

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

Paul G. McDonald, David R. Wilson, and Christopher S. Evans

Department of Brain, Behaviour and Evolution, Centre for the Integrative Study of Animal Behaviour, Macquarie University, Sydney 2109, Australia

Models of parent–offspring conflict and nestling begging honesty often assume that signaling is associated with increased predation risk. However, little evidence exists that begging actually increases predation in the context in which it evolved, especially when the potentially modulating effects of parental defense are taken into account. We measured the cost of begging in cooperatively breeding bell miners (*Manorina melanophrys*) by baiting 168 inactive nests with a wax egg and broadcasting sounds from nearby speakers. Nests were randomly assigned to 1 of 3 treatments: silence, unmanipulated begging calls, or shaped white noise pulses that matched the amplitude envelope of each corresponding begging call. Moreover, half of the nests were placed outside and half inside bell miner colonies, where miners vigorously mob potential nest predators. Predation was not influenced by vegetation cover, distance of the nest from the speaker, or placement inside the colony. Sounds were costly, however, as nests broadcasting begging signals or white noise were predated more often and more quickly than silent controls. Contrary to theoretical predictions regarding “stealthy” design, we found that predators were just as likely to locate nests with broadband white noise playback as nests broadcasting begging signals. Further, there was an interaction between playback amplitude and predator type (avian vs. rodent): Louder playback led to decreased nest survival for those taken by avian predators. As increased begging drives provisioning rates in many species, including bell miners, this reveals an inescapable trade-off between nestling begging intensity, parental provisioning effort, and predation risk. *Key words:* costs of signals, parent–offspring conflict, predator–prey interactions, signal design. [*Behav Ecol* 20:821–829 (2009)]

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

Differences in begging intensity between brood mates can also affect within-brood competition (Briskie et al. 1994; Cotton et al. 1996; Bulmer et al. 2008). For example, more intense begging has been documented in species with high levels of extrapair fertilizations and thus low levels of within-brood relatedness (Briskie et al. 1994). This conflict over resource allocation has generated considerable theoretical work investigating the factors that lead to evolutionarily stable strategies (ESS) of signaling (“honest signaling”; Johnstone and Godfray 2002). Although some models reach equilibrium utilizing cost-free signals, their broad applicability remains doubtful (Brilot and Johnstone 2003). More commonly, models rely on 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, nonmutually 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 are 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). Although 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,

Address correspondence to P.G. McDonald. E-mail: paul@galliform.bhs.mq.edu.au.

Received 9 November 2008; revised 27 February 2009; accepted 1 April 2009.

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 Kendal 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 1988) and thus potentially reduce predation risk costs associated with begging. Although 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 (i.e., nest location, amplitude, and rate of begging) 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 revisited 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, and temporal and acoustic properties of begging) and identified a positive relationship between begging intensity and provisioning effort (e.g., Poiani 1993; McDonald, Kazem, et al. 2008; McDonald, te Marvelde, et al. 2008; McDonald et al. 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 mobbing predators within the colony) and outside miner colonies, utilizing hundreds of exemplars of age-specific recordings of nestlings.

In the current study, we assessed the following questions: 1) Do begging signals cause increased predation relative to silence? 2) 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: 3) Are louder vocalizations more risky? 4) 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 4 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 mobbing predators within the colony) and 21 outside of colonies (undefended nests, note that 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, the latter with the same amplitude characteristics as the 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 of 113 calls obtained for each age from 6 to 10 days posthatch. On each of 5 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, Kazem, et al. 2008; McDonald, te Marvelde, et al. 2008) 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 (McDonald, Kazem, and Wright 2007). Begging calls were collected from nestlings between 6 and 10 days posthatch. This corresponds to the days immediately prior to fledging (10–12 days posthatch) when provisioning rates and thus begging rates are maximal (te Marvelde et al. 2009).

