

Convergent characteristics of begging vocalisations in Australian birds

Mark A. Jurisevic

School of Biological Sciences, Flinders University of South Australia, G.P.O. Box 2100, Adelaide, South Australia, 5001, Australia.

Abstract

The acoustic structure and sound pressure level (i.e. loudness) of begging calls from nestlings and fledglings were examined for 12 species of Australian passerines and three species of parrots. There was a great deal of variation in the acoustic structure of the begging calls between species. Some calls were quite short in duration (0.06-0.1 s) while others were very long (0.98-1.51 s). However, most begging calls were loud and covered a wide range of frequencies consisting of noisy and/or harmonic components. These acoustic characteristics, which were observed in all species, presumably allow for efficient detection and location of the calling bird by parents, as well as signalling the birds' nutritional requirements. The potential negative consequences of producing these vocalisations are an increased risk of detection by predators and a high metabolic cost. The findings of this study suggest that the potential risks associated with begging in Australian birds are offset by the benefits gained from producing loud, wide band vocalisations that can be easily detected and located by parents.

Keywords: begging calls, convergent structure, passerines and parrots

Introduction

Begging vocalisations are of particular interest as they represent an adaptive compromise between positive and negative selection factors. Begging vocalisations are beneficial as they convey information regarding the nutritional requirements of chicks, which induces feeding by the parents, and along with other forms of activity such as wing fluttering, stretching, gaping and pushing, are used to compete with siblings for food (e.g. Redondo & Arias de Reyna, 1988; Redondo & Castro, 1992b; Cotton et al., 1996). The negative effects of conspicuous activity associated with begging are elevated energy requirements (Leech & Leonard, 1996; Bachman & Chappell, 1999; Jurisevic et al., 1999) and an increased likelihood of predation (Redondo & Arias de Reyna, 1988; Redondo & Castro, 1992a; Haskell, 1994; Briskie et al., 1999; Dearborn, 1999) particularly by predators that may use acoustic cues to locate nests (Dunn, 1977).

Comparative studies on begging vocalisations have only been carried out on Northern Hemisphere species and show the acoustic structure to be quite variable. Many species produce begging calls which provide abundant cues for detection and location; acoustic energy which is noisy or harmonic covering a wide frequency spectrum (Redondo & Arias de Reyna, 1988; Popp & Ficken, 1991). By contrast, the calls of nestlings from other Northern Hemisphere species have structural properties which suggest that they may be difficult to detect and/or locate

(i.e. narrow band, high frequency sounds; Popp & Ficken, 1991; Briskie et al., 1999).

In the present study, begging vocalisations were recorded and analysed from several species of Australian passerines and parrots. This is the first detailed comparative study of begging vocalisations in Australian birds, and is one in which call loudness and structure were measured. As previous studies have demonstrated some differences between the alarm calls of Australian and Northern Hemisphere birds (Jurisevic & Sanderson, 1994a), there might also be differences in the begging calls of these groups. This study: (1) describes and compares the begging vocalisations in several species of nestling and fledgling Australian birds; and (2) determines whether the calls of the species investigated are easy or difficult to detect and/or locate, thereby providing some insight into their function.

Methods

Species Recorded and Sources of Recording

Begging vocalisations were recorded and analysed by sonagram from nestling and fledgling birds from two orders: Passeriformes (oscines) (ten species) and Psittaciformes (parrots) (three species). Refer to Table 1 for complete listing of species, individuals recorded and measurements of physical parameters of begging calls. Most of the recordings of begging calls were obtained from birds under the care and supervision of members of the Bird Care and Conservation Society of South Australia. The ages of birds could only be estimated since they were handed over by members of the public to Bird Care members.

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Measurements of call loudness or sound pressure level (SPL) in decibels (dB) were also taken from the 13 species plus two others, the House Sparrow (*Passer domesticus*) and Blackbird (*Turdus merula*) (see Table 2). The calls of these two species were not recorded and analysed by sonagram. Observations and recordings were conducted in line with ethics approval by the Flinders University Bioethics Committee. There were no deaths related to any of the experimental procedures.

Recording Apparatus

Vocalisations were recorded with a Realistic VSC-2001 stereo cassette recorder and Realistic Directional Electret Condenser Microphone (80-18000 Hz) on to low noise/high output magnetic audio tapes. Sonographic analysis was carried out on a personal computer using a 12 bit DT2801 A-D card and the sound analysis software "Ultrasound" (Uniquet, University of Queensland 1988). The sampling frequency for sound was 20 kHz, allowing for analysis of sound from 0-10 kHz to an accuracy of 0.1 kHz and 0.01 s. Call loudness was measured with a Philips PM 6400 SPL Meter set on "FAST" (fast meter indication) and A weighting scale.

