



Begging to differ: scrubwren nestlings beg to alarm calls and vocalize when parents are absent

GOLO MAURER*, ROBERT D. MAGRATH*, MARTY L. LEONARD*†, ANDREW G. HORN*† & CHRISTINE DONNELLY‡

*School of Botany and Zoology, Australian National University

†Department of Biology, Dalhousie University

‡Statistical Consulting Unit, Australian National University

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Nestling birds face a dilemma: they can increase parental provisioning by begging more intensively, but by doing so may also increase their risk of predation. Nestlings could deal with this dilemma by reducing begging intensity after parents have warned them of a nearby predator. We therefore tested experimentally whether nestling scrubwrens, *Sericornis frontalis*, increase begging intensity with hunger but reduce it after adult alarm calls. Single 5- and 8-day-old nestlings were temporarily taken into the laboratory for playback experiments. Over a 90-min period of food deprivation we simulated parental visits every 10 min by playing back adult feeding calls. Hungrier nestlings begged louder and longer to simulated parental visits, but contrary to expectation did not beg less if they had previously heard playback of alarm calls, and even begged to the alarm calls themselves. The results were similar for both 'mobbing' and 'flee' alarm calls. Nestlings also gave distinctive calls in the 10-min interval between simulated parental visits, and the number of these calls increased with hunger and after playback of alarm calls. We suggest that nestlings acquire the ability to respond appropriately to alarm calls late in the nestling period and that therefore parents might be selected to avoid alarm calling when defending young nestlings.

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The conspicuous begging calls of nestling birds stimulate parental feeding (reviewed by Budden & Wright 2001a) but can also attract predators to the nest (Redondo & Castro 1992; Haskell 1994; Leech & Leonard 1997). Nestlings therefore have to trade off the nutritional benefit of begging against the cost of predation. Reducing this cost of begging could be done on evolutionary and ecological timescales (Lima & Dill 1990). There is good evidence of an evolutionary response, because species with a higher predation risk have less conspicuous begging calls (Briskie et al. 1999; Haskell 1999). It is unclear, however, whether nestlings respond to a high predation risk on an ecological timescale as well. One way they might do this is by adjusting their begging intensity, if predation risk varies from one parental feeding to the next. Nestlings could gauge that risk by monitoring alarm calls that their parents give in the interval between visits.

A trade-off between acquiring food and avoiding predators assumes that more intense begging stimulates

greater parental provisioning. The begging display in passerines consists of various acoustic and visual features whose intensity increases with hunger. These features can include the duration, amplitude and number of calls, and vigour of the visual display or intensity of mouth colour (Mondloch 1995; Price et al. 1996; Kilner & Davies 1998; Leonard & Horn 1998, 2001a). More intense and more conspicuous begging of hungrier nestlings stimulates greater provisioning by parents to broods (reviewed by Budden & Wright 2001a) and to particular nestlings (Leonard & Horn 2001b).

The trade-off between food acquisition and safety from predation also depends on the fact that nestling begging increases the risk of predation. Interspecific comparisons suggest that nestlings of vulnerable species can evolve less conspicuous begging (Briskie et al. 1999; Haskell 1999), showing that begging, at least historically, carried a cost (Haskell 2002). Playback experiments using artificial nests suggest that begging may also carry a current cost (Haskell 1994; Leech & Leonard 1997; Dearborn 1998), but do not take into account the effects of parental behaviour. In a natural situation parents could reduce the risk of begging by giving alarm calls to lead the predator away from the nest before it comes into hearing distance (Greig-Smith 1980; Knight & Temple 1986). Parental behaviour might

Correspondence: R. D. Magrath, School of Botany and Zoology, Australian National University, 0200 Canberra, Australia (email robert.magrath@anu.edu.au). M. L. Leonard and A. G. Horn are now at the Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada. C. Donnelly is at the Statistical Consulting Unit, Australian National University, 0200 Canberra, Australia.

be one of the reasons why studies at natural nests do not provide consistent evidence that begging increases predation. Redondo & Castro (1992) found that broods of magpies, *Pica pica*, with more begging nestlings suffered more predation and that nestlings that begged more readily were more likely to be taken by a predator. Other studies, however, found no effect of increased begging on nest predation (Cresswell 1997; Halupka 1998; Dearborn 1999). Despite the crucial role of begging costs for theoretical models on the evolution of begging as an honest signal (Maynard Smith 1991; Godfray & Johnstone 2000), little is known about the extent of the predation costs of begging in natural situations. A full assessment of predation risk must incorporate the behaviour of parents as well as nestlings.

No study so far has examined whether nestling begging during a parental feeding visit is affected by hearing parental alarm calls before the parent arrives at the nest. A field study by Halupka (1998) on meadow pipits, *Anthus pratensis*, suggested that parents somehow communicated an increased risk of predation (simulated by a person near the nest) to their nestlings so that they were silent at the following feeding visit. However, it is not clear from that study whether it was the alarm calls that silenced the nestlings rather than other aspects of parental behaviour, or a decrease in hunger level. Other studies have experimentally investigated the effect of alarm calls on nestlings that were already begging before they heard the alarm calls. In these cases alarm calls did cause the nestlings to become quiet and crouch (Greig-Smith 1980; Knight & Temple 1986).

In this study, we examined experimentally whether single nestling white-browed scrubwrens, *Sericornis frontalis*, begged more intensively when hungrier, and then tested whether begging became less intense after playback of adult alarm calls.