To re-create the natural begging rate of 32 bouts per hour throughout all daylight hours (McDonald, te Marvelde, et al. 2008; 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 1 day (i.e., 25 broods in total). Begging sequences were relatively long ($7.8 \text{ s} \pm 3.3\text{SD}$, standard deviation) and consisted of intermittent vocalizations (hereafter “syllables”) punctuated by brief periods of silence ($11 \pm 5\text{SD}$ syllables per sequence; Figure 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, United States). The brief periods of silence between syllables were also filtered across all frequencies using Raven. Finally, all sequences were high-pass filtered (138 at 1200 Hz; remainder at 1800 Hz) using Signal software (Engineering Design; United States; 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

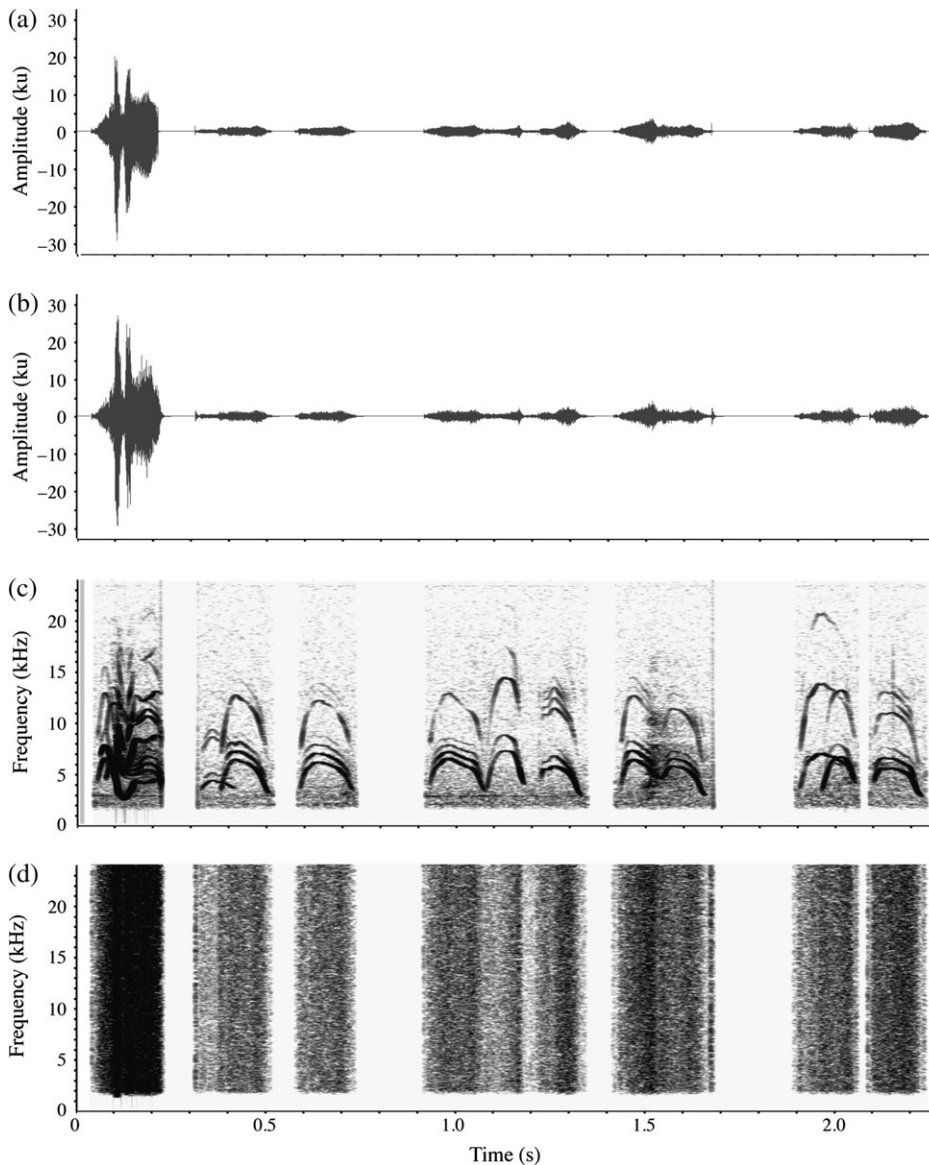


Figure 1

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, whereas (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%. Gray scale represents a 52-dB range.

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 -1 dB and combined as separate channels into a single stereo file using Quicktime v7.5 (Apple; United States). This process generated 567 pairs of files, which 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 (Figure 1; see ESM).

