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Nestling begging increases predation risk, regardless of spectral characteristics or
avian mobbing

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2 Abstract

3 Models of parent-offspring conflict and nestling begging honesty often assume
 4 that signaling is associated with increased predation risk. However, little evidence
 5 exists that begging actually increases predation in the context in which it evolved,
 6 especially when the potentially modulating effects of parental defense are taken
 7 into account. We measured the cost of begging in cooperatively breeding bell
 8 miners (*Manorina melanophrys*) by baiting 168 inactive nests with a wax egg and
 9 broadcasting sounds from nearby speakers. Nests were randomly assigned to one
 10 of three treatments: silence, unmanipulated begging calls, or shaped white noise
 11 pulses that matched the amplitude envelope of each corresponding begging call.
 12 Moreover, half of the nests were placed outside and half inside bell miner
 13 colonies, where miners vigorously mob potential nest predators. Predation was
 14 not influenced by vegetation cover, distance of the nest from the speaker, or
 15 placement inside the colony. Sounds were costly, however, as nests broadcasting
 16 begging signals or white noise were predated more often and more quickly than
 17 silent controls. Contrary to theoretical predictions regarding ‘stealthy’ design, we
 18 found that predators were just as likely to locate nests with broadband white noise
 19 playback as nests broadcasting begging signals. Further, there was an interaction
 20 between playback amplitude and predator type (avian versus rodent): louder
 21 playback lead to decreased nest survival for those taken by avian predators. As
 22 increased begging drives provisioning rates in many species, including bell miners,

23 this reveals an inescapable trade-off between nestling begging intensity, parental
24 provisioning effort and predation risk.

25 **Keywords:** Parent-offspring conflict, signal design, costs of signals, predator-prey
26 interactions.

27

28 **Introduction**

29 Solicitation of food from parents is accompanied by some form of begging display
30 in many taxa (e.g. Furlow 1997; Kilner and Johnstone 1997; Rauter and Moore
31 1999; Bell 2008). In the case of altricial nestling birds, offspring are totally reliant
32 upon their parents and/or nest attendants for nutrition, and typically signal for
33 food via multiple modalities, including a colorful gape, altered posture and
34 conspicuous vocalizations (Wright and Leonard 2002). There is now considerable
35 evidence that begging intensity and, in particular, the acoustic component of
36 begging, acts as the proximate cue for parental adjustment of feeding rates in
37 many species (Kilner and Johnstone 1997; Wright and Dingemanse 1999; Budden
38 and Wright 2001; Wright and Leonard 2002; M^cDonald et al. 2009).

39 Differences in begging intensity between brood mates can also affect within-brood
40 competition (Briskie et al. 1994; Cotton et al. 1996; Bulmer et al. 2008). For
41 example, more intense begging has been documented in species with high levels
42 of extra-pair fertilizations, and thus low levels of within-brood relatedness (Briskie
43 et al. 1994). This conflict over resource allocation has generated considerable
44 theoretical work investigating the factors that lead to evolutionarily-stable
45 strategies (ESS) of signaling ('honest signaling'; Johnstone and Godfray 2002).
46 While some models reach equilibrium utilizing cost-free signals, their broad
47 applicability remains doubtful (Brilot and Johnstone 2003). More commonly,
48 models rely upon an inherent cost of begging to balance parental and offspring

needs, thereby preventing begging intensity from escalating endlessly (e.g. Godfray 1991). Understanding the precise mechanisms by which costs are incurred for begging is thus fundamental to understanding the evolution and maintenance of these signals.

Two, non-mutually exclusive, costs of begging are commonly evoked: increased metabolic costs and an enhanced risk of predation (see Chappell and Bachman 2002; Haskell 2002 for reviews). The metabolic costs associated with producing even the most conspicuous acoustic signals is only a small fraction of the daily metabolic requirements of nestlings. Given the substantial nutritional rewards that nestlings might acquire by increasing begging intensity (e.g. Kilner and Johnstone 1997; Wright and Dingemanse 1999), these metabolic costs seem insufficient to prevent escalation of begging levels, though few studies have examined these costs directly (e.g. Kilner 2001; Rodríguez-Gironés et al. 2001; Leonard and Horn 2008; reviewed in Chappell and Bachman 2002).

The most convincing evidence of begging costs is via enhanced predation risks in experimental studies broadcasting begging calls (Haskell 1994, 1999; Leech and Leonard 1997; Dearborn 1999). While results have been promising, they have also been, to some extent, equivocal (Haskell 2002). Researchers have concluded that begging leads to greater predation than silence (Haskell 1994, 1999; Leech and Leonard 1997), and that higher rates of begging lead to higher rates of predation

(Haskell 1994; Dearborn 1999). Furthermore, playing back begging calls from species with high predation rates (e.g. ground nesters) leads to greater predation than playing back begging calls from species with relatively low predation rates (e.g. cavity-nesters; Haskell 1999).

If the acoustic nature of begging does indeed carry a cost via increased predation, we might expect the structure of these calls to have been modified by selection to reduce conspicuousness. This appears to be the case for at least some systems, where species that are subject to higher overall nest predation rates beg at both lower amplitudes and with a higher dominant frequency (Redondo and Arias de Reyna 1988; Briskie et al. 1994, 1999); a design similar to that of cryptic avian alarm calls (e.g. Marler 1955; Wiley and Richards 1982; Wood et al. 2000).

Moreover, nestlings respond to alarm signals of adults by reducing or even ceasing to produce begging signals in several taxa (Davies et al. 2004; Platzen and Magrath 2004; Madden et al. 2005).

Several authors have highlighted problems with the approaches previously used to measure the predation costs of nestling begging. For example, artificial nest structures such as cane baskets may evoke predator neophobia, or even attract an entirely new subset of predators (see Major and Kendall 1996; Thompson and Burhans 2004 for reviews). Similarly, previous work has been unable to realistically replicate many biologically relevant conditions. For example, begging calls have

been broadcast at abnormally high rates (Leech and Leonard 1997) or throughout the night when nests would normally be silent (Dearborn 1999). Moreover, the influence of nest defense by parents has received little attention, despite the ability of parents to drive predators from the nest area (Montgomerie and Weatherhead 1998) and thus potentially reduce predation risk costs associated with begging. While parental alarm calls can silence begging nestlings (e.g. Davies et al. 2004), the pertinent point when assessing begging costs *per se* is whether or not nest defense can deter predators while nestlings continue to beg, as even the most sophisticated alarm call system is unlikely to perfectly warn of approaching predators. In sum, predation costs of a begging signal from a focal species have yet to be established in the natural context (ie nest location) in which the signal evolved (Haskell 2002). Further, a cost associated with begging *per se*, as opposed to any noise from the nest area, has yet to be detected.