Measurement of Begging Vocalisations

Seven call variables were measured. Variables 1-6 were determined from sonographic analysis: (1) peak frequency (the highest frequency detected by the sonagram); (2) minimum frequency (the lowest frequency detected by the sonagram), which was often the fundamental frequency for harmonic calls; (3) the peak dominant frequency (the uppermost level of the dominant frequency); (4) the minimum dominant frequency (the lowest level of the dominant frequency); (5) duration of individual call pulses; (6) inter-pulse spacing (duration between successive pulses); and (7) SPL measured in dB. The peak frequency was often around 10 kHz at the upper limit of measurement used, therefore these values are presented with a + symbol indicating that the peak frequency may have been higher than 10 kHz.

Recording and SPL Measurements of Begging Vocalisations

Vocalisations were recorded from birds that were enticed to beg by the presentation of food. Recordings were made with the microphone held 20-30 cm from the bird. For the measurement of SPLs, the meter was held at a distance of 1 m directly in front of the calling bird. Begging calls of nestling Crimson Rosellas (*Platycercus elegans*, race *flaveolus*) were enticed by movement of their artificial nest box. Where possible, recordings and measurements of SPL were performed at the same time every morning prior to and during the first feeding of the day.

The final feed of the day was performed at approximately the same time each evening (20:30 hrs). Due to differences in feeding behaviour and preferred food types between taxonomic groups (parrots and passerines) and size differences between nestlings of different ages and different species, there was no standardised amount of food given. Therefore, in an attempt to

standardise feeding protocol, each bird was fed until it was satiated (i.e. until it stopped begging). This ensured that any given bird was in a similar state of hunger (i.e. motivational state) when recordings and measurements were taken. This allowed for valid comparisons of call structure and amplitude within an individual, as well as for comparisons between individuals within and between species.

Data Transformation

The loudness (amplitude) of begging calls was initially measured as SPL in dB. Since a change of 3 dB in SPL corresponds to a factor of two change in sound intensity (Watts/m²) each dB reading was converted to the equivalent sound intensity value to calculate the average value. The mean sound intensity value was then converted to dB.

Results

Sonagrams of begging calls are presented in Figures 1 (passerines) and 2 (parrots) according to taxa, with quantitative measurements of call parameters presented in Tables 1 and 2. In all species, begging calls were highly repetitive vocalisations produced at relatively high amplitudes (Table 2). The amplitude of begging calls varied according to the motivational state or degree of begging activity. Begging calls were louder prior to the first feeding, with begging activity and amplitude waning as feeding continued. Furthermore, in some individuals there was fluctuation in call amplitude during a bout of begging.

Structural Properties and Amplitude of Begging Calls in Passerines

Begging calls of passerines covered a wide frequency range with a great deal of variation in acoustic structure, both within and between species. With the exception of some calls of the Silvereye (*Zosterops lateralis*), most calls had low dominant frequencies (Table 1). The three honeyeaters gave chip like begging calls, which were sharp descending whistles in the White-plumed Honeyeater (*Lichenostomus penicillatus*) (Figure 1b) or short duration harmonic calls in the Noisy Miner (*Manorina melanocephala*) (Figure 1c) and Red Wattlebird (*Anthochaera carunculata*) (Figure 1e). The Red Wattlebird also emitted a harsher call while begging (Figure 1d). Begging calls of the White-plumed Honeyeater and Noisy Miner were loud penetrating sounds reaching 69 and 86 dB respectively at 1 m (Table 2). The SPL of Red Wattlebird calls were slightly lower, ranging between 47-64 dB. Begging calls of other passerines such as the Silvereye, Common Starling (*Sturnus vulgaris*), Australian Magpie-lark (*Grallina cyanoleuca*), Black-faced Cuckoo-shrike (*Coracina novaehollandiae*), White-winged Chough (*Corcorax melanorhamphos*), Australian Magpie (*Gymnorhina tibicen*) and Little Raven (*Corvus mellori*) were longer in duration with either a noisy (harsh) or harmonic structure (see Figure 1a, g-l). In all passerines, begging calls were repeated continuously with short time intervals between successive pulses (Table 2). One starling emitted two types of begging calls, with a more harmonic call emitted during higher levels of begging activity (Figure 1f). This call was also characterised by shorter inter-pulse spacings