Preparation of artificial nests

Intact nests previously used by bell miners were collected, after completion of nesting attempts during previous studies (McDonald, Kazem, et al. 2008; McDonald, te Marvelde, et al. 2008) and stored in sealed plastic bags. Artificial eggs were constructed using microcrystalline wax (All Australian Candle Making Supplies, Australia). Comparisons revealed

no difference in predation rates between real (*Poephila acuticauda*) eggs (3 of 9) and similarly sized wax eggs (6 of 9) placed on the ground to encourage rodent predation, the most likely predators to utilize olfactory cues. Mold size was chosen to provide a close match to bell miner eggs (molds: 22×16 mm $L \times W$, Home Chocolate Factory; United Kingdom; bell miner eggs 24×16 mm; Beruldsen 1980). Eggs were constructed according to the methods outlined in McEntee (2007), with the addition of a small fishing line swivel (Size 8; Jarvis Walker, Australia) inserted into the egg to provide an attachment point for a monofilament line (15 kg, low visibility; Penn, United States) used to secure the eggs.

Playback apparatus

Playbacks were conducted over 4 trials ($n = 42$ nests per trial; $n = 168$ nests in total), during the breeding season (3 February–8 April 2008) at Ourimbah State Forest ($33^{\circ}18'22''S$, $151^{\circ}19'17''E$), approximately 60 km north of Sydney, Australia. Boundaries of the 4 different bell miner colonies were determined on foot by walking along focal roads. This could be done confidently to ± 10 m, as individual miners inhabit relatively small and static active spaces (Clarke

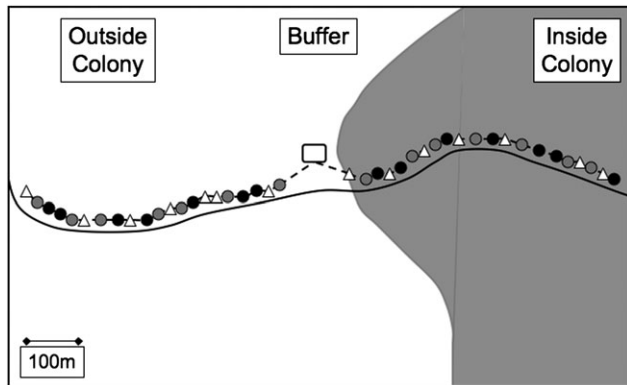


Figure 2

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.

and Fitz-Gerald 1994) are extremely vociferous and are obligate colonial species; individuals do not move outside the colony boundary except on very rare dispersal events.

All speakers and artificial nests were placed along the edge of vegetation lining unsealed (unpaved) tracks through the forest. To begin, we laid 2 rows of speaker cable (17 gauge, 2×0.14 mm; Radio Parts Group, Melbourne, Australia) for 520 m through an area occupied, and thus defended, by bell miners (Figure 2). Two rows of cable were used to carry the 2 channels of the stereo files used as stimuli. Cable was placed in dense undergrowth 2–3 m from the edge of tracks and was covered with additional leaf litter. After this, beginning at the edge of the colony, we ran another 100 m of paired cable adjacent to the track in the opposite direction. This point was the center of the layout, where playback equipment was eventually situated (see below). We then replicated this initial 620 m “arm” of the design by laying cable away from the bell miner colony (Figure 2).

Speakers ($n = 42$; SPG6555; Redback, Australia) were then placed below likely nesting places at 26-m intervals along each 520-m section of cable, leaving the 2 center 100-m sections without speakers. This distance was based on the mean separation between bell miners in other studies ($26.4 \text{ m} \pm 5.4\text{SD}$; Poiani 1993; McDonald P, unpublished data; $n = 71$ nests). Speakers and artificial nests were not placed within 26 m of active nests of any species. Thus, we placed 21 nests inside each bell 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 4 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 ($34.3 \text{ cm} \pm 11.7\text{SD}$ from speakers; range 12–67 cm, $n = 168$). Suitable sites were chosen based on P.M.’s experience with this species and were similar in characteristics to actual nest sites (e.g., nest height: $1.5 \text{ m} \pm 0.3\text{SD}$, $n = 168$ this study; cf. $2.1 \text{ m} \pm 1.8\text{SD}$, $n = 137$ nests, McDonald P, unpublished 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 2 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 base of the tree in which the nest was placed. If eggs were moved substantially, the monofilament was stretched, dislodging the plastic, closing the timer circuit, and starting the clock.