Given this, we re-visited the predation costs of nestling begging in a species amenable to manipulations of this kind, the cooperatively breeding and colonial bell miner (*Manorina melanophrys*). Previous research on this species has quantified important parameters required for realistic deployment of experimental nests (nesting density, nest site placement, temporal and acoustic properties of begging), and identified a positive relationship between begging intensity and provisioning effort (e.g. Poiani 1993; McDonald et al. 2008ab, 2009). Further, all bell miners in a colony, not simply the breeding individuals, vigorously

mob potential predators whenever they are in the colony area, regardless of their current reproductive state (Loyn et al. 1983; Clarke and Fitz-Gerald 1994). This behavioral trait provides an ideal system in which to examine the effects of nest defense without manipulating breeding birds directly. These attributes allowed us to conduct an experiment that addressed the deficiencies of previous work, by comparing predation rates on ‘natural’ nests near silent or operational speakers, both within (where nests were observed being indirectly defended by miners that mob predators within the colony boundaries) and outside miner colonies, utilizing hundreds of exemplars of age-specific recordings of nestlings.

In the current study, we assessed the following questions: i) Do begging signals cause increased predation than silence? ii) Can nest defense ameliorate any costs associated with begging vocalizations? Finally, acoustic characteristics of begging signals may also be important for determining predation pressure, thus we also asked: iii) Are louder vocalizations more risky? iv) Is the acoustic structure of these vocalizations in any way more cryptic than white noise with similar amplitude and temporal characteristics?

Methods

Overview

A total of 168 nests from previous breeding attempts of bell miners were hung in typical situations for this species over four trials (n = 42 nests/trial). Within a trial 21 nests were placed within a bell miner colony (and thus were actively defended against potential predators by bell miners driving predators from their colony) and 21 outside of colonies (undefended nests, not each trial occurred within a different bell miner colony). All nests had a speaker placed next to it that was either silent or played back either a begging call or a paired-white noise equivalent with the same amplitude characteristics as a given begging call. Unique begging calls, and thus white noise correlates, were obtained from 567 begging bouts from bell miner nestlings of known age, with an average 113 calls obtained for each age from 6-10 days post-hatch. On each of five days of playback per trial calls from a given nestling age were broadcast from speakers at a rate typical of bell miner nestlings, with silence interspersing begging bouts. Order of call playback was randomized on a given day across trials. Nests were monitored daily, and the predator of specific nests determined by marks left on wax eggs placed within nests.

Acquisition and preparation of playback stimuli

Begging calls were recorded during previous work (McDonald et al. 2008ab) from known-age bell miner broods that each contained 2 nestlings. Briefly this involved

placing a small microphone (ECM-77B; Sony, Japan) 20 cm below the nest cup. Calls were then recorded from each provisioning event (48 kHz/16 bits) using a solid state recorder (Marantz PMD670; Japan) placed at least 10 m from the nest — a distance known not to cause disturbance in this species (M^cDonald et al. 2007a). Begging calls were collected from nestlings between 6 and 10 days post-hatch. This corresponds to the days immediately prior to fledging (10-12 days post-hatch) when provisioning rates and thus begging rates are maximal (te Marvelde et al. 2009).

To recreate the natural begging rate of 32 bouts per hour throughout all daylight hours (M^cDonald et al. 2008a; te Marvelde et al. 2009), we extracted a total of 567 begging bouts, with 113 (+/- 1) calls extracted per brood age. A total of 5 broods were recorded at each nestling age, and no brood was recorded on more than one day (i.e. 25 broods in total). Begging sequences were relatively long ($7.8 \text{ sec} \pm 3.3\text{SD}$), and consisted of intermittent vocalizations (hereafter 'syllables') punctuated by brief periods of silence ($11 \pm 5\text{SD}$ syllables per sequence; Fig. 1). Some syllables were inevitably masked by interference from other acoustic sources. When this occurred, we filtered out the affected syllables, removing $1.1 \pm 1.2\text{SD}$ sections per sequence with Raven 1.3 (Cornell Lab of Ornithology; USA). The brief periods of silence between syllables were also filtered across all frequencies using Raven. Finally, all sequences were high-pass filtered (138 at 1200Hz; remainder at 1800Hz) using Signal software (Engineering Design; USA; version

4.03.01). High-pass filtering above these frequencies removed the maximum amount of background noise without filtering any component of the signal of interest.

We wished to isolate effects of signal design at the level of the syllable, to distinguish these from aspects of gross structure at the level of call bouts. This required control stimuli that were identical to begging calls in the time and amplitude domains, but which had a different spectral structure. We used Signal to create 567 amplitude envelopes from the waveforms of each of the 567 begging calls. Each amplitude envelope was then used to generate a white noise signal (48 kHz) that had identical amplitude and temporal characteristics to the original begging call from which it was derived. White noise signals were then high-pass filtered in precisely the same fashion as their corresponding begging calls (i.e. 1200 or 1800 Hz). The original begging calls and the matched-pair white noise controls were then normalized to -1dB and combined as separate channels into a single stereo file using Quicktime v7.5 (Apple; USA). This process generated 567 pairs of files, that were identical in the time and amplitude domains, but which had a different distribution of energy in the frequency domain. This design permitted a comparison of the complex frequency modulated structure of begging calls with the random frequency profile of white noise (Fig. 1; see ESM).

188 *Preparation of artificial nests*

189 Intact nests previously used by bell miners were collected, following completion of
 190 nesting attempts during previous studies (McDonald et al. 2008ab), and stored in
 191 sealed plastic bags. Artificial eggs were constructed using microcrystalline wax (All
 192 Australian Candle Making Supplies; Australia). Comparisons revealed no difference
 193 in predation rates between real (*Poephila acuticauda*) eggs (3 of 9) and similarly-
 194 sized wax eggs (6 of 9) placed on the ground to encourage rodent predation, the
 195 most likely predators to utilize olfactory cues. Mould size was chosen to provide a
 196 close match to bell miner eggs (moulds: 22 x 16 mm L x W, Home Chocolate
 197 Factory; UK; bell miner eggs 24 x 16 mm; Beruldsen 1980). Eggs were constructed
 198 according to the methods outlined in McEntee (2007), with the addition of a small
 199 fishing line swivel (Size 8; Jarvis Walker; Australia) inserted into the egg to provide
 200 an attachment point for a monofilament line (15 kg, low visibility; Penn; USA) used
 201 to secure the eggs.