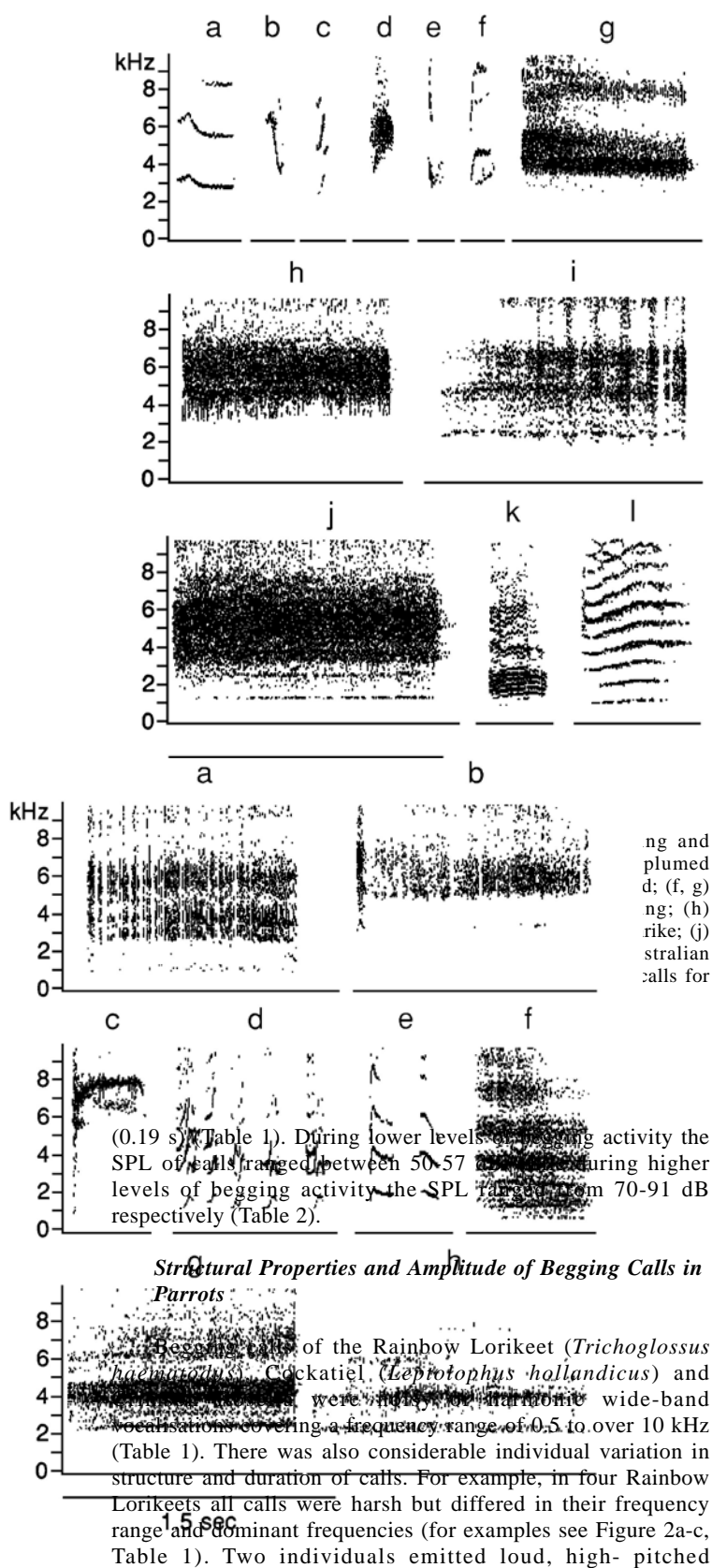


Figure 2 - Sonagrams of begging calls of nestling and fledgling parrots: (a-c) Rainbow Lorikeet; (a, b) long duration harsh calls from different birds; (c) loud high pitch call, mean dominant frequency 6.5-8.5 kHz; (d, e) nestling/fledgling Crimson Rosella calls (race *adelaidae*) from different birds; (f) nestling Crimson Rosella (race *flaveolus*); (g, h) nestling/fledgling Cockatiel, with (g) higher intensity than (h). Apart from (h), calls were relatively high intensity. Sound pressure levels (SPL) of calls for each species are shown in Table 2.

harmonic/noisy calls with a mean dominant frequency between 6.5-8.5 kHz (Figure 2c). Other call types produced were longer in duration (sometimes over a second), were harsh and had dominant frequencies with a wider frequency range (4.1-6.9 kHz) (Figure 2a, b). Three main types of begging calls were recorded from two races of the Crimson Rosella. Those from race *adelaidae* were recorded from birds in the late nestling or fledgling stage and consisted of two main types; a trill like vocalisation with 5-14 individual pulses of a harmonic or noisy nature (Figure 2d), and a clear harmonic call which was emitted more sporadically (Figure 2e). The vocalisations recorded from race *flaveolus* were noisy in structure and were recorded from a young nestling (Figure 2f).