In the center of the loudspeaker array, we used a Macintosh computer (G4 MacMini, 1.44 GHz, 2 GB RAM) housed in a weather-proof box to play back call sequences simultaneously at each speaker using iTunes software, a digital/analogue converter (FCA202; Behringer, Germany; 48 kHz/16 bits) and an amplifier (AH500 180W; Behringer). This setup was powered by an inverter (300W; Dick Smith Electronics; Australia) attached to 2 deep-cycle batteries (US2200; US Battery, United States) and was programed to broadcast calls from 30 min before sunrise through to 30 min after the local sunset. Bell miners typically begin and end daily provisioning at these relative times (McDonald P, unpublished data). We used iCal and Applescripts software to control the computer and initiate and terminate playback as appropriate, adjusting for changes in day length for each trial.

Playback rate and amplitude were based on natural data from typical bell miner nests, which average 32 provisioning visits per hour, a rate that is stable between the ages of 6 and 10 days posthatch (te Marvelde et al. 2009). To introduce natural variability into the timing of playbacks, while maintaining hourly averages of 32 sequences interspersed with silence, across the 5 days, we played calls at rates of either 28, 30, 32, 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 4 trials, a new randomized call order was used. Each playback was of a particular begging bout from 1 of the 5 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 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 (days 6–10, measured using a Realistic 33-2050 SPL meter, “C” weighting, fast response; Radioshack, United States). 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 1 or 2 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: 1) height of nest cup above ground (cm), 2) distance of speaker from nest cup (cm), 3) height of nest tree (m), 4) diameter of nest tree trunk at 1.5 m (mm), 5) percentage cover of foliage above and to the north, south, east, and west of the nest tree (to the nearest 25%), and 6) distance to the next nest along the cable arm (m).

Monitoring regime and scoring criteria

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

At the conclusion of all 4 trials, all remaining eggs were placed in single bags marked only with trial number and position. After all 4 trials had been completed, all eggs, regardless of initial classification, were assessed again in the laboratory under standardized lighting conditions by P.M. and D.W., with a consensus reached as to predator guild. Any conclusion that was in disagreement with initial field notes was subsequently reexamined 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 2 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 stepwise (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 stepwise 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 2-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 4 trials, a total of 113 were predated, with 57 nests being taken from inside the bell miner

Table 1

Daily predation rates (proportion predated) for all nests within a trial and for those located immediately adjacent to a predated nest

Playback age (days)	<i>n</i>	Daily predation rate	Adjacent rate	<i>P</i> 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.

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 6 “noisy” adjacent nests throughout the entire 4 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 1 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 1 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. Although 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 h, with 1 afternoon event at 1636 h. Rodent predation always occurred overnight, between 1959 and 0309 h ($n = 4$).

Factors influencing nest survival

A PCA examining nest-site characteristics extracted 2 components. The first (eigenvalue 2.016), hereafter referred to as

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

Predator guild	Specific name	Confident	Probable
Rodents			
Black rat	<i>Rattus rattus</i>	6	1
House mouse	<i>Mus domesticus</i>	48	0
Insufficient detail to identify		17	0
Total		71	1
Birds			
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/violaceus</i>	0	1
Insufficient detail to identify		22	0
Total		32	9

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

“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, $df = 1$, $P = 0.016$; Figure 3). Indeed, no silent control nests ($n = 56$) were taken in the first day of the experiment in any of the 4 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; Figure 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 $2.3 \text{ km} \pm 0.3SD$), 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 3 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

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
a) Survival through the experiment (all nests)			
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
b) Daily survival of nests (predated playback nests only)			
Final model			
Predator (avian or rodent)	0.960	1	0.327
Amplitude	9.610	1	0.002
Predator × amplitude	4.368	1	0.036
Other factors			
Trial (1–4)	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 0, models including amplitude excluded these nests from analysis. All 2-way interactions were assessed, with significant results only presented for brevity.

amplitude (Final model: $\chi_3^2 = 10.61$, $P = 0.014$; Figure 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 that 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, while 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 (Figure 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