202 *Playback apparatus*

203 Playbacks were conducted over 4 trials ($n = 42$ nests per trial; $n = 168$ nests in
 204 total), during the breeding season (3 February—8 April 2008) at Ourimbah State
 205 Forest (33°18'22"S, 151°19'17"E), c.60 km north of Sydney, Australia. Boundaries
 206 of the four different bell miner colonies were determined on foot by walking along
 207 focal roads. This could be done confidently to ± 10 m, as individual miners inhabit
 208 relatively small and static active spaces (Clarke and Fitz-Gerald 1994), are

209 extremely vociferous and are obligate colonial species; individuals do not move
210 outside the colony boundary except on very rare dispersal events.

211 All speakers and artificial nests were placed along the edge of vegetation lining
212 unsealed (unpaved) tracks through the forest. To begin, we laid 2 rows of speaker
213 cable (17 gauge, 2x0.14 mm; Radio Parts Group, Melbourne; Australia) for 520 m
214 through an area occupied, and thus defended, by bell miners (Fig. 2). Two rows of
215 cable were used to carry the two channels of the stereo files used as stimuli. Cable
216 was placed in dense undergrowth 2-3 m in from the edge of track and was covered
217 with additional leaf litter. After this, beginning at the edge of the colony, we ran
218 another 100 m of paired cable adjacent to the track in the opposite direction. This
219 point was the centre of the layout, where playback equipment was eventually
220 situated (see below). We then replicated this initial 620m 'arm' of the design by
221 laying cable away from the bell miner colony (Fig. 2).

222 Speakers ($n = 42$; SPG6555; Redback; Australia) were then placed below likely
223 nesting places at 26 m intervals along each 520 m section of cable, leaving the two
224 centre 100 m sections without speakers. This distance was based on the mean
225 separation between bell miners in other studies ($26.4 \text{ m} \pm 5.4\text{SD}$; Poiani 1993;
226 McDonald unpubl. data; $n = 71$ nests). Speakers and artificial nests were not placed
227 within 26 m of active nests of any species. Thus we placed 21 nests inside each bell
228 miner colony, beginning at the edge of the area defended and moving deeper

within it, and 21 nests outside the colony, with this entire setup being repeated at four different colonies/locations. Nests outside the colony were a minimum 200 m from the nearest miners. No active nests of any species were observed outside miner colonies, ensuring mobbing pressure was very likely to have been considerably greater within as opposed to outside bell miner colonies.

Disused but intact miner nests were placed in a suitable fork in the vegetation (34.3 cm \pm 11.7SD from speakers; range 12-67 cm, n = 168). Suitable sites were chosen based on PM's experience with this species and were similar in characteristics to actual nest sites (e.g. nest height: 1.5 m \pm 0.3SD, n = 168 this study; cf. 2.1 m \pm 1.8SD, n = 137 nests, M^cDonald unpubl. data). Treatment order was then assigned randomly for trios of nests on each arm (control, white noise or begging calls). We wired speakers for sound playback into either the left or right channel, as appropriate and attached sections of cable connecting the control speakers to the main cable arm, so that these silent speakers were visually identical to those in the other treatments. One wax egg was then placed in each nest, with monofilament stretched taut from the egg swivel, down through the base of the nest and tied off on a branch, preventing predators from removing eggs completely. To this line we added a small piece of insulating plastic held in place by two solder lugs (HP1350; Jaycar; Australia) mounted next to the speaker. This was used to break a circuit between a small battery and a clock (Y1009, Dick Smith Electronics; Australia), which was buried in the leaf litter 3-4 m from the

250 base of the tree in which the nest was placed. If eggs were moved substantially,
251 the monofilament was stretched, dislodging the plastic, closing the timer circuit
252 and starting the clock.

253 In the centre of the loudspeaker array we used a Macintosh computer (G4
254 MacMini, 1.44 GHz, 2 GB RAM) housed in a weather-proof box to play back call
255 sequences simultaneously at each speaker using iTunes software, a
256 digital/analogue converter (FCA202; Behringer; Germany; 48kHz/16 bits) and an
257 amplifier (AH500 180W; Behringer). This setup was powered by an inverter (300W;
258 Dick Smith Electronics; Australia) attached to two deep-cycle batteries (US2200;
259 U.S. Battery; USA) and was programmed to broadcast calls from 30 min before
260 sunrise through to 30 min after the local sunset. Bell miners typically begin and
261 end daily provisioning at these relative times (M^cDonald unpubl. data). We used
262 iCal and Applescripts software to control the computer and initiate and terminate
263 playback as appropriate, adjusting for changes in daylength for each trial.

264 Playback rate and amplitude were based upon natural data from typical bell miner
265 nests, which average 32 provisioning visits per hour, a rate that is stable between
266 the ages of 6 and 10 days post-hatch (te Marvelde et al. 2009). To introduce
267 natural variability into the timing of playbacks, whilst maintaining hourly averages
268 of 32 sequences across the five days, we played calls at rates of either 28, 30, 32,
269 34 or 36 begging events per hour (thus 32 on average overall, with rates assigned

at random to each call on each day). For each of the four trials, a new randomized call order was used. Each playback was of a particular begging bout from one of the five nests recorded at a given age, with order of presentation randomized. Natural peak amplitudes of begging sequences were determined by monitoring begging at 4 nests, all broods of 2, at different ages near to the study area. Peak amplitude of begging averaged $65.8 \text{ dB} \pm 5.1\text{SD}$ at 1 m from the nest across the measured ages (day 6-10, measured using a Realistic 33-2050 SPL meter, "C" weighting, fast response; Radioshack; USA). At the beginning of each playback, we adjusted the amplitude of the signal from the middle nest in each arm to this peak value using a white noise standard. Middle nests were calibrated, as signals unavoidably attenuated with increasing physical distance from the amplifier. To include this in analyses, we also explicitly measured amplitude at each specific speaker (range of all nests 50-89 dB; mean $66.6 \text{ dB} \pm 10.8\text{SD}$, $n = 112$). Amplitude did not differ significantly between treatments (excluding silent controls: $F_{1,110} = 0.008$, $p = 0.931$).