As already mentioned, the loudness or amplitude of begging calls fluctuated in some species during a begging bout and waned during the course of feeding as a bird became satiated. The mean SPL of begging calls in the parrots ranged

from 58 dB in the Cockatiel to 79 dB in the Rainbow Lorikeet. In the latter species, some call pulses reached 88 dB, which is comparable to the SPL of distress calls in many species (Jurisevic & Sanderson 1998). Interestingly there was some variation in the SPL of begging calls of Cockatiels. Some individuals produced very low amplitude calls (i.e. below 50 dB), which is represented by a lighter and dispersed shading on the sonagram with only a narrow area of significant acoustic energy (between 4.5-5.0 kHz) (Figure 2h). Figure 2g shows a call that has a SPL of over 60 dB.

Discussion

Acoustic Structure of Begging Vocalisations

The acoustic structure of begging vocalisations observed in the current study, coupled with their relatively high amplitudes suggest that they are highly locatable signals which may be detected over considerable distances. In fact the begging calls of some species, such as the White-winged Chough, were as loud as the distress calls given by adults (see Table 2 and Jurisevic & Sanderson, 1998). The characteristics of the begging calls suggest that detectability or locatability of the signal may be the major selection force influencing the structure of these vocalisations.

The begging vocalisations recorded in this study are similar to those documented in numerous Northern Hemisphere passerine and non-passerine species, (i.e. a harsh or harmonic structure covering a wide frequency spectrum with abrupt transients, see for example, Redondo & Arias de Reyna, 1988; Popp & Ficken, 1991). The overall similarity in begging call structure between these species suggests that the vocalisations are convergent in nature, similar to that documented in the distress, terrestrial alarm and mobbing vocalisations of Northern and Southern Hemisphere birds (Marler, 1955, 1957; Jurisevic & Sanderson, 1994a; Jurisevic & Sanderson, 1998).

It is interesting to note, however, that some Northern Hemisphere species emit begging calls that are low in amplitude and cover only a narrow frequency spectrum (Popp & Ficken, 1991). These calls are similar in acoustic structure to the aerial alarm calls given by Northern Hemisphere passerines, which are difficult for airborne predators to detect (Klump et al., 1986). Begging calls of this structure may reduce the risk of detection by passing raptors while still providing a stimulus for the parent. No begging calls of this structure were observed in the present study. Due to the extensive variation of “nestling” call structure observed in their study, Popp & Ficken (1991) argue that signal locatability is only a minor selection pressure acting on call structure. Rather, ontogenetic and phylogenetic constraints, as well as reducing predation, are suggested as the major factors influencing call structure. The latter hypothesis may be true for the Northern Hemisphere species that produce begging calls similar to aerial alarm calls. However, the Australian species recorded in this study produced calls that were loud and harsh, characteristics that would make the caller relatively easy to detect and locate. Calls of this structure may inadvertently reveal the position of the nest to “non-intended receivers” such as predators and brood parasites (Gochfeld, 1979; O’Brien & Dow, 1979; Redondo & Castro, 1992a). Direct evidence that begging behaviour increases the risk of

predation or nest parasitism is available (Redondo & Castro, 1992a; Haskell, 1994; Leech & Leonard, 1997; Dearborn, 1999).

Role of Predation on Begging Call Structure and Behaviour

Begging vocalisations function in signalling the chick’s nutritional state and attracting feeders (parents, and helpers in co-operative breeding species, O’Brien & Dow, 1979). The benefits associated with producing loud, conspicuous vocalisations must outweigh potential costs such as predation; otherwise the behaviour would not be an evolutionary stable strategy. Therefore, strategies have been developed to minimise the risk of detection by predators, particularly in species that are more vulnerable to predation.

In the present study, the intensity of begging behaviour and amplitude of calls reduced significantly during feeding, with birds becoming quiet on becoming satiated or with removal of the food stimulus. Bullfinch (*Pyrrhula pyrrhula*) and Chaffinch (*Fringilla coelebs*) nestlings produce low amplitude calls when parents are sighted 1-2 meters from the nest, become louder when the parent lands on the nest, are continued at a lower amplitude for a few seconds when the parent departs, and then stop (Wilkinson, 1980, 1990). This behavioural pattern ensures that loud vocalisations are only emitted just prior to, or during the course of feeding, thereby reducing the likelihood of detection by predators. Redondo & Castro (1992a) showed that higher levels of begging activity in Magpies (*Pica pica*) resulted in higher rates of predation, and that broods with a significantly lower rate of begging activity were not preyed upon. Within broods, predators more readily took nestlings with a higher motivation to beg.