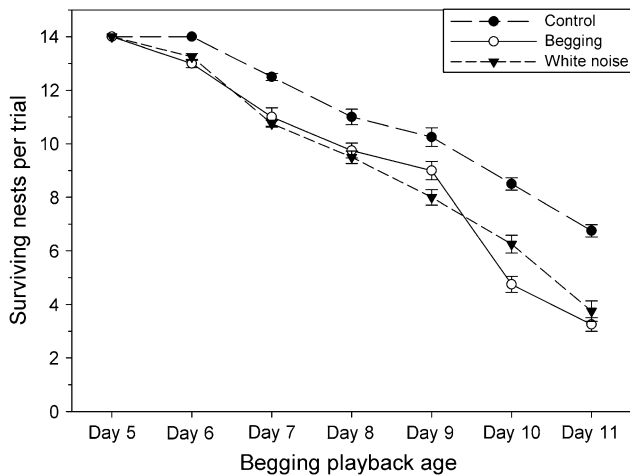


Figure 3
 Mean number of nests surviving for each treatment (control, begging, or white noise playback) for each of 4 trials. Playback age is the age of broods from which begging sequences were obtained, in days posthatch (range 6–10). Thus, day 5 represents the beginning and day 11 the end of the experimental period, before and after playback, respectively. Error bars represent 1 standard error.

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). Although 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.

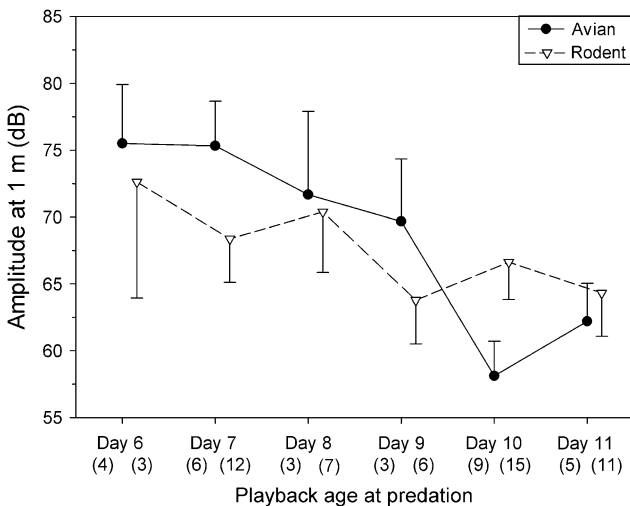


Figure 4
 Mean amplitude of sound playback from nests that survived to a given day during the experiment, according to whether they were eventually predated by either avian (filled circles) or rodent predators (open triangles). Error bars represent 1 standard error, numbers in parentheses refer to sample sizes. Rodent data are offset to the right slightly for clarity.

Similarly, other potential measures of conspicuousness (e.g., speaker proximity) also failed to influence predation, as in several other nest predation studies (Major and Kendal 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 Kendal 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 2 days of heavy rain, whereas all other trials were conducted in dry periods. The results reported (all bar 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 (McDonald et al. 2009; Wright et al. [forthcoming]). 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 (McDonald, Heathcote, et al. 2007; McDonald 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 (McDonald, te Marvelde, et al. 2008; McDonald 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 (50–89 dB). 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 (Figure 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, they clearly did so here, as the limited number of nests for which accurate times of predation were recorded were all predated overnight, while 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 while 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. [forthcoming]). 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. Although 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.

FUNDING

Macquarie University Research Fellowship to P.M.

Forests NSW kindly allowed fieldwork to be undertaken on their land. Sidney McDonald assisted with constructing the timer systems and Mike Clarke provided some of the nests used from his studies. Sarah Pryke and James Brazill-Boast provided finch eggs. Walter Boles and Sandy Ingleby facilitated access to specimens at the Australian Museum collection for predator identification. Alan Taylor provided helpful advice on the statistical analyses. The research was approved by the Macquarie University Animal Ethics committee (license ARA2007/010) and Forests NSW (license XX38571).