Equipment was placed in the field over a period of either one or two days. The first day of playback (i.e. of a 6 day-old brood), began just prior to dawn on the first day after setup was complete. Nests were only loaded with artificial eggs at dusk the day prior to playback onset, after first checking that no potential predators (e.g. corvids), were in the vicinity. Before this, we took the following measures of the immediate environment surrounding each nest: i) height of nest cup above ground

291 (cm), ii) distance of speaker from nest cup (cm), iii) height of nest tree (m), iv)
292 diameter of nest tree trunk at 1.5 m (mm), v) percentage cover of foliage above
293 and to the north, south, east and west of the nest tree (to the nearest 25%) and vi)
294 distance to the next nest along the cable arm (m).

295 *Monitoring regime and scoring criteria*

296 We checked nests daily over the five days of playback during the hottest part of
297 the day, c.1300-1500 hrs, maintaining playback to confirm equipment was
298 operating correctly. Playback was stopped briefly (typically less than 5 min) daily to
299 change the batteries powering the computer and amplifier. When moving
300 between nests, we walked along the roadside, rather than through the vegetation,
301 and again checked for the presence of potential predators prior to examining each
302 nest contents. Eggs that had been predated were removed and marked with a
303 number indicating the trial number and position in the setup, independent of
304 treatment. Notes were taken on the condition of eggs, likely predator guild
305 (rodent or avian) and, if the timer had been activated, the time of the predation
306 event.

307 At the conclusion of all four trials, all remaining eggs were placed in single bags
308 marked only with trial number and position. After all four trials had been
309 completed, all eggs, regardless of initial classification, were assessed again in the
310 lab under standardized lighting conditions by PM and DW, with a consensus

reached as to predator guild. Any conclusion that was in disagreement with initial field notes was subsequently re-examined after perusal of these notes. This was valuable when no marks were visible on the egg, but it had been lifted out of the nest in such a way that the movement could only have been caused by a predator. After initial categorization into predator guild, marks on eggs were examined relative to measurements taken from museum specimens of likely predators for specific predator identification.

Statistical analyses

We assessed independence of predation events within trials by calculating the likelihood of predation occurring across all nests each day. We then estimated the probability of predation for nests adjacent to a predated nest on that day, testing differences with binomial tests. As some of the nest-site variables were correlated, data were simplified with a principal components analysis (PCA) including the variables nest and tree height, tree branch diameter and the 5 measures of vegetative cover. We extracted components with eigenvalues over 1 for subsequent analyses.

Predation events were analyzed in two ways. First, factors influencing whether a nest was predated or not throughout the entire experiment were assessed using logistic regressions, with the variables of trial (1-4), colony (inside or outside bell miner areas), treatment (control, begging or white noise playback), distance

between nest and speaker, amplitude and the 2 components from the nest-site PCA. Terms were eliminated from the model step-wise (if $p > 0.05$), although both final models had similar results with respect to statistical significance when all terms were included. Second, we conducted a daily survival analysis that examined the daily rate of predation for those nests that were eventually predated in the experiment. This was done using the Efron method of Cox's regression (Hertz-Picciotto and Rockhill 1997) and a step-wise elimination technique ($p < 0.05$ required for factor retention). Factors assessed in this analysis were as above, with the addition of predator guild. Note that as amplitude was 0 for all control nests, models including this factor were restricted to assessing white noise or begging playback nests only. All biologically relevant two-way interactions were tested in both analyses, although significant ($p < 0.05$) terms only are presented for brevity. Binomial tests and logistic regressions were carried out using SPSS v16 for Mac and survival analyses with Stata v10.

Results

Independence of nest within each trial

Of the 168 nests laid out over the four trials, a total of 113 were predated, with 57 nests being taken from inside the bell miner colonies, and 56 nests from outside the colonies. A total of 29 controls, 41 white noise and 43 begging playback nests

were predated. There was no significant daily variation in predation rates over the 6 days of playback, nor could we detect changes in the probability of a nest adjacent to a predated one also being attacked (Table 1). Indeed, the only significant effect was that nests were *less* likely to be taken on the first day if they were adjacent to a nest also taken on that day, the opposite to that predicted if predation events were not independent. The same result is obtained if control nests are excluded from these analyses. Further, no evidence of spatial clustering of nests taken on a given day was found, with only six ‘noisy’ adjacent nests throughout the entire four trials predated on the same day (total number of pairs of adjacent ‘noisy’ nests excluding controls = 62). This rate of predation (9.6%) is much less than the overall predation rate of white noise and begging playback nests (75%, 84 of 112). Further, playback from one nest was rarely audible in the field from an adjacent nest, with the exception of the loudest, central 3 nests on each arm. However, these inner nests were never predated on the same day, further indicating predators were not using playback heard at one nest to find adjacent nests in the array. Predators are also unlikely to have been presented with a supernormal stimulus of multiple nests begging simultaneously. As predators were not apparently receiving multiple cues from nests at any one time, we consider the playback design to be robust against problems associated with pseudoreplication. Further, we specifically included the term ‘trial’ in models to control for differences between replicates. Together, these data indicate that each

nest was an independent datapoint, and we proceeded with the analyses with this assumption.

Predators and time of predation events

Of the nests predated, 73 were scored as being from a rodent predator, and 40 from avian predators. While every egg was readily identifiable as being attacked by either a rodent (e.g. incisor marks) or avian predator (e.g. straight, sharp triangular mandible marks), 8 species of predators were identifiable to the species level ($n = 74$ separate predation events; Table 2). Due to technical difficulties (e.g. condensation shorting timers), times of predation were not obtained for every event. Avian predation occurred at 7 known times, 6 of which were in the morning between 0744 and 1006 hrs, with one afternoon event at 1636 hrs. Rodent predation always occurred overnight, between 1959 and 0309 hrs ($n = 4$).

Factors influencing nest survival

A PCA examining nest site characteristics extracted two components. The first (eigenvalue 2.016), hereafter referred to as 'tree', explained 25.2% of variation, and was mainly correlated with tree height (factor loading score: 0.887), tree diameter (0.823), the level of cover above nests (0.624) and nest height (0.341). The second component, hereafter 'cover', explained an additional 23.2% of variation (eigenvalue 1.855), and primarily loaded with the variables vegetative

cover to the south (0.719), east (0.676) and north (0.304) of nests. The tree and cover components replaced raw nest site measures in all subsequent analyses.