There has been much speculation on the role of nesting habits and predation risk acting on the structure of begging calls. One of the major factors affecting predation risk is nest accessibility (Lack, 1968; Roëll, 1978). Species that build open (exposed) nests are at greater risk of predation than species that use holes or tunnels as nests (Lack, 1968; Martin & Clobert, 1996). This trend has also been documented in species that nest both in cavities and open nests. For example, Jackdaws (*Corvus monedula*) that build open nests are more prone to predation than Jackdaws that nest in holes (Roëll, 1978).

Briskie et al. (1999) showed that species at risk of higher levels of nest predation produced calls that were higher in frequency and lower in amplitude than species exposed to a lower threat of predation. These acoustic properties would make it difficult for potential predators to detect or accurately locate the calling bird (Klump et al., 1986; Briskie et al., 1999). Similarly, ground-nesting species that occupy shrub and grassland habitats suffer from greater levels of predation than above-ground nesting species (Martin, 1993). Haskell (1999) suggests that ground-nesting wood warblers (Parulidae) reduce predation by having begging calls higher in frequency and less rapidly modulated than those of tree-nesting wood warblers. However, there was no appreciable difference in the amplitude of begging calls between the two groups. Cavity-nesters, which suffer less from predation, have calls with a wider frequency range and lower medium frequencies than open-nesters (Redondo & Arias de Reyna, 1988). Sounds with these acoustic

Begging vocalisations in Australian birds

Table 1 - Summary of numerical parameters (mean \pm S.D.) of begging vocalisations. Note: some species (Silvereye, Red Wattlebird, Common Starling and Crimson Rosella) produced two or three structurally distinct vocalisations while begging and thus were analysed separately. Recordings of Crimson (Yellow) Rosella (race *flaveolus*) begging calls were made at the Monarto Division of the Department of Environment and Natural Resources, South Australia. White-winged Choughs (three individuals) and Little Ravens (three) were obtained from a private property within the Murray Mallee (39°0'S 139°20'E) at about 5-9 days of age. Recordings and sound pressure level (SPL) measurements were also taken from three Australian Magpies, one fledgling Common Starling and one fledgling Noisy Miner which were found on Flinders University campus, either abandoned by their parents or dislodged from their nest by high winds.

* = introduced species.