REFERENCES

- Bell MB. 2008. Strategic adjustment of begging effort by banded monogoose pups. *Proc R Soc Lond B*. 275:1313–1319.
- Beruldsen G. 1980. A field guide to nests and eggs of Australian birds. Adelaide (Australia): Rigby Publishers Limited.
- Bristol BO, Johnstone RA. 2003. The limits to cost-free signalling of need between relatives. *Proc R Soc Lond B*. 270:1055–1060.
- Briskie JV, Martin PR, Martin TE. 1999. Nest predation and the evolution of nestling begging calls. *Proc R Soc Lond B*. 266:2153–2159.
- Briskie JV, Naugler CG, Leech SM. 1994. Begging intensity of nestling birds varies with sibling relatedness. *Proc R Soc Lond B*. 258:73–78.
- Budden AE, Wright J. 2001. Falling on deaf ears: the adaptive significance of begging in the absence of a parent. *Behav Ecol Sociobiol*. 49:474–481.
- Bulmer E, Celis P, Gil D. 2008. Parent-absent begging: evidence for sibling honesty and cooperation in the spotless starling (*Sturnus unicolor*). *Behav Ecol*. 19:279–284.
- Chappell MA, Bachman GC. 2002. Energetic costs of begging behavior. In: Wright J, Leonard ML, editors. *The evolution of begging: competition, cooperation and conflict*. Dordrecht (the Netherlands): Kluwer Academic Publishers. p. 143–162.
- Clarke MF, Fitz-Gerald GF. 1994. Spatial organisation of the cooperatively breeding bell miner *Manorina melanophrys*. *Emu*. 94:96–105.
- Cotton PA, Kacelnik A, Wright J. 1996. Chick begging as a signal: are nestlings honest? *Behav Ecol*. 7:178–182.
- Davies NB, Madden JR, Butchart SHM. 2004. Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species. *Proc R Soc Lond B*. 271:2297–2304.
- Dearborn DC. 1999. Brown-headed cowbird nestling vocalizations and risk of nest predation. *Auk*. 116:448–457.
- Eggers S, Griesser M, Ekman J. 2008. Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. *Behav Ecol*. 19:1056–1062.
- Furlow FB. 1997. Human neonatal cry quality as an honest signal of fitness. *Evol Human Behav*. 18:175–193.
- Gaunt AS, Nowicki S. 1998. Sound production in birds: acoustics and physiology revisited. In: Hopp SL, Owren MJ, Evans CS, editors. *Animal acoustic communication: sound analysis and research methods*. Berlin: Springer. p. 291–322.
- Godfray HCJ. 1991. Signalling of need by offspring to their parents. *Nature*. 352:328–330.
- Haskell DG. 1994. Experimental evidence that nestling begging behavior incurs a cost due to nest predation. *Proc R Soc Lond B*. 257:161–164.
- Haskell DG. 1999. The effect of predation on begging-call evolution in nestling wood warblers. *Anim Behav*. 57:893–901.
- Haskell DG. 2002. Begging behaviour and nest predation. In: Wright J, Leonard ML, editors. *The evolution of begging: competition, cooperation and conflict*. Kluwer Academic Publishers. p. 163–172.
- Hatchwell BJ. 1999. Investment strategies of breeders in avian cooperative breeding systems. *Am Nat*. 154:205–219.
- Heinsohn RG, Legge S. 1999. The cost of helping. *TREE*. 14:53–57.
- Hertz-Picciotto I, Rockhill B. 1997. Validity and efficiency of approximation methods for tied survival times in Cox regression. *Biometrics*. 53:1151–1156.
- Higgins PJ, Peter JM, Steele WK. 2001. *Handbook of Australian, New Zealand and Antarctic birds*. Vol. 5: Tyrant-flycatchers to chats. Melbourne (Australia): Oxford University Press.
- Johnstone RA, Godfray HCJ. 2002. Models of begging as a signal of need. In: Wright J, Leonard ML, editors. *The evolution of begging:*