METHODS

Study Species and Population

The white-browed scrubwren is a small (11–15 g) ground-nesting passerine of the endemic Australian passerine family Acanthizidae (Schodde & Mason 1999). Its breeding biology is typical of the family. The three young hatch synchronously after about 18 days of incubation, remain in the dome-shaped nest for another 15 days, and are fed for about 6 weeks after leaving the nest (Magrath et al. 2000). Nestling starvation is virtually absent but the risk of nest predation is high, with only 54% of broods that hatch surviving to fledge (Magrath & Yezerinac 1997). Furthermore, daily mortality increases from 2 to 5% from the incubation to the nestling stage, consistent with a cost of begging. Pied currawongs, *Strepera graculina*, are a major predator of nestling scrubwrens (Prawiradilaga 1996; D. Platzen & R. D. Magrath, unpublished data), and casual observations suggest they locate the nests of small passerines by both sight and sound (D. Green, M. Double & R. D. Magrath, unpublished data). Scrubwrens live in pairs or cooperatively breeding groups containing additional males (Magrath &

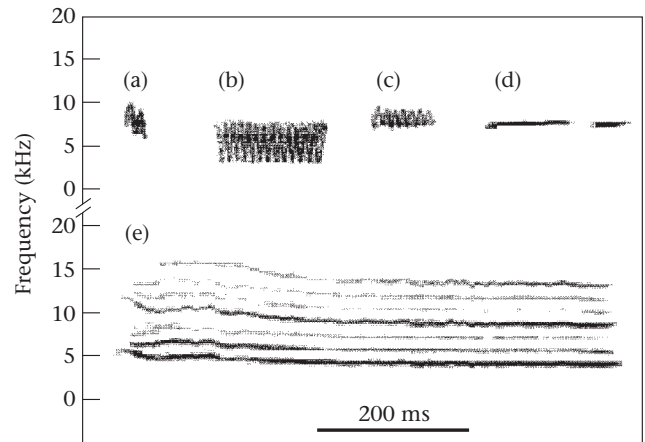


Figure 1. Spectrograms of adult and nestling scrubwren calls: (a) adult chip; (b) adult buzz alarm; (c) adult trill alarm; (d) nestling peeps; (e) nestling whine.

Whittingham 1997; Whittingham et al. 1997). The study population lives in the Australian National Botanic Gardens, Canberra, Australia, where it has been studied since 1992 (Magrath et al. 2000; Magrath 2001). The study was conducted between September and December 2000.

Adult scrubwrens give a variety of calls near the nest, including two associated with feeding young. ‘Chip’ calls are usually given while approaching the nest and often also upon arrival at the nest entrance. In the field, nestlings often beg immediately after they have heard these calls (A. G. Horn, M. L. Leonard & R. D. Magrath, unpublished data). Chip calls are short (ca. 50 ms), broadband, with a rapid onset (Fig. 1a). Adults may also give specific ‘provisioning calls’, especially to very young nestlings, when they arrive at the nest. These calls sound like a soft territorial song and stimulate silent nestlings to beg (A. G. Horn, M. L. Leonard & R. D. Magrath, unpublished data).

Scrubwrens have two types of alarm calls that can also be given in the vicinity of the nest. ‘Buzz’ alarms are broadband calls (ca. 3–10 kHz; Fig. 1b) often given repetitively when a predator is nearby either perched or on the ground. They appear to function as mobbing calls, as scrubwrens and other bird species often approach and give similar calls. ‘Trill’ alarm calls are short, high-frequency calls (ca. 7–8 kHz; Fig. 1c), usually given to predatory birds in flight and they prompt other scrubwrens to flee for cover (R. D. Magrath & H. Browning, unpublished data). At the study site, trill calls are most commonly given to pied currawongs and laughing kookaburras, *Dacelo novaeguineae*, both large omnivores. The design of the two alarm calls is consistent with their apparent function as mobbing and flee alarms (Evans et al. 1993; Bradbury & Vehrencamp 1998).

Experimental Box and Playback Sounds

Experiments were conducted in a plywood box especially designed for playback to nestlings. The box was asymmetrical (38 cm wide at front, 33 cm wide at back,

33 cm deep and 28 cm high) and lined with carpet to prevent echoing and standing sound waves. The top 10 cm of the front board could be removed for feeding nestlings before and after the experiments. A padded and heated nest cup (diameter 9 cm) was mounted in a false floor. Electrical heating tape (Raychem BTV autotrace self-regulating heater at 6 W/m) was coiled around the nest cup below the false floor and could be switched on or off from outside the box to keep the temperature inside the nest cup at 40°C for 5-day-old nestlings and at 37°C for the 8-day-old nestlings; temperature was monitored continuously via a thermocouple. Similar temperatures have been found in natural nests of other small passerines (Choi & Bakken 1990; Bachman & Chappell 1998), and scrubwren nestlings neither shivered nor panted at these temperatures.

A speaker and microphone were mounted on the ceiling of the box to enable simultaneous playback and recording. An Audio-Technica ATM 15a condenser tie-clip microphone was pointed directly at the nest cup from a distance of 20 cm, and vocalizations were recorded with a digital audiotape recorder (Sony TCD-D100). Adult calls were played back to nestlings from a Macintosh PowerBook 5300cs computer, via a Toshiba SB/A10 amplifier and a loudspeaker (DAI-1CHI, Dome Tweeter, DT-89, 8 Ohms, 80–100 W) 22 cm from the nest. A black and white infrared video camera directly above the nest allowed constant monitoring of nestlings during experiments. Between the loudspeaker and the video camera was a hole 4 cm in diameter, through which light could fall into the box to create the impression of a nest entrance.