Species	N individuals	N pulses analysed	Peak frequency (kHz)	Minimum frequency (kHz)	Peak dominant frequency (kHz)	Minimum dominant frequency (kHz)	Pulse duration (s)	Inter-pulse spacing (s)
Silvereye	1	6-10	8.7 \pm 1.5	3.2 \pm 0.65	4.9 \pm 1.4	3.4 \pm 0.65	0.32 \pm 0.07	0.86 \pm 0.53
	14-22	9.4 \pm 0.59	3.8 \pm 0.32	8.6 \pm 1.2	7.0 \pm 1.3	0.23 \pm 0.12	0.12 \pm 0.06	
White-plumed Honeyeater	2	24-40	9.3 \pm 1.0	3.3 \pm 0.4	6.6 \pm 0.49	3.8 \pm 0.69	0.1 \pm 0.02	0.97 \pm 0.41
Noisy Miner	4	54-64	9.1 \pm 0.93	2.5 \pm 0.19	6.7 \pm 0.38	4.9 \pm 0.9	0.08 \pm 0.03	0.38 \pm 0.11
Red Wattlebird	2	22-31	8.8 \pm 1.0	3.2 \pm 0.56	6.6 \pm 0.37	5.0 \pm 0.47	0.1 \pm 0.02	0.64 \pm 0.29
	5-15	7.6 \pm 1.1	2.6 \pm 0.18	4.3 \pm 1.4	3.7 \pm 1.3	0.06 \pm 0.05	0.37 \pm 0.1	
Common Starling*	3	22-27	8.9 \pm 0.78	2.7 \pm 0.2	5.1 \pm 0.73	4.0 \pm 0.63	0.13 \pm 0.03	0.19 \pm 0.14
	37-42	8.9 \pm 1.6	2.3 \pm 0.74	5.0 \pm 0.54	3.5 \pm 0.54	0.73 \pm 0.18	0.41 \pm 0.14	
Australian Magpie-lark	7	45-71	9.8 \pm 0.48	1.9 \pm 0.45	7.0 \pm 0.42	4.8 \pm 0.63	1.24 \pm 0.4	0.34 \pm 0.35
Black-faced Cuckoo-shrike	3	27-42	9.9 \pm 0.15	1.7 \pm 0.18	6.0 \pm 0.8	4.0 \pm 0.57	0.8 \pm 0.31	0.19 \pm 0.16
White-winged Chough	3	65-74	9.95 \pm 0.2	1.2 \pm 0.21	6.3 \pm 0.58	3.4 \pm 0.43	1.02 \pm 0.32	0.23 \pm 0.23
Australian Magpie	3	41-46	9.9 \pm 0.16	1.0 \pm 0.23	6.4 \pm 0.75	3.8 \pm 0.53	0.42 \pm 0.11	0.22 \pm 0.16
Little Raven	3	64-80	8.4 \pm 1.2	1.0 \pm 0.45	3.6 \pm 1.1	2.0 \pm 0.46	0.3 \pm 0.1	0.27 \pm 0.18
Cockatiel	4	24-38	7.5 \pm 1.6	2.3 \pm 0.48	5.3 \pm 0.87	3.4 \pm 0.5	1.51 \pm 0.41	0.1 \pm 0.02
Rainbow Lorikeet	4	18-19	10.0+ \pm 0.08	1.6 \pm 1.1	6.9 \pm 0.83	4.1 \pm 1.0	0.98 \pm 0.21	0.84 \pm 0.52
	34-37	10.0+ \pm 0.2	1.9 \pm 1.1	8.5 \pm 0.46	6.5 \pm 0.84	0.68 \pm 0.21	0.49 \pm 0.24	
Crimson Rosella								
race <i>adelaidae</i>	8	47-72	9.6 \pm 0.63	1.2 \pm 0.2	4.9 \pm 0.85	2.9 \pm 0.4	0.1 \pm 0.03	0.09 \pm 0.03
	9-92	9.9 \pm 0.29	1.5 \pm 0.19	5.6 \pm 0.72	2.7 \pm 0.56	0.15 \pm 0.03	0.14 \pm 0.06	
race <i>flaveolus</i>	1	6	9.9 \pm 0.16	0.5 \pm 0.08	3.1 \pm 1.3	1.3 \pm 0.47	0.84 \pm 0.13	-

features are less attenuable by environmental constraints and are thus detectable over longer distances. A wider frequency range also offers more cues for accurate localisation by means of binaural comparison (Marler, 1955, 1957; Brown, 1982). Cavity-nesters also have shorter bouts of incubation and make more frequent nest trips, while species that are prone to high levels of predation have incubation periods characterised by long on- and off-bouts of incubation that minimises activity that could attract predators (Conway & Martin, 2000).

In the present study, both cavity nesters (parrots and Common Starling) and open nesters (all other passerine species) produced calls with locatable characteristics. Both groups generally produced loud, wide band calls with low dominant frequencies, which were long in duration. Species such as the Crimson Rosella (race *adelaidae*), White-plumed Honeyeater, Noisy Miner and Red Wattlebird produced shorter duration calls that were rapidly repeated and characterised by an abrupt onset and termination. O'Brien & Dow (1979) also showed that the begging calls of Noisy Miners contain the aforementioned properties as well as having maximum amplitude at the beginning or end of the vocalisation.

Species that build open nests may reduce predation by

building nests high off the ground and having large social units to help protect young. Australian Magpies, White-winged Choughs and Little Ravens usually build nests 6-16 m off the ground (Frith, 1977). Furthermore, the adults of these species are large, reaching 44, 47 and 50 cm, and are thus capable of defending nests from predators. White-winged Choughs and Australian Magpies can occur in groups of up to 16 and 24 individuals respectively with the latter species being very aggressive and territorial, particularly during the breeding season, actively attacking intruders including humans (Frith, 1977; Heinsohn & Cockburn, 1994). Other open nesters, such as honeyeaters are also pugnacious birds and actively mob predators (Dow, 1975). Noisy Miners, for example, are co-operative breeders with colonies consisting of up to 200 birds. This species will actively mob and drive off intruders in large numbers, including large lizards (Dow, 1970, 1975; O'Brien & Dow, 1979).

Energetic Cost of Begging Vocalisations

Another potential cost associated with begging is energy expenditure. Measurements of oxygen consumption in begging

birds show that nestlings use significantly more oxygen during begging than when resting. McCarty (1996) showed that the active metabolic rate while begging was 1.05 times the resting metabolic rate in Tree Swallows (*Tachycineta bicolor*), and 1.27 times the resting metabolic rate in Common Starlings. Leech & Leonard (1996) showed similar values, again in the Tree Swallow, in which begging required 28% more energy than resting, and Bachman & Chappell (1998) had almost identical findings in the House Wren (*Troglodytes aedon*). Jurisevic et al. (1999) also observed significant increases in oxygen consumption above resting levels during begging in six species of Australian passerines.