Two factors were important in influencing the probability of nests 'surviving' to the end of the experiment: treatment and trial (Final model: Wald statistic = 22.338, df = 5, $p < 0.001$, Nagelkerke $R^2 = 0.173$; Table 3a). This model correctly classified 95.8% of predated nests ($n = 113$) and 16.4% of surviving nests (9 of 55). When this was assessed further, the predation rate of nests placed near control speakers was significantly less than those placed near speakers playing either begging (Wald = 7.941, df = 1, $p = 0.005$) or white noise sequences (Wald = 5.810, df = 1, $p = 0.016$; Fig. 3). Indeed, no silent control nests ($n = 56$) were taken in the first day of the experiment in any of the four trials. There was remarkably little difference in the predation rates of nests placed near speakers issuing either begging or white noise (41 begging and 43 white noise nests taken; Fig. 3). The trial effect (trials are labeled sequentially) was primarily due to the first trial run having fewer nests predated (19) than either trial 2 (31 nests taken; Wald = 7.29, df = 1, $p = 0.007$), trial 3 (33 nests; Wald = 9.890, df = 1, $p = 0.002$) or trial 4 (30 nests; Wald = 6.128, df = 1, $p = 0.013$). Importantly, both of these effects remained significant even when nests taken by avian (Trial: $p = 0.048$, treatment = 0.037) and rodent predators (Trial: $p = 0.006$, treatment = 0.018) were assessed separately. As it is very unlikely that rodents moved between trials (mean distance between trials 2.3 km \pm 300 m SD), it is also unlikely that this effect was due to a 'learned' response

by predators. Instead this difference is likely due to inclement weather during the first trial and fine, sunny weather during the latter three trials (see Discussion).

Factors influencing the rate of nest predation

Daily survival of nests issuing playback, regardless of whether it was white noise or begging sequences, were influenced by a significant interaction between predator type and playback amplitude (Final model: $\chi^2_3 = 10.61$, $p = 0.014$; Fig. 4; Table 3b). This interaction was the result of a significant decrease in survival with increasing amplitude among avian (Wald = 9.610, $df = 1$, $p = 0.002$) but not rodent-based predation events (Wald = 1.210, $df = 1$, $p = 0.271$).

Discussion

Significant predation costs from begging are often assumed, despite evidence for this being equivocal. Here we were able to overcome many of the problems which have challenged previous work. We used real nests of the focal species, played back hundreds of different age-specific exemplars of both begging and amplitude-matched white noise sequences at the appropriate rate, whilst also assessing the potential benefits of nest defense. There was a clear predation cost for nests placed near speakers emitting begging signals over those placed near silent controls. Moreover, nests placed near speakers emitting white noise pulses suffered predation rates that were nearly identical to those placed near speakers playing begging calls (Fig. 3). We hence find no evidence to support the idea that begging call frequency is designed to reduce detectability or locatability (cf. Marler 1955; Wiley and Richards 1982; Wood et al. 2000). Moreover, these effects persisted even when predation by avian or rodent predators was analyzed independently. Finally, speakers emitting louder sequences of any type were more likely to be attacked, particularly if the predator was avian. Together, this is the first experimental evidence that begging vocalizations are costly, in terms of attracting predators to a nest area, in the context in which they have evolved.

Despite bell miners reputation for monopolizing large tracts of forest with high levels of interspecific aggression (Loyn et al. 1983), placing nests within the boundaries of a colony did not reduce the probability of predation. This finding has

important implications for hypotheses proposed to account for both social living and cooperative breeding, as larger group sizes are typically predicted to be more successful at repelling potential predators (Kruuk 1964; Wiklund and Andersson 1994). While the level of nest concealment has been found to influence predation in some systems (Martin et al. 2000; Eggers et al. 2008), this was not the case here. Similarly, other potential measures of conspicuousness (e.g. speaker proximity) also failed to influence predation, as in several other nest predation studies (Major and Kendall 1996).

Predation rates were similar to those reported for natural bell miner nests. The predators that could be identified to species level were also those previously reported for bell miners in this region (Major and Kendall 1996; Higgins et al. 2001). We conclude that a biologically relevant predator suite was targeted by the experiment, implying that the relationships reported are likely to be representative of those affecting natural nests. Tests for temporal and spatial clustering of predation events showed that attacks on experimental nests were independent. We did observe a trial effect, in that the nests tested in the first trial experienced a lower number of predation events. However, this was likely due to inclement weather, as the first trial experienced two days of heavy rain, whereas all other trials were conducted in dry periods. The results reported (all but trial effects) remain significant if the initial trial is excluded from analyses, indicating that these patterns were also robust with regard to weather conditions.

It is striking that we could detect no difference in predation rates of nests located near speakers broadcasting begging versus matched broadband white noise sequences, which are theoretically some of the easiest acoustic signals to locate (Wiley and Richards 1982). This experimental finding conflicts with correlational evidence suggesting that begging call spectral properties have been selected to be acoustically cryptic (Redondo and Arias de Reyna 1988; Briskie et al. 1994, 1999; Haskell 1999). Our results clearly indicate that any acoustic signal produced at the nest can be used as a cue by eavesdropping predators. Indeed, the fact that predators were attracted to novel white noise stimuli suggests that they were not using the specific frequency structure of begging calls to recognize nest sites, but rather were investigating any intermittent noise. Presumably visual and possibly olfactory cues were then used to find the exact nest location once predators were in the correct vicinity.

Developmental constraints may prevent the production of more cryptic begging signals. In some species, spectral changes in nestling begging occur as nestlings age and presumably gain increased control over the vocal tract (e.g. Wright 1998; Leonard and Horn 2006), a process that is well-documented in production of bird song (Gaunt and Nowicki 1998). Alternatively, nestlings may be using their conspicuous begging signals as a form of ‘blackmail’ over parents and other nest attendants to ensure an adequate supply of food (Zahavi 1977). From this study, it

is clear that nest attendants observing a begging brood face a trade-off between increasing provisioning, at considerable energetic cost (Hatchwell 1999; Heinsohn and Legge 1999), and the predation risk associated with allowing the nestlings to continue to beg loudly. This hypothesis is supported by the finding that when faced with increased begging amplitude, both helpers and parent bell miners in this cooperative species increase their provisioning rates (M^cDonald et al. 2009; Wright et al. in review). Further experimental work examining changes in provisioning effort relative to begging intensity for broods of different fitness value (e.g. brood sizes) would be beneficial in testing this idea.