Digital recordings for playbacks were obtained in the Botanic Gardens from wild scrubwrens with a Sony TCD-D100 digital audiotape recorder. We recorded chip calls at the nest, using a lapel condenser microphone (Genexxa 33-300). The microphone was set up 22 cm from the nest entrance when the nestlings were 4 and 7 days old. Adult buzz alarms were recorded with a Sennheiser MKH 816T directional microphone 5–10 m from the bird. We prompted buzzes by placing a mounted kookaburra about 2 m from a nest containing nestlings 9 days or older. The trill alarm calls were recorded from adults with nestlings or fledglings. The calls were either given in response to a flying pied currawong or they were prompted by a model currawong thrown past the adult scrubwren. The calls appeared the same on spectrograms regardless of the prompt. Each nestling used in the experiments heard unique playbacks of chips and alarm calls, thereby avoiding the problem of pseudoreplication (Kroodma et al. 2001). Because of the difficulty of recording trill alarms (they are short and infrequent and most were prompted by the unpredictable appearance of a flying predator) we could not prepare exemplars from the parents of each nestling. We therefore exclusively played back the alarm and chip calls of adults other than those given by the members of the nestling's own group. This allowed us to avoid any potential confounding effects of 'familiar' and 'unfamiliar' calls.

Control sounds for buzz and trill alarm call experiments consisted of natural background noise recorded

under identical conditions and within seconds of the recording of alarm calls. The control was designed to ensure that any responses by nestlings were due to the adults' alarm calls, and not to sounds produced by the playback equipment or any environmental sounds recorded simultaneously with the alarm calls. This type of control is appropriate because we wanted to know whether parental alarm calls affected nestling vocalizations, and so the appropriate control was to compare the response to alarm calls with background noise occurring at the same time, which is what the nestling would have heard if the adult had not vocalized. In contrast, this control was not designed to test what features of these alarm calls affected nestling behaviour, or whether other sounds or calls would have similar effects. These are also important questions, but they require a different experimental design, including different controls.

All the recordings for the playback experiments were transferred from digital audiotapes on to a computer at 44 kHz and 16 bits. We then prepared spectrograms in Canary 1.2.4 (Charif et al. 1995), using a filter bandwidth of 699.4 Hz, and filtered out all noise below 2 kHz. We then simulated a parental visit using playback of a sequence of chip calls, consisting of a single chip at 62–72 dB, a 20-s break, and the same chip played back twice in short succession (ca. 100 ms) at 72–78 dB. All dB values are re 1 pW/m², and were measured with a Genrad GR 1981 B Precision sound level meter placed in the nest cup in the experimental box. These amplitudes were within the natural range determined from field recordings at the nest ($\bar{X} \pm SE = 74.2 \pm 5.4$ dB). The alarm calls were played back at 46–52 dB and the background at 40 dB. The loudness of the alarm call playbacks in the experimental box was also adjusted to the loudness of parent calls measured at the nest with the sound level meter placed in nearby vegetation. Measurements were obtained when birds about 2–5 m from the nest 'buzzed' to the stuffed kookaburra. Buzzes had a mean loudness $\pm SE$ of 51 \pm 9 dB and the background was 38 \pm 3 dB. Because of the unpredictable nature of trill calls only one measurement (46 dB) was obtained for a bird 2–5 m away during the recording.

Food Deprivation and Begging

We took 10 nestlings from the wild when they were 5 days old and again when they were 8 days old. On the day of the experiment, before 0900 hours, we marked all the nestlings in a brood by clipping specific tufts of down, weighed them and measured their tibias. A randomly chosen nestling was then transferred to the laboratory for the experiment; those taken later in the day were remeasured and reweighed. After a 15-min acclimation period in the experimental box, the nestling was stimulated to beg with playback of an adult's provisioning call (at 66 dB) and fed with grated cheese. The same playback was used for all nestlings so that they were equally stimulated to beg. We started the experiment as soon as the nestling stopped begging, presumably because it was satiated.

We simulated parental visits by playing back the chip call sequence every 10 min for 90 min, a rate similar to the frequency of adult feeding visits (Magrath & Yezerinac 1997). The nestlings reliably called in response to both the first single chip and following double chip, so we analysed responses only in the 5 s after the first chip. Nestling calls between simulated parental visits were recorded and analysed as well, using the 7 min starting 2 min after one simulated parental visit and ending 1 min before the next. After the experiment nestlings were weighed again, fed to satiation and taken back to their nest. We followed the same protocol when each nestling was 5 and 8 days old, with any one individual receiving the same unique chip call sequence to simulate parental visits at each occasion.

The nestling begging calls were transformed into spectrograms (using the same settings as for the field recordings) and analysed in Canary 1.2.4 (Charif et al. 1995) on a Macintosh PowerPC 7300/180. For each call within the 5-s period after the simulated parental visit (i.e. after the first chip), we measured the duration and, average amplitude, and the minimum, maximum and peak frequencies. We measured fundamental frequencies, which were the loudest and lowest frequency bands, but excluded harmonics. We measured the same variables for one randomly chosen vocalization in every minute of the 7-min interval between simulated parental visits, and also counted the total number of nestling vocalizations during this interval.

Alarm Calls and Begging

The alarm call experiments used the same general design as the food deprivation experiment, except that before the simulated parental visits at 20 and 30 min (early) and again at 70 and 80 min (late), either an alarm call or the corresponding control sound was played back before the begging stimulus. We measured responses both early and late to determine whether hunger affected the response, and carried out 10 buzz and 10 trill alarm experiments to allow a comparison of alarm type. Each nestling in a buzz experiment was paired to a sibling used in a trill experiment. To avoid order effects we played back alarm calls before control sounds in half the experiments and the reverse in the remainder. The younger nestlings were 4 ($N=6$), 5 ($N=12$) or 6 ($N=2$) days old; the older nestlings were 7 ($N=6$) or 8 ($N=14$) days old.