Despite these increases in oxygen consumption, it has been suggested that the energy requirements for begging are quite low compared to other avian behaviours, and that metabolic cost does not play a considerable role in influencing the signalling of nutritional need by nestlings (Vehrencamp et al., 1989; Eberhardt, 1994; McCarty, 1997; Bachman & Chappell, 1998). For example, in House Wrens, over a 24 hr period the cumulative energy assigned to begging ranged from 0.02% of the energy budget in 3-day-old nestlings, to 0.22% in 10-day-old nestlings. In comparison, non-begging movements accounted for 2% in 3-day-old chicks and 9% in 10-day-old chicks (Bachman & Chappell, 1998).

Furthermore, the amount of time spent begging, as well as the intensity of begging behaviour does not appear to have a significant effect on energetic cost in one 10-day-old House Wrens, Common Starlings and 5-day-old Tree Swallows (Leech & Leonard, 1996; McCarty, 1996; Bachman & Chappell, 1998); although Leech & Leonard (1996) suggest that energy expenditure was significantly related to begging intensity in older Tree Swallow nestlings (10 days of age). The reduction in begging vigour and call amplitude observed during feeding of birds in the present study may be an adaptive behaviour to help conserve energy (as well as reduce detection by predators). Great-spotted Cuckoos (*Clamator glandarius*) and Magpies have also been shown to cease begging after ingesting enough food (Soler et al., 1999).

Family Specific Traits of Begging Vocalisations

The structures of begging vocalisations may be family-specific. Corvids have typically wide-band calls that are either harsh or harmonic (e.g. Chamberlain & Cornwell, 1971; Richards & Thompson, 1978; Redondo & Exposito, 1990; Redondo 1991). Hirundinidae have complex begging calls comprised of frequency modulated non-related harmonic bands (Loesche et al., 1991; Medvin et al., 1993). Popp & Fickens' (1991) comparative analysis of "nestling" calls in 71 species of passerines and four species of woodpeckers provides evidence that this is true for a variety of avian groups.

The present study also provides evidence that begging calls may be similar in related groups of birds: the three honeyeater species gave begging calls which began and ended abruptly, were broad band and of very short duration. Furthermore, in all three honeyeaters the calls were very similar to contact calls emitted by adults (Jurisevic & Sanderson, 1994b). The White-winged Chough and Little Raven also emitted begging calls that were very similar to adult calls (Jurisevic, 1999). These similarities are not surprising as begging calls form the basis

for the development of adult vocalisations (Wilkinson & Huxley, 1978; Redondo & Exposito, 1990; Wilkinson, 1990).

Variation in Begging Call Structure Within Species

Although sample sizes in the present study were generally low, some individual variation was observed in begging call structure. The largest differences were found for the calls of the Rainbow Lorikeet and Crimson Rosella. Two possible explanations for this are the occurrence of age related differences in begging calls and differences in the motivational state or hunger of the birds.

Crimson Rosellas that were early nestlings produced harsh calls while older birds (late nestlings or fledglings) produced more tonal harmonic calls similar to those of adults. Age related changes in begging call structure have also been observed in Bank Swallows (*Riparia riparia*) (Beecher et al., 1981), Warbling Vireos (*Vireo gilvus*) (Howes-Jones, 1984), Little Ravens and White-winged Choughs (Jurisevic, 1999), Magpies (Redondo & Exposito, 1990), Chaffinches (Wilkinson, 1980), Bullfinches (Wilkinson, 1990), Lazuli Buntings (*Passerina amoena*) (Thompson, 1976) and Budgerigars (*Melopsittacus undulatus*) (Brittan-Powell et al., 1997). In general, begging calls become more complex and variable with age, changing in physical structure (i.e. either more harsh or tonal), duration, peak frequency, bandwidth and frequency modulation (Popp & Ficken, 1991; Brittan-Powell et al., 1997; Jurisevic, 1999). The changes in acoustic structure are probably due to physical changes as the bird matures (e.g. an increase in body size, length of the vocal tract and size of the resonance cavities; Brittan-Powell et al., 1997). Popp & Ficken (1991) and Brittan-Powell et al. (1997) both found a significant relationship between body size and high and low frequency components in the calls of developing Budgerigars and numerous species of passerines and woodpeckers.