As sounds from the nest attract predators, it is worth considering that bell miners are one of the few species in which nest attendants give distinctive, loud vocalizations when provisioning young at the nest, despite these not being essential for efficient food transfer (M^cDonald et al. 2007b; M^cDonald and Wright 2008). Recent analyses have concluded that calls given by attendants in these contexts also serve a social cohesion function, helping to coordinate interactions between colony members away from the nest area, such as during mobbing events (M^cDonald et al. 2008a; M^cDonald and Wright 2008). The benefits of such a signaling system in this and other species must be considerable for this mode of communication to persist in the face of increased predation risk to nestlings.

The amplitude of begging signals has been shown to correlate negatively with overall mean level of predation across species (Briskie et al. 1999), although the validity of this comparative analysis has been questioned (Haskell 2002). Dearborn (1999) also experimentally examined the role of amplitude on nestling predation rates, but failed to find a significant difference between calls from passerine (74 dB) versus cowbird nestlings (80 dB). By controlling signal structure and broadcasting over a wider range of amplitudes, we were able to show a pronounced amplitude effect on a finer scale that included nests being taken across all amplitude ranges presented (50 - 89dB). The positive relationship between predation rate and amplitude was part of an interaction with predator guild that was driven by avian predators taking louder nests more quickly. This fits the expectation that avian predators use acoustic cues to locate nests, and that louder cues are more easily found. Importantly, there was no interaction between amplitude (as a proxy of distance from the central playback equipment) and colony in either model, indicating that predation pressure did not decline the further nests were placed within bell miner colonies.

In contrast to nests taken by avian predators, the effect of amplitude on nest survival for those eventually taken by rodents was not significant (Fig. 4), despite rodents taking more playback nests as opposed to silent controls. Rodents are not typically thought of as using acoustic cues to locate nests (e.g. Haskell 2002). However clearly they did so here, as the limited number of nests for which

accurate times of predation were recorded were all predated overnight whilst they were silent. This, in conjunction with a lack of amplitude effect on nest survival, suggests that largely nocturnal rodents investigate areas of interest that are identified whilst inactive during the day. This is consistent with recent findings that mobbing calls broadcast from nest boxes during daylight hours attract nocturnal mammalian predators over subsequent nights, again in the absence of a signal during these periods (Krams et al. 2007). The predation risks of begging during daylight hours therefore apparently extends to attracting nocturnal predators eavesdropping on potential cues of nest locations even when inactive.

The results of the present study have important implications for theories of parent-offspring conflict and the evolution of parental care, as increased begging is associated with increases in provisioning rates in many species (Wright and Leonard 2002), including the bell miner (McDonald et al. 2009; Wright et al. in review). Our finding that begging vocalizations increase predation rate is consistent with Zahavi's (1977) suggestion that begging may function as a form of 'blackmail', forcing parents and/or attendants to increase provisioning levels.

While alarm calls from attendants may reduce predation costs by inhibiting begging in some systems (e.g. Davies et al. 2004; Platzen and Magrath 2004), any such mitigation is unlikely to be completely effective. In addition, predators may detect begging nestlings before attendants are able to give alarm calls, as is likely the case for nocturnal rodents. In the absence of error-free modulation of call

production, nestlings face an inescapable trade-off between within-brood competition and/or parent-offspring conflict over limited resources. Both of these favor increased call production, as well as a concurrent increased risk of predation. This study therefore provides unequivocal evidence for predation costs being associated with nestling begging, a critical component of the majority of ESS models examining the evolution of this signal.

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- 696

697 **Table 1. Daily predation rates (proportion predated) for all nests within a trial,**
 698 **and for those located immediately adjacent to a predated nest.**

Playback age (days)	<i>n</i>	Daily predation rate	Adjacent rate	p value
6	168	0.042	0	0.001
7	161	0.149	0.333	0.136
8	137	0.117	0.063	0.426
9	121	0.099	0.250	0.108
10	109	0.284	0.194	0.181
11	78	0.295	0.130	0.060

Results for binomial tests assessing the significance of differences are also

presented. Significant values are in bold.

Table 2. Predators of the 113 artificial wax eggs identified to the species level.

Predator guild	Specific name	Confident	Probable
<i>rodents</i>			
Black rat	<i>Rattus rattus</i>	6	1
House mouse	<i>Mus domesticus</i>	48	0
Insufficient detail to identify		17	0
<i>Total</i>		71	1
<i>Birds</i>			
Australian magpie	<i>Gymnorhina tibicen</i>	2	1
Australian raven	<i>Corvus coronoides</i>	1	2
Grey shrike-thrush	<i>Colluricincla harmonica</i>	4	3
Laughing kookaburra	<i>Dacelo novaeguineae</i>	0	1
Pied currawong	<i>Strepera graculina</i>	3	1
Green catbird/Satin bowerbird	<i>Ailuroedus crassirostris/</i> <i>Ptilonorhynchus violaceus</i>	0	1
Insufficient detail to identify		22	0
<i>Total</i>		32	9

Identification based on comparisons of marks on wax eggs with teeth/bills of

potential predators.

Table 3. Results from a) logistic regressions assessing the probability of nests surviving the entire playback period and b) Cox's regressions of daily survival rates of nests.

Factor	Wald statistic	df	p value
<i>a) Survival through the experiment (all nests)</i>			
Final model:			
Trial (1 through 4)	12.710	3	0.005
Treatment (begging, white noise, control)	9.650	2	0.008
Other factors:			
Speaker distance from nest	0.840	1	0.360
Cover	0.485	1	0.486
Tree	0.376	1	0.540
Colony (within/outside miner colony)	0.071	1	0.790
Amplitude	0.244	1	0.621
<i>b) Daily survival of nests (predated playback nests only)</i>			
Final model:			
Predator (avian or rodent)	0.960	1	0.327
Amplitude	9.610	1	0.002
Predator x amplitude	4.368	1	0.036
Other factors:			
Trial (1 through 4)	7.440	3	0.059
Cover	0.608	1	0.432
Tree	0.281	1	0.598
Treatment (begging, white noise)	0.044	1	0.832
Speaker distance from nest	0.137	1	0.709
Colony	0.040	1	0.839

Significant terms in bold, with values for remaining factors presented when added to final models. Dropped factors are presented from most recent to first dropped terms. Note that, as the control treatment had an amplitude of zero, models including amplitude excluded these nests from analysis. All two-way interactions were assessed, with significant results only presented for brevity.