The buzz playback started 27 s before the corresponding simulated parental visit (i.e. the first chip). A single buzz was given initially, followed by 1 s of silence and another 5 s of playback with 25–30 buzzes. The trill playbacks followed the same routine as the buzz playbacks but entailed fewer repeats. A single trill was followed by 1 s of silence and then two more trills. The trill playback was started only 24 s before the corresponding simulated parental visit to achieve the same 20-s break between alarm call and simulated parental visit as in the buzz experiment. Both the buzz and the trill playbacks were designed to simulate the natural delivery of the calls (R. D. Magrath & G. Maurer, personal observation). The control sound playbacks for buzz and for trill experiments

matched the timing and duration of the corresponding alarm call playbacks.

The response of the nestlings to alarm calls or control sounds was measured during three periods: (1) the simulated parental visit following the alarm, again sampling the 5-s period after the first chip; (2) the 5 s immediately after the first alarm call itself but before the simulated parental visit; and (3) the 7-min period before the next simulated parental visit. These periods were designed to test whether nestlings: (1) beg less intensively during a simulated parental visit shortly after an alarm call; (2) become quieter after an alarm call; and (3) remain quieter in the interval between the two following simulated parental visits. The recordings were analysed in Canary 1.2.4 in the same way as for the food deprivation experiment. However, nestling responses sometimes overlapped playback of an alarm call, so it was not always possible to measure amplitude. We therefore restricted the analysis to frequency and duration of calls (which correlate with other features including amplitude; see below).

In the alarm call experiment (and also in the food deprivation experiment), 5-day-old nestlings often did not respond at all to the early simulated parental visits, presumably because they did not get hungry as fast as 8-day-old nestlings. Therefore the data for 5-day-old nestlings did not allow a comparison of the response to alarm call playbacks early and late in the experiment, and so the analysis of the alarm call experiment was restricted to 8-day-old nestlings.

Statistical Analyses

We used restricted maximum likelihood estimation (REML) mixed-modelling analyses, implemented in Genstat 5 (Genstat Committee 1993). REML estimation was required because the data were unbalanced for some variables (individuals did not all vocalize at all times) and contained both random and fixed effects as explanatory variables (Bennington & Thayne 1994; Sokal & Rohlf 1995). The effect of an explanatory variable was assessed by the change in deviance caused by dropping the variable from a more inclusive model.

Analyses of the food deprivation experiment were designed to test the effect of hunger and age on begging. The two main explanatory variables were: (1) time during the experiment, corresponding to time since satiation and therefore assumed to reflect nestling hunger; and (2) age of the nestling. We examined five more variables to ensure that they did not obscure or confound the effects of hunger and age: weight in the morning, tibia length, date, time of day and nestling sex. None of these additional variables had a strong or consistent effect on begging and so are not considered further. The data for the food deprivation experiment had three levels: individual nestling (random effect), and time since satiation and nestling age (both fixed effects).

We analysed the effect of hunger on begging calls and on vocalization during the intervals between simulated parental visits. The begging calls were quantified as: (1) mean amplitude; (2) sum of time spent calling within the

5-s sample; and (3) mean frequency range. We substituted the total number of vocalizations in the intervals for the sum of time spent vocalizing, since these calls are very short.

Analyses of the alarm call experiment assessed the effects of the type of playback (buzz versus trill, each compared with the control sound) and timing of the playback (early versus late) on call duration, frequency range and the number of interval calls. The values for frequency range were transformed with a natural logarithm to satisfy assumptions of normality of residuals and constant variance. In addition, we included as random effects the brood from which the two siblings came, the individual bird and the minute of the playback. Nestlings also increased their begging responses with increasing hunger in the alarm call experiment, but because the effect of hunger was analysed in the previous experiment, the analyses focused on the effect of alarm calls.

Ethical Note

To carry out this study, it was necessary: (1) to remove nestlings from their nests and hold them in captivity for 2 h; (2) to deprive them of food for 90 min; and (3) to play back adult alarm calls. We consider each of these issues. First, temporary removal itself did not cause problems as the nestlings did not yet show a 'fear' response and parents never abandoned broods during or after the experiments. While visiting nests, we first searched the area to avoid being observed by predatory birds, which are the major source of predation (Prawiradilaga 1996; D. Platzen & R. D. Magrath, unpublished data). Furthermore, we fed nestlings to satiation before returning them to the nest, to ensure they did not beg unusually loudly. Overall, 64% of experimental broods fledged, which is roughly that expected from the long-term data (66–70% should survive from 7 or 8 days old to fledging at 15 days, based on a 5% daily mortality rate). Second, a period of food deprivation was necessary to examine the relation between a standardized level of hunger and begging and was crucial for assessing a possible trade-off between begging and predation. We chose a period of 90 min as covering the natural range of intervals between feeds during the day in the wild (see Discussion), yet shorter than the 110 min used without harm on 31 species of small insectivorous passerines studied by Kilner & Davies (1998). Following Kilner & Davies' study, we also fed nestlings to satiation before and after the period of deprivation. Third, alarm calls are naturally given many times a day in the wild, so we assumed that playback of two alarm calls within 90 min was unlikely to cause the birds greater distress than in the wild. As it turned out, nestlings actually begged to the alarm calls, so they appeared not to find them stressful at all. In addition to these specific issues, we used the minimum number of nestlings consistent with robust statistical analyses, by using pairwise designs coupled with generalized linear modelling and true replication of playback tapes. The study was carried out under an ethics permit granted by the Australian National University Ethics Committee.