Many vocalisations appear to be derived from begging calls as they share common acoustic features, or are maintained in the vocal repertoire and given in different behavioural contexts as adults (Howes-Jones, 1984; Wilkinson, 1990; Jurisevic, 1999). The contact calls of fledgling Budgerigars are a shortened version of the "patterned food-begging call" of nestlings, which serves as an acoustic basis for the recognition of young by parents or siblings (Brittan-Powell et al., 1997). The begging call of the Chaffinch and Warbling Vireo is used as a social contact call or mobbing call when birds become independent from parents as juveniles (Marler, 1956; Howes-Jones, 1984). The suggestion here is that contact other calls of the adult vocal repertoire develop from begging calls (Marler, 1956; Clemmons & Howitz, 1990; Wilkinson, 1990; Brittan-Powell et al., 1997).

Since most of the birds recorded in this study were not hand reared but rather obtained fortuitously from outside sources, the ages of birds could not be determined. Therefore it was difficult to make age specific comparisons of call structure between and within species. Age related comparisons of begging call structure would be of interest as fledglings and post-fledglings have different priorities than nestlings (e.g. they need to be located away from the nest by parents, are less dependant, more mobile and can evade predators better than nestlings).

Table 2 - Sound pressure level (SPL) of begging vocalisations in decibels (dB) at 1 m. * = introduced species

Species	N individuals	N of pulses measured	Mean sound pressure level in decibels (dB)	Range (dB)
House Sparrow*	2	24	59	54-64
Blackbird*	2	16	57	40-61
Silvereye	1	15	50	42-57
White-plumed Honeyeater	2	22	62	52-69
Noisy Miner	4	107	72	49-86
Red Wattlebird	5	94	57	47-64
Common Starling*	3	25	65	50-70
Australian Magpie-lark	10	159	65	55-71
Black-faced Cuckoo-shrike	2	35	67	57-71
White-winged Chough	3	441	78	52-91
Australian Magpie	3	41	64	55-71
Little Raven	1	72	64	54-70
Cockatiel	4	46	58	47-64
Rainbow Lorikeet	2	29	79	61-88
Crimson Rosella (race <i>adelaidae</i>)	5	85	72	64-80

In the present study, variation in call structure related to motivational state was observed in Rainbow Lorikeets, with high-pitched vocalisations given during higher levels of begging activity (i.e. during food presentation), and wide-band harsher calls with lower dominant frequencies given prior to the presentation of food. Silvereyes also showed changes in call structure; louder calls with higher dominant frequencies were emitted during higher levels of begging activity, which also included more exaggerated begging postures and wing fluttering. The begging calls of young Black-headed Gull (*Larus ridibundus*) chicks also change in relation to motivational state. Calls given when the bird is “satiated, hungry and warm” and “hungry and cold” differ in temporal characteristics, number of harmonics and frequency modulation (Impeken, 1971).

Parents can differentiate between hungrier broods and chicks from those less hungry based on the intensity of their calling and overall begging behaviour, resulting in more food being brought to the nest (e.g. Bengtsson & Rydén, 1983; Whittingham & Robertson, 1993; Redondo & Castro, 1992b). It is possible that parents also have the ability to recognise the motivational state (e.g. degree of hunger) of chicks by changes in the acoustical features of their begging calls. Passerines and parrots exhibit extremely acute hearing abilities. For example, Zebra Finches (*Taeniopygia guttata*) and Budgerigars are capable of detecting alterations in the timbre and harmonic integrity of complex harmonic signals (Lohr & Dooling, 1998). Many species are specially attuned to the physical characteristics of their own species’ calls showing an enhanced proficiency to discriminate among calls of their own species over the calls of others (Park et al., 1989; Okanoya & Dooling, 1990, 1991; Dooling et al., 1992). Budgerigars, for example, can discriminate the calls of their young from those of others, as well as discriminate between various calls of the same nestling based on temporal and spectral characteristics such as

duration, bandwidth, peak frequency and rate of frequency modulation (Brittan-Powell et al., 1997).

In summary, unlike many Northern Hemisphere birds (e.g. Popp & Ficken, 1991), the acoustic features of begging vocalisations in Australian passerines and parrots suggest that many species have developed signals which provide abundant cues for ease of detection and location; high amplitude harsh or harmonic signals covering a wide frequency spectrum. Although sounds with these properties may attract predators, several mechanisms appear to have been developed to help reduce detection by predators (e.g. nesting behaviour, reducing intensity of begging behaviour and call amplitude after feeding), thereby maintaining loud, conspicuous vocalisations as a viable strategy of nestling and fledgling begging behaviour.

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