

Locatability of begging calls in nestling altricial birds

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Abstract. Nestling begging calls of altricial species of birds have design features (wide frequency range, abrupt onsets and modulation in amplitude and frequency) that make them easily located by birds and mammals, and so may attract predators to the nest. To be maintained by natural selection, such calls must also be beneficial. It is argued here that sibling competition for food during the early stages of nestling development favours locatability of begging calls, presumably because noisy nestlings attract the attention of parents. In the magpie, *Pica pica*, begging calls of nestlings have a wider frequency spectrum before the nestlings' eyes have opened, a trait that increases their locatability. A strategy of having locatable calls should spread if favoured by mechanisms that overcome the increased predation risk associated with such calls. Two mechanisms are proposed: increased attenuation of the signals by emphasizing higher frequencies (a feature commonly found in begging calls) and dispersion of energy over a wide time-frequency range, a trait that, because of sound degradation, probably masks the estimate of source distance by predators. This hypothesis agrees with predictions of models of intra-brood conflict: when predation costs are higher, level of solicitation (locatability) should decrease. Hole-nesting species, which have a lower risk of predation, have calls with wider frequency ranges and lower (less attenuable) medium frequencies than those of open-nesting species of a similar weight.

The locatability of avian calls has played a major role in the evolution of their structural design (Marler 1955). Certain features of calls (tonal quality, high pitch, absence of modulation and smooth gradients of amplitude variation at the onset or the end of the call, usually referred to as transients) make it difficult for mammals and birds to locate them, while the opposite traits (broad frequency range, abrupt transients and modulation in amplitude and frequency) allow them to locate source position accurately (Marler 1955; Rooke & Knight 1977).

Humans are able to locate sound sources by comparing differences of intensity, phase and time of arrival between the sounds reaching the two ears. Based on this evidence, Marler (1955) deduced those features of a call that favour its location. Binaural differences in intensity become appreciable only when the wavelength of incident sound is less than about four times the smallest distance between the ears. Phase differences are useful when the wavelength is greater than twice the inter-aural distance, and differences in time of arrival are facilitated by discontinuities and detectable changes in frequency and intensity of the sound (Rooke & Knight 1977).

Further experimental studies confirmed Marler's

hypothesis (Brown 1982). Birds and mammals use different mechanisms to locate sounds so we should not extrapolate to birds results obtained with human subjects (Lewis & Coles 1980). Nevertheless, evidence suggests some general features in a call that make them easy to locate by both groups of animals. Birds and mammals locate broad-band signals more accurately than pure tones, and frequency-modulated tonal sounds better than non-modulated ones (Brown 1982; Klump & Shalter 1984). Differences in time of arrival are expected to be negligible in a pressure-gradient acoustic receiver like the avian ear (Lewis & Coles 1980) but the so-called temporal cues (abrupt onsets and terminations and interruptions) have been much less studied than the spectral ones. Experimental evidence about the ability of birds to use temporal differences in locating sounds is still needed. However, birds show a very high acoustic time resolution (they can discriminate differences of about 0.5 ms) and such ability may greatly facilitate sound location based upon temporal differences (Rooke & Knight 1977).

Marler (1955, page 7) presented a sonagram of a wren, *Troglodytes troglodytes*, begging call as an example of a barely locatable call. In his words: 'Many juvenile passerines, which are very suscep-

tible to predation, have calls which are difficult for man to locate . . . and which resemble the "hawk" call in structure and frequency'. The wren's call has a mean frequency of about 6 kHz and lasts about 0.16 s. The equivalent figures for a 'hawk' call are approximately 7 kHz and 0.25 s (Marler 1955, page 7). As Rooke & Knight (1977) have already noted, Marler did not specify the band-width of the filter used during the production of these sonagrams but presumably both the alarm and the begging calls were obtained under the same conditions (wide-band filter). If so, the frequency range of the begging call is about twice that of the alarm call (1.3/0.75 kHz). Moreover, the onset of the begging call appears much less gradual than that of the alarm call. These facts suggest that the begging call of a young wren may contain more information about the sender's position than Marler initially supposed. This case is not unique, nor exceptional. Begging calls of several species have a structure that makes them easy to locate (O'Brien & Dow 1979; Howes-Jones 1984).

In this paper, we analyse the structure of nestling begging calls of altricial species, focusing on those of the family Corvidae, in relation to their locatability, and briefly discuss the roles that intra-brood competition and nest predation have presumably played in modelling the acoustical design of such calls during their evolution.

MATERIALS AND METHODS

The idea that nestling begging calls are easy to locate came to us in the course of a study of corvid begging calls. We analysed 110 calls of carrion crows, *Corvus corone* (15 nestlings from nine nests), 110 of jackdaws, *Corvus monedula* (10 nestlings from eight nests), 477 of magpies, *Pica pica* (58 nestlings from 23 nests) and 14 of azure-winged magpies, *Cyanopica cyana* (two birds from one nest, 7–10 days old). We also obtained sonagrams from a blackbird, *Turdus merula*, 6–11 days old. Nests were found at several sites in Andalusia, southern Spain, during the springs of 1985 and 1986. Calls were recorded in the absence of the parents, using a Uher 4200 Report Monitor tape-recorder through a condenser microphone AKG 568 EB, at 9.5 cm/s speed. Recordings were analysed in a Kay sound spectrograph model Voice Identification Inc. 700 from the Zoology Museum of Barcelona, using the wide-band filter (300 Hz)

and sonagrams obtained for a scanned frequency range of