RESULTS

Nestling Vocalizations

Nestlings gave two distinct types of calls. 'Peep' calls were short with a small frequency range, usually lacked sidebands and harmonics, and were relatively quiet (mean intensity in 8-day-old, hungry nestlings 42 dB; Fig. 1d). 'Whine' calls were given only in response to chip or provisioning calls and were long with a broad frequency range, had one to four sidebands, one to three harmonics, and were loud (mean intensity in 8-day-old, hungry nestlings 51 dB; Fig. 1e). The peak frequency of whines was usually much lower than that of peeps (about 5 versus 7 kHz in 8-day-old, hungry nestlings). Nestlings normally opened their bills during whines but kept their bills closed or only slightly open during peeps. In the interval between parental visits nestlings only ever gave peeps; however, they sometimes gave peeps rather than whines in response to a parent's simulated visit, or started with whines and then reverted to peeps. In the following, we refer to calls given during simulated parental visits as 'begging calls', and those given in the intervals between those visits as 'interval calls'. Begging calls can thus include both types of nestling call, while interval calls contain only peeps.

Food Deprivation Experiment

Begging calls

All measures of begging calls increased with duration of food deprivation (Fig. 2). This was true for both 5- and 8-day-old nestlings, although the effect of hunger was sometimes greater for older nestlings. Average amplitude increased strongly and linearly with time since last fed (time: change in deviance₁=156.83, $P<0.001$) and the increase in amplitude was slightly greater for older nestlings (time × age: change in deviance₁=5.90, $P=0.02$). The total duration of begging within a 5-s sample increased with time since satiation (time: change in deviance₁=38.5, $P<0.001$), and 5- and 8-day-old nestlings showed a similar increase (time × age: change in deviance₁=0.02, $P=0.89$). The frequency range increased with hunger (time: change in deviance₁=49.24, $P<0.001$), and this increase was slightly greater for 8-day-old nestlings (time × age: change in deviance₁=5.78, $P=0.02$). Throughout we give information on main effects even when there were significant interactions; we do so because main effects were strong and linear, whereas interactions were relatively weak.

Interval calls

All measures of the vigour of calling in the intervals between simulated parental visits also increased with hunger, and more strongly for older nestlings (Fig. 3). Average amplitude of the peeps increased (time: change in deviance₁=64.81, $P<0.001$), and the increase was smaller for nestlings at day 5 than at day 8 (time × age: change in deviance₁=4.86, $P=0.03$). The number of calls in the interval between simulated parental visits increased dramatically with time since satiation (time:

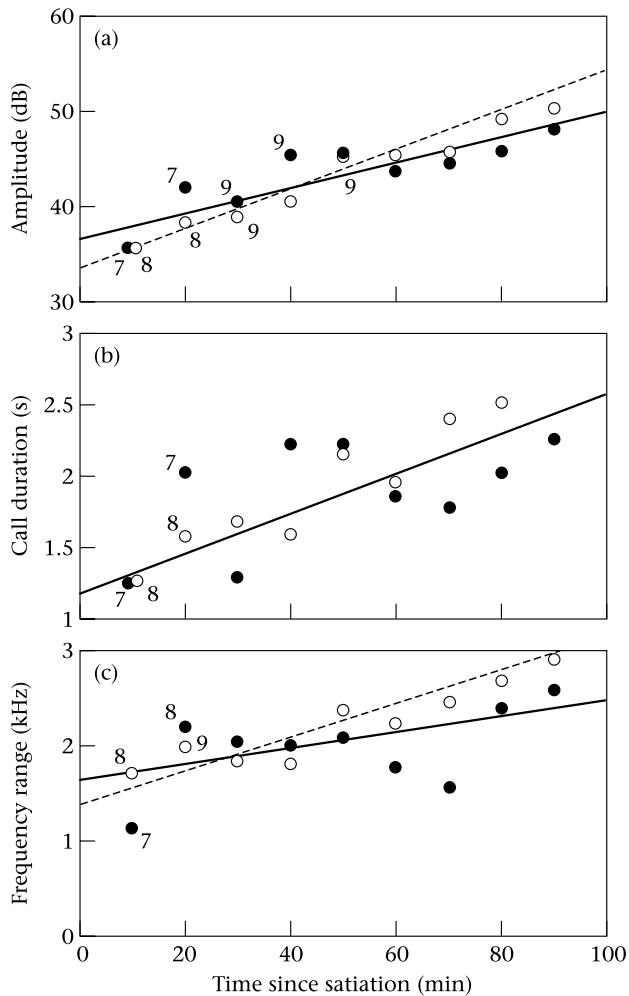


Figure 2. Begging intensity in relation to hunger. Circles indicate the mean values for 5-day-old (●) and 8-day-old (○) nestlings and the lines show estimates from mixed-model analyses for begging of 5-day-old (—) and 8-day-old (---) nestlings. Numbers near means are sample sizes; if no number is given $N=10$. (a) Amplitude, (b) duration and (c) frequency range.

change in deviance₁=143.49, $P<0.001$), and the increase was stronger for older nestlings (time \times age: change in deviance₁=5.57, $P=0.02$). The frequency range increased with hunger (time: change in deviance₁=54.75, $P<0.001$), more strongly for older nestlings (time \times age: change in deviance₁=17.3, $P<0.001$).