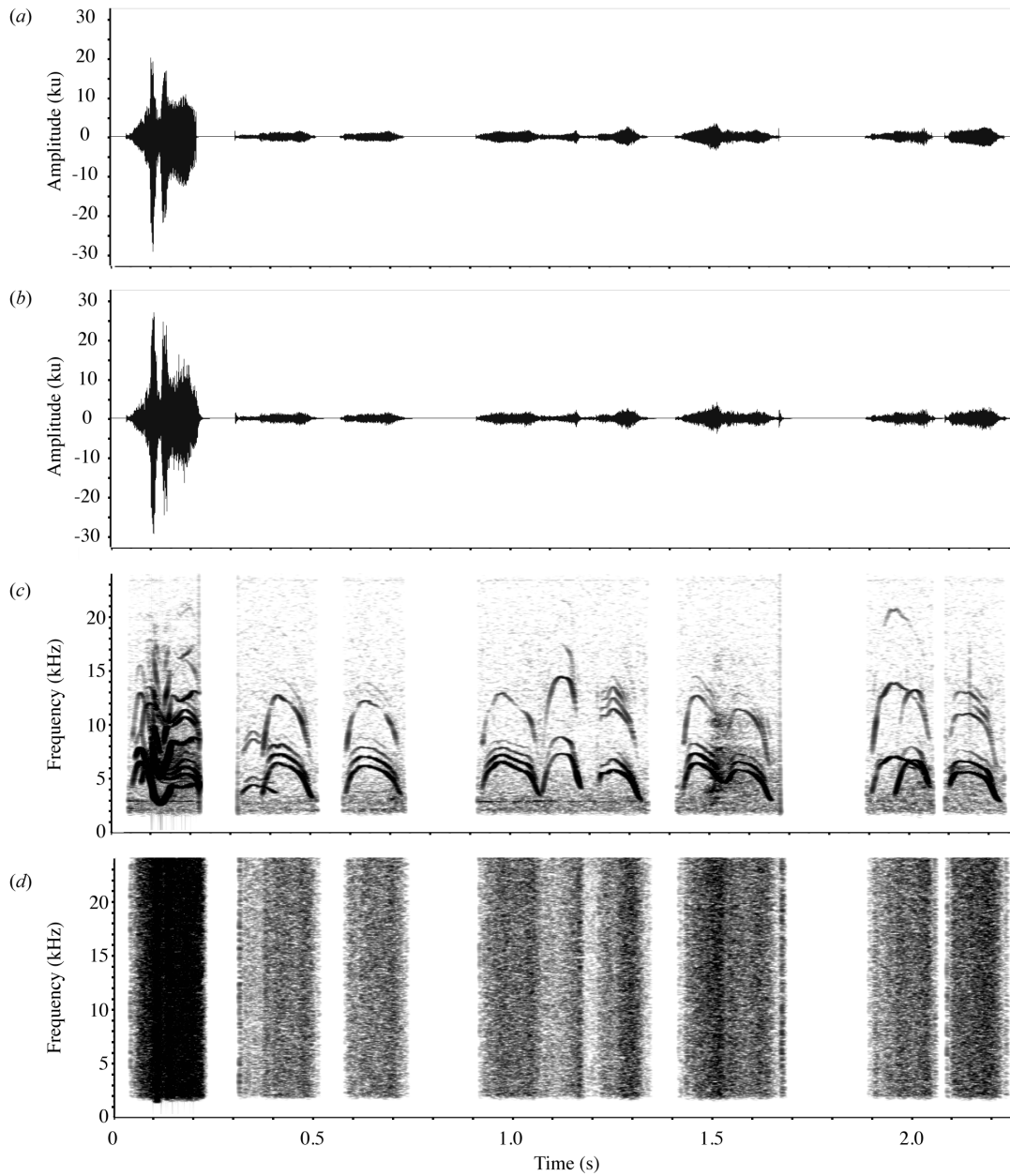


Figure 1. A representative example, depicted as both waveforms (a,b,) and spectrograms (c,d), of a section of the playback stimuli used. a,c) represent the begging playback treatment, while b,d) depict the amplitude and temporally matched equivalent white noise sequence. Spectrograms constructed with a Hanning window function at a sample rate of 1024, 3 dB bandwidth filter at 61 Hz and overlap set to 94.9%. Grey scale represents a 52 dB range.

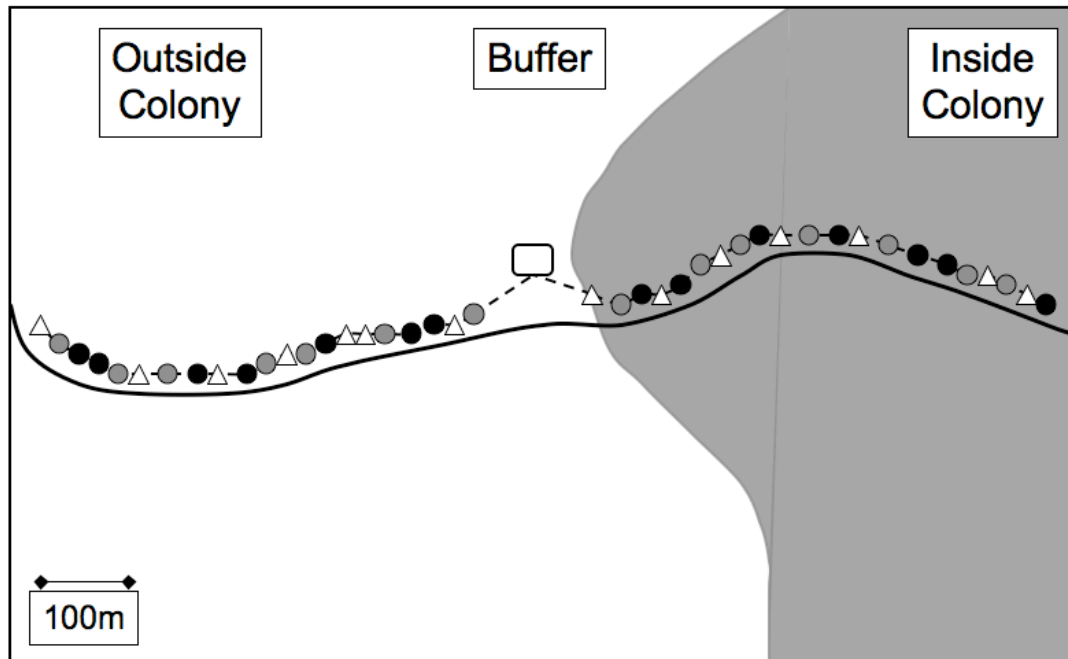


Figure 2. A schematic of a typical playback array (trial 2). Different treatments are indicated by filled circles (Controls), shaded circles (Begging playback) or triangles (White noise playbacks). Roads (solid lines), speaker cable (dashed lines), computer location (open rectangle) and areas defended by miners (shaded) are also depicted.

