestling calling during feeding visits), played during adult visits. All nestling playbacks were of parents’ own nestlings. To ensure that parents were not responding to the properties of background sounds in recordings, we presented background noise as a control. No broods were completely silent during background playbacks, and so we effectively compared adult response with nestling calling at high rates with response at moderate or low rates of nestling calling. Playbacks were presented continuously for at least 30 min, or until both parents had visited the nest. Further details about experimental set-up and playback methods are available in the electronic supplementary materials.

In stage 2, we manipulated parents’ perception of risk to nestlings using taxidermic models. Models were either: (i) a predator, a pied currawong, or (ii) a control, a common, harmless parrot (crimson rosella, Platycercus elegans; see the electronic supplementary material). Models were placed on the ground 2 m from the nest and presented for 2 min. Stage 2 occurred immediately after stage 1. Models were presented to a single parent, which was maintained as the focal parent during subsequent trials (see electronic supplementary material). Playback of nestlings or background noise continued during model presentation. Nestlings calling during model presentation are within the range of natural behaviour, as broods occasionally respond slowly or ignore adult alarms [15].

Each nest received all four combinations of playback treatment and model type. We alternated playback and model presentation order between nests to control for effects of order or brood value [11]. This matched design allowed us to measure differences in adult calling within each nest under different levels of perceived nestling vulnerability (see electronic supplementary material).

We recorded nestling and adult vocal responses during model presentation, as well as commentary on adult behaviour. For each focal parent at each trial, we recorded: (i) number of buzz alarms and (ii) number of chip contact calls (see electronic supplementary material).

We were not able to improve data normality through transformation, and so used non-parametric statistics. We compared adult call rates using matched designs with Friedman ANOVA and Wilcoxon signed-rank tests. We tested the prediction that adults would give more alarm calls when nestlings were noisy and a predator was present than when they were less noisy or
Figure 2. Difference in the number of calls given by focal parents between playback treatments in response to model presentations, calculated as the number of calls during noisy brood playbacks minus the number calls during background playbacks; (a) buzz alarms and (b) chip contact calls. Positive values represent increased calling during noisy brood treatments; negative values represent an increase during background treatments.

there was no predator. We therefore calculated the difference in calling as the number of alarm calls during nestling calling playbacks minus the number of alarm calls during background playbacks, and compared these differences between predator and control model presentations. We similarly compared differences in chip contact calls, as a control. We used an alpha level of 0.05 and two-tailed statistics for all tests, which we carried out in SPSS Statistics v. 19.0. The sample size was 20 for all tests.

3. Results
Supporting our key prediction, adults gave alarm calls specifically when a predator was near a noisy brood. Parents alarm called more when playbacks were of noisy broods in response to predator, but not control models, near nests (figure 2; $Z = -2.94$, $p = 0.003$). This response was not due to a change in chip calling in general, as there was no increase in the number of chip contact calls to either model type during noisy playbacks to either model type (figure 2; $Z = -1.21$, $p = 0.23$; see electronic supplementary material for further control analyses).

4. Discussion
Parents alarm called most when a model predator was near nests and playbacks simulated noisy broods vulnerable to eavesdropping. By contrast, nestling behaviour did not affect alarm calling when control models were nearby. These results control for brood value and suggest that adults assess the tradeoff between warning young and betraying the location of nests. We thus demonstrate that noisy broods can affect alarm signalling by parents [2,10], and that the presence of heterospecific eavesdroppers can affect signalling between parents and offspring [1]. Furthermore, whereas most theoretical models assume that the direct costs of signalling are borne by the sender alone [20], these results demonstrate a system in which the costs and benefits of signaling are likely to be borne more heavily by receivers.

Adults did not alarm call more when nestlings were noisy simply to ensure that young were able to detect their calls, which might be expected if nestling calling masked parental vocalizations [21]. If this had been the case, playback of noisy broods during control model presentations should have led to an increased number of adult chip contact calls [19]. Instead, chip call rates were similar between playback types during control model presentations. This suggests that parental alarm calling has been selected to reduce risk to young, rather than to overcome acoustic masking.

The fact that parents can mediate risk to nestlings by responding to changes in mean predation risk and altering reproductive strategies is well established [22], but flexible strategies for response to short-term risk are less well documented. Here, we show that parents can synthesize information on current nestling behaviour and predation risk to reduce short-term changes in offspring vulnerability.

Studies showing that the vulnerability of an intended audience affects alarm calling have previously centred on primates [1]. Male blue monkeys, Cercopithecus mitis stuhlmanni, monitor the level of threat to their audience, and give more alarm calls when playbacks simulate a predator closer to group members [8]. In Thomas langurs, Presbytis thomasi, males continue to alarm call in response to a terrestrial predator until all group members call in response, possibly to ensure that all are aware of the risk [23]. Our study demonstrates that other taxonomic groups can also adjust alarm calling based on audience vulnerability to detection by predators. Given the tradeoffs that can arise between alarm calling and audience predation risk [12], such assessment of receiver vulnerability is probably widespread.

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References