Alarm Call Experiment

Begging to simulated parental visits

Contrary to expectation, scrubwren nestlings did not reduce the duration and frequency range of their begging calls during simulated parental visits after alarm calls, and the type of alarm call had little or no effect on the response. Alarm calls did not affect the duration of begging calls (alarm versus control: change in deviance₁=0.13, $P=0.7$; Fig. 4a), and the lack of response was similar for trills and buzzes (alarm versus control \times alarm type: change in deviance₁=0.02, $P=0.9$). Similarly, alarm

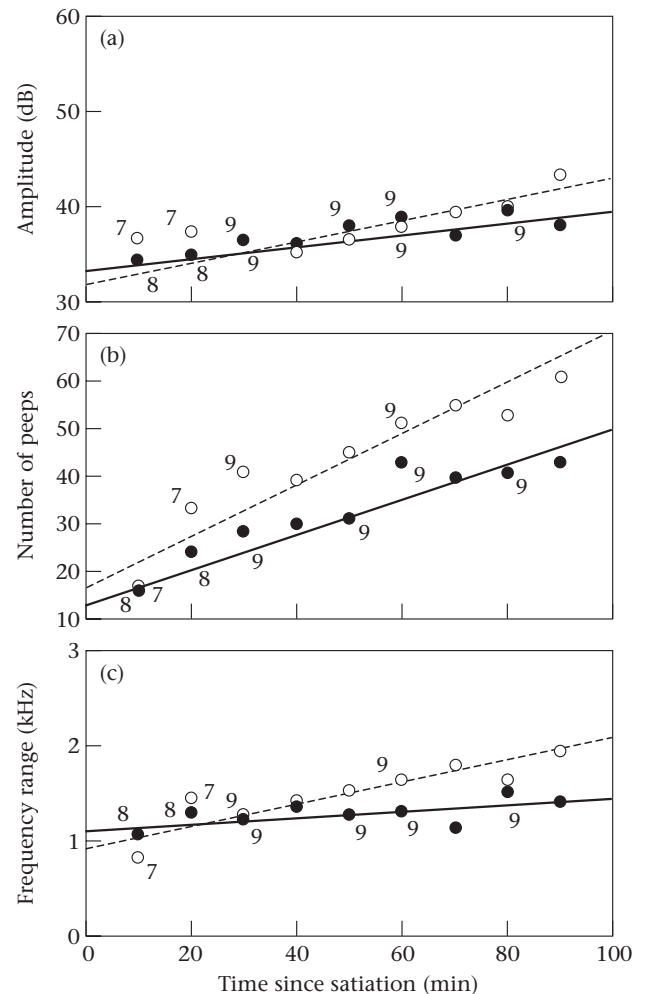


Figure 3. Calling between parental visits in relation to hunger. Circles indicate the mean for 5-day-old (●) and 8-day-old (○) nestlings and the lines show estimates from mixed-model analyses for begging of 5-day-old (—) and 8-day-old (---) nestlings. Numbers near means are sample sizes; if no number is given $N=10$. (a) Amplitude, (b) number of peeps and (c) frequency range.

calls did not affect the frequency range of begging calls (alarm versus control: change in deviance₁=0.03, $P=0.9$; alarm versus control \times alarm type: change in deviance₁=2.84, $P=0.09$). As in the hunger experiment, the vigour of begging calls was greater after a longer period of food deprivation, but this increase affected alarm calls and control sounds equally.

Begging to alarm calls

Alarm calls themselves prompted conspicuous begging calls (Fig. 4b). Nestlings begged for longer periods after either of the alarm playbacks compared with control playback (alarm versus control: change in deviance₁=17.37, $P<0.001$; alarm type: change in deviance₁=0.23, $P=0.6$). Calls given in direct response to either type of alarm call also had a greater frequency range (alarm versus control: change in deviance₁=23.56, $P<0.001$; alarm versus control \times alarm type: change in deviance₁=0.46, $P=0.5$).

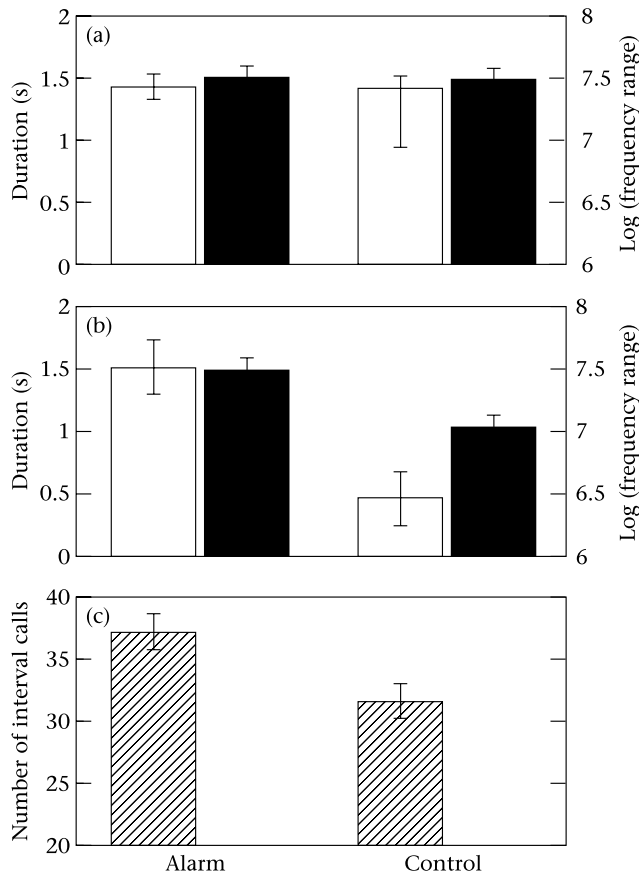


Figure 4. Nestling responses to adult alarm calls. (a) Duration of begging to simulated parental visits; $N=19$. (b) Duration of begging to alarm calls; $N=18$. (c) Number of calls in the absence of parents after alarm calls; $N=19$. Bars show means estimated from mixed models for duration (\square), log frequency range (\blacksquare) and number of calls (\hatched). The vertical lines indicate 2 SEDs for the comparison of the alarm with the control.

Calls between simulated parental visits

Nestlings gave more peeps in the interval between subsequent parental visits following either type of alarm call playback than in intervals that followed control playback (playback type: change in deviance₁=11.5, $P<0.001$; alarm versus control \times alarm type: change in deviance₁=1.41, $P=0.2$; Fig. 4c).