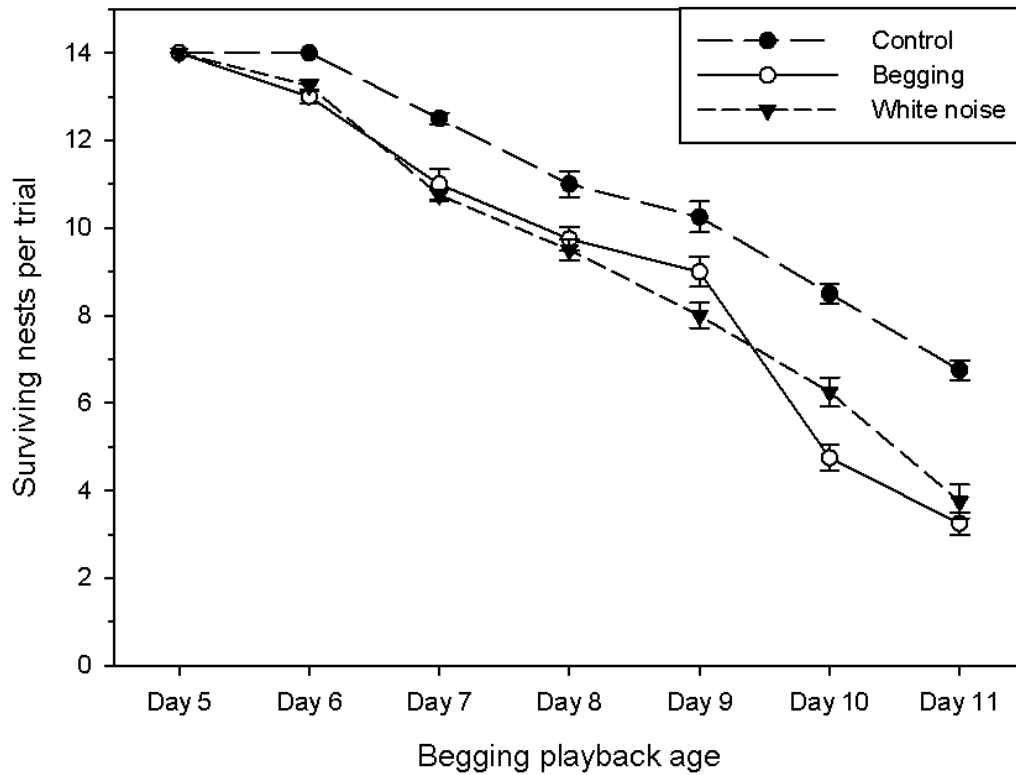
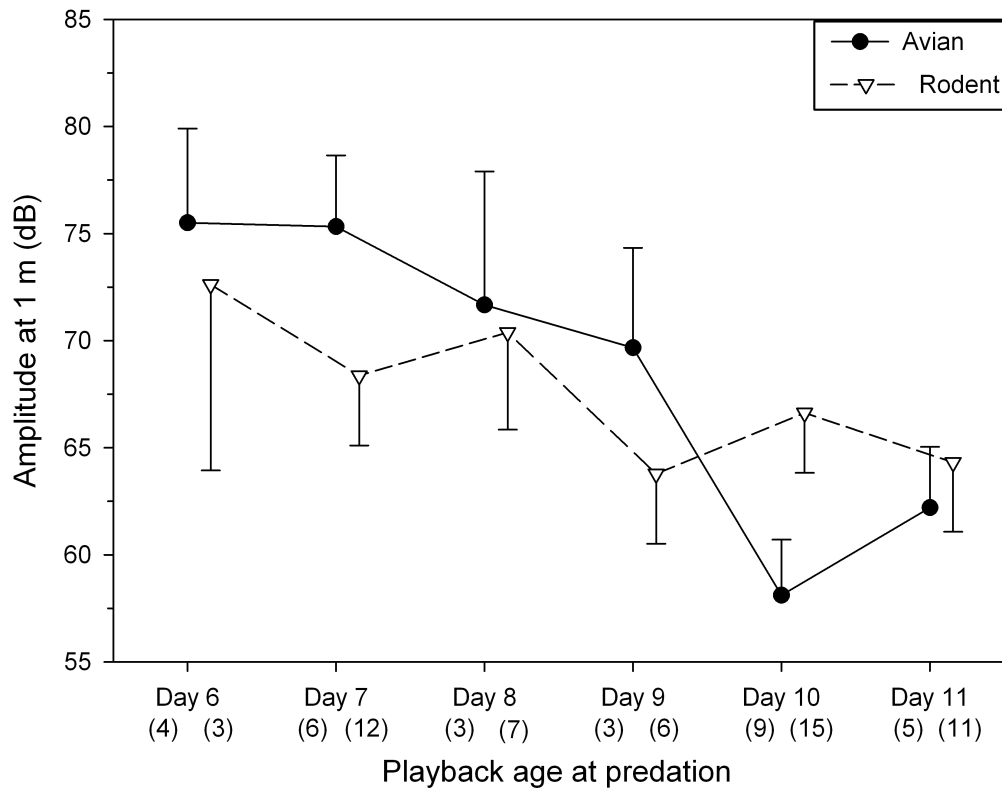


Figure 3. Mean number of nests surviving for each treatment (control, begging or white noise playback) for each of four trials. Playback age is the age of broods from which begging sequences were obtained, in days post-hatch (range 6 -10). Thus day 5 represents the beginning and day 11 the end of the experimental period, before and after playback, respectively. Error bars represent one standard error.



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Figure 4. Mean amplitude of sound playback from nests that survived to a given day during the experiment, according to whether they were eventually predated by either avian (filled circles) or rodent predators (open triangles). Error bars represent one standard error, numbers in parentheses refer to sample sizes. Rodent data are offset to the right slightly for clarity.