- competition, cooperation and conflict. Dordrecht (the Netherlands): Kluwer Academic Publishers. p. 1–20.
- Kilner RM. 2001. A growth cost of begging in captive canary chicks. *Proc Natl Acad Sci.* 98:11394–11398.
- Kilner RM, Johnstone RA. 1997. Begging the question: are offspring solicitation behaviours signals of need? *TREE.* 12:11–15.
- Krams I, Krama T, Igaune K, Mand R. 2007. Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behav Ecol.* 18:1082–1084.
- Kruuk H. 1964. Predators and anti-predator behaviour of the black-headed gull (*Larus ridibundus* L.). *Behav Suppl.* 11:1–129.
- Leech SM, Leonard ML. 1997. Begging and the risk of predation in nestling birds. *Behav Ecol.* 8:644–646.
- Leonard ML, Horn AG. 2006. Age-related changes in signalling of need by nestling tree swallows (*Tachycineta bicolor*). *Ethol.* 112:1020–1026.
- Leonard ML, Horn AG. 2008. Does ambient noise affect growth and begging call structure in nestling birds? *Behav Ecol.* 19:502–507.
- Loyn RH, Runnalls RG, Forward GY. 1983. Territorial bell miners and other birds affecting populations of insect prey. *Science.* 221:1411–1413.
- Madden JR, Kilner RM, Davies NB. 2005. Nestling responses to adult food and alarm calls 2: Cowbirds and red-winged blackbirds reared by eastern phoebe hosts. *Anim Behav.* 70:629–637.
- Major RE, Kendal CE. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis.* 138:298–307.
- Marler P. 1955. Characteristics of some animal calls. *Nature.* 176:6–8.
- Martin TE, Scott J, Menge C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc R Soc Lond B.* 267:2287–2293.
- McDonald PG, Heathcote CF, Clarke MF, Wright J, Kazem AJN. 2007. Provisioning calls of the cooperatively breeding bell miner *Manorina melanophrys* encode sufficient information for individual discrimination. *J Avian Biol.* 38:113–121.
- McDonald PG, Kazem AJN, Clarke MF, Wright J. 2008. Helping as a signal: does removal of potential audiences alter helper behavior in the bell miner? *Behav Ecol.* 19:1047–1055.
- McDonald PG, Kazem AJN, Wright J. 2007. A critical analysis of ‘false-feeding’ behaviour in a cooperatively breeding bird: disturbance effects, satiated nestlings or deception? *Behav Ecol Sociobiol.* 61:1623–1635.
- McDonald PG, Kazem AJN, Wright J. 2009. Cooperative provisioning dynamics: fathers and unrelated helpers show similar responses to manipulations of begging. *Anim Behav.* 77:369–376.
- McDonald PG, te Marvelde L, Kazem AJN, Wright J. 2008. Helping as a signal and the effect of a potential audience during provisioning visits in a cooperative bird. *Anim Behav.* 75:1319–1330.
- McDonald PG, Wright J. 2008. Provisioning vocalizations in cooperative bell miners: more than a simple stimulus for nestling begging? *Auk.* 125:670–678.
- McEntee D. 2007. Use of artificial nests to monitor predators in braided river systems (Masters). Christchurch: Lincoln University.
- Montgomerie RD, Weatherhead PJ. 1988. Risks and rewards of nest defence by parent birds. *Q Rev Biol.* 63:167–187.
- Platzen D, Magrath RD. 2004. Parental alarm calls suppress nestling vocalization. *Proc R Soc Lond B.* 271:1271–1276.
- Poiani A. 1993. Reproductive biology of the Bell Miner (*Manorina melanophrys*, Meliphagidae) at Healesville, South-eastern Victoria. *Wild Res.* 20:579–598.
- Rauter CM, Moore AJ. 1999. Do honest signalling models of offspring solicitation apply to insects? *Proc R Soc Lond B.* 266:1691–1696.
- Redondo T, Arias de Reyna L. 1988. Locatability of begging calls in nestling altricial birds. *Anim Behav.* 36:653–661.
- Rodríguez-Gironés MA, Zúñiga JM, Redondo T. 2001. Effects of begging on growth rates of nestling chicks. *Behav Ecol.* 12:269–274.
- te Marvelde L, McDonald PG, Kazem AJN, Wright J. 2009. Do helpers really help? Provisioning biomass and prey type effects on nestling growth in the cooperative bell miner. *Anim Behav.* 77:727–735.
- Thompson FR III, Burhans DE. 2004. Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. *Cons Biol.* 18:373–380.
- Wiklund CG, Andersson M. 1994. Natural selection of colony size in a passerine bird. *J Anim Ecol.* 63:765–774.
- Wiley RH, Richards DG. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Kroodsma DE, Miller EH, Ouellet H, editors. *Acoustic communication in birds Vol. 1: Production, perception, and design features of sounds.* New York: Academic Press. p. 131–181.
- Wood SR, Sanderson KJ, Evans CS. 2000. Perception of terrestrial and aerial alarm calls by honeyeaters and falcons. *Aust J Zool.* 48:127–134.
- Wright J. 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. *Behav Ecol Sociobiol.* 42:423–429.
- Wright J, Dingemanse NJ. 1999. Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. *Anim Behav.* 58:345–350.
- Wright J, Leonard ML, editors. 2002. *The evolution of begging: competition, cooperation and communication.* Dordrecht (the Netherlands): Kluwer Academic Press.
- Wright J, McDonald PG, te Marvelde L, Kazem AJN. (Forthcoming). Direct versus indirect fitness benefits: male and female helpers respond to begging for different reasons.
- Zahavi A. 1977. Reliability in communication systems and the evolution of altruism. In: Stonehouse B, Perrins C, editors. *Evolutionary ecology.* London: Macmillan Press. p. 253–259.