DISCUSSION

Nestling scrubwrens increased the intensity of their begging calls when hungry but contrary to our predictions alarm calls did not cause nestlings to reduce begging to simulated parental visits. Even more surprisingly, the alarm calls themselves stimulated nestlings to beg. Also unexpectedly, nestlings were vocal in the intervals between simulated parental visits, and increased the number of interval vocalizations when they were hungry and in the intervals following alarm calls. We examine in turn the relation between hunger and begging calls, the effect of adult alarm calls on nestling vocalizations, and the potential function of vocalizations given in the absence of parents.

Hunger and Begging

Nestling scrubwrens increased every measure of begging intensity with increasing hunger. An increase in begging with hunger is consistent with the idea that begging honestly reflects nestling need and is also found in many other species (reviewed by Kilner & Johnstone 1997; Budden & Wright 2001a). We assume, as have others, that hunger increases with duration of food deprivation, and that the increase in begging with time is caused by hunger (Budden & Wright 2001a). This assumption has never been tested directly, although the longer nestling canaries, *Serinus canaria*, are deprived of food, the more they must be fed before they will stop begging (R. Kilner, personal communication).

The increased begging intensity of hungrier scrubwrens probably makes them more vulnerable to predation. Hungrier nestlings have louder and longer begging calls with a broader frequency range. These features make calls easier for predators to detect and locate (Marten & Marler 1977; Richards & Wiley 1980; Klump 1996), and suggest that scrubwren nestlings should trade nutritional benefits of begging against safety from predation.

Alarm Calls and Begging

Unchanged begging during simulated parental visits following alarm calls

Contrary to our prediction, nestlings did not beg less conspicuously during simulated parental visits if they had heard either type of alarm call within the previous 30 s. Why did they not respond as predicted?

Developmental constraints. The 8-day-old nestlings might have been too young to have developed the ability to recognize different adult calls, possibly because their nervous systems were not sufficiently developed or because they had not had enough time to learn the call types. Khayutin (1985) found that nestling pied flycatchers, *Ficedula hypoleuca*, develop the ability to recognize parental alarm calls and respond appropriately only when 6 days old, even though they are already able to perceive them when they are 4 days old. Perhaps scrubwren nestlings develop this ability even later than pied flycatcher nestlings. Unfortunately, older scrubwren nestlings could not be tested with the current protocol because after 9 days old they can jump out of the nest when disturbed.

The chip as an all-clear signal. Nestling scrubwrens might not beg less conspicuously to simulated parental visits following alarm calls because the chip call given after the alarm call could be an all-clear signal. Therefore the nestling would not have to trade safety against intensive begging for food. However, this hypothesis appears to be irrelevant to scrubwrens because nestlings begged to the alarm calls themselves before they heard a chip (below), rendering an all-clear signal superfluous.

Experimental design and apparatus. The experimental design and experimental apparatus might have influenced the results in three ways. (1) Nestlings may recognize only alarm calls given by adults attending the nest, and not the playbacks of alarm calls of strange adults. This explanation seems unconvincing because nestlings begged, apparently normally, to a stranger's chips and provisioning calls. It is also unclear why it would be adaptive to respond to the alarm calls only of specific adults; predators should be avoided regardless of the informant. (2) The nestlings might have been unnaturally hungry and so begged regardless of risk. However, the time from feeding until the first alarm call playback at 20 or 30 min was well within the natural range of feeding intervals in scrubwrens, so they should not have been unnaturally hungry. For broods of three, by far the most common brood size, 55% of broods received nine or fewer feeds/h, and 31% six or fewer, indicating average feeding intervals of 20 and 30 min per head, respectively ($N=583$ watches 1992–1998; R. D. Magrath, unpublished data). Furthermore, we fed the nestlings to satiation before the experiment, and so they were probably 'unnaturally' well fed when the experiment started. (3) The experimental box might have been so alien as to result in generally abnormal behaviour. However, we strived to mimic a natural situation as closely as possible by using playbacks of adult calls; others have relied on artificial sounds as begging stimuli (e.g. Price et al. 1996; Rodriguez-Girones et al. 2001). The transfer to the artificial system itself did not prevent scrubwrens from showing 'normal' behaviour: nestlings begged to both adult call types associated with feeding in the wild (i.e. provisioning calls and chips) and readily took food when offered in combination with the provisioning call. Nestlings of a variety of other species also appeared to behave normally after transfer to artificial nests in boxes (e.g. Kilner & Davies 1998; Leonard & Horn 2001a).

Begging to the alarm call itself

Begging to the alarm calls seems paradoxical because it is unlikely to stimulate immediate parental feeding and might draw the predator's attention to the nestling. After alarm calls, nestlings begged for longer with calls that had a greater frequency range; unfortunately, we were unable to measure amplitude (see above), which is perhaps the simplest way to change audibility. None the less, all three features increased with hunger (see above), suggesting that nestlings probably also begged more loudly. No other study has reported begging to alarm calls. Nestlings of other species crouch and stop begging after alarm calls (Greig-Smith 1980; Khayutin 1985; Knight & Temple 1986; Buitron & Nuechterlein 1993; Kleindorfer et al. 1996), or jump out of the nest when they are older (Kleindorfer et al. 1996). Given how little is known about nestling responses to alarm signals, however, it is unclear whether scrubwrens are unique. In fact the occurrence of 'mistaken' begging to a variety of stimuli (see below), suggests that begging even to alarm signals could be common. Why, then, did nestlings beg to alarm calls?

Developmental constraints. Again, the 8-day-old nestling scrubwrens may not yet have developed the ability to recognize parental alarm calls as such, but may recognize them as those of adult scrubwrens and respond for that reason. Another possibility is that nestlings under a certain age respond with begging to almost any noise. In support of the latter idea, young during the first half of the nestling period have been stimulated to beg with many artificial stimuli, including the human voice (Rodriguez-Girones et al. 2001) or tapping sounds (Price et al. 1996). Few studies have systematically investigated the types of stimuli to which nestlings respond and how the responses change with age. Khayutin (1985) found that the begging stimulus for nestling great tits, *Parus major*, changed with age, from the sound of a parent landing at the box to a luminosity change and, shortly before fledging, to the species' song. Very hungry great tit nestlings, however, begged to almost any sound except alarm calls.

Slow development of the ability of nestlings to recognize parental alarm signals and respond appropriately would have implications for parental nest defence. Parents should be selected to refrain from alarm calling near the nest before the nestlings are old enough to respond appropriately. This could provide another explanation for more rigorous defence of the brood as nestlings age. As suggested by Curio (1998), nestling behaviour could make it necessary to modify the predictions of brood value and vulnerability hypotheses (Montgomerie & Weatherhead 1988). In support of this idea, parent moustached warblers, *Acrocephalus melanopogon*, start to give alarm calls near the nest only when nestlings are 6 days old, corresponding to the age at which they crouch to humans (Kleindorfer et al. 1996). In that study, however, there was no test of the effect of alarm calls on the behaviour of younger nestlings.

Begging does not incur a predation cost. Perhaps begging to alarm calls does not carry a cost and therefore has not been selected against. Alarm calls might distract predators or mask begging calls so that the predator cannot detect them. Masking by buzz alarms is possible because they are loud, given repeatedly, and have a broad frequency range that overlaps with that of begging calls. However, masking cannot be a complete explanation because nestlings begged as much to trill alarms, which are short, given only a few times and have a narrow frequency range. The few repeats of trill alarms also seem unlikely to distract a predator. Furthermore, neither masking nor distraction can explain why nestlings also increased the number of peeps in between the simulated adult visits following alarm calls (see below).

Begging to alarm calls signals hunger. Adult alarm calls indicate that parents are near the nest and a nestling could use this opportunity to signal its hunger. In support of this hypothesis, hungrier nestlings did beg more to alarm calls. Such begging would make sense if it did not increase the risk of predation and if the parents could hear their nestlings above their own alarm calls and increase their feeding later.

Another possibility is that nestlings blackmail their parents by begging to attract predators when hungry, thereby forcing their parents to bring more food than would otherwise be optimal (Zahavi 1977; Johnstone 1996). A nestling could similarly blackmail siblings to acquire first access to the food. Intensive begging of hungry nestlings to alarm calls is consistent with blackmail, as it might be particularly effective, but the idea remains to be tested.

Vocalizations in the Absence of Parents

Nestling scrubwrens called regularly in the intervals between simulated parental visits, in the absence of any obvious stimulus. These peeping calls were different in structure from the whines given in response to simulated parental feeding. Calling in the intervals between parental visits has rarely been described for other bird species (but see: Greig-Smith 1980; Wright & Cuthill 1990; Price & Ydenberg 1995; Roulin et al. 2000; Budden & Wright 2001b; Leonard & Horn 2001c). In other species, furthermore, these calls appear to resemble begging calls given during parental visits and might be a result of nestlings mistakenly begging to inappropriate stimuli (Leonard & Horn 2001c). The difference between peeps and begging whines suggests that in scrubwrens these calls are not just mistakes but might have a specific function. Although our study was not designed to test hypotheses about these calls, because we discovered them during the study, they beg interpretation.

Peeps are short, have a low amplitude, high frequency and narrow frequency range compared with whines. All these characteristics are likely to make them difficult for predators to overhear or locate (see above). None the less, at times they are given at rates of over 65 calls/min, facilitating detection of the nest even for human observers (R. D. Magrath & G. Maurer, personal observation), so they may still be detectable to nearby predators. We consider potential functions of peeping, according to potential receivers.

Communication of hunger to parents

The rate of peeping increased markedly with hunger. Nestlings might therefore signal hunger to parents, without the parents having to visit the nest. Thus parents might be able to minimize the number of visits to the nest and thereby reduce the risk of revealing the nest to predators (Martin et al. 2000). The increase in peeps in the 10 min after hearing alarm calls might mean that parents can assess hunger even when a predator is watching. Price & Ydenberg (1995) also suggested that nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, might communicate with parents near the nest.

Communication with siblings

Nestling calling between feeding might serve as a mechanism to reduce sibling competition and ensure that the most needy nestling receives the next food item brought to the nest (Roulin et al. 2000). Nestlings might 'negotiate' ahead of time about who will be fed at the

parent's next visit, thereby reducing competition when the parent arrives. Roulin et al. (2000) argued that this is true of barn owls, *Tyto alba*. The increase of peeping with hunger in scrubwrens is consistent with this hypothesis, except that hungrier nestlings also begged more at simulated parental visits, so peeping could be superfluous. Furthermore, the nestlings in our experiments were always alone, so we could not test the idea of 'negotiation'.

Conclusions

In conclusion, scrubwren nestlings begged more vigorously when they were hungrier, but their behaviour after alarm calls appears paradoxical. We consider the most plausible explanation of begging to alarm calls is that scrubwren nestlings had not yet developed the ability to recognize alarm calls and respond appropriately to them, a result that has important consequences for parental behaviour. The distinctive calls that scrubwren nestlings give when their parents are not at the nest are also puzzling; the function and the receiver of these calls are unclear. Our results suggest that it is vital to consider parent-offspring communication when examining the potential risks of begging, and that more attention should be focused on vocalizations in the absence of parents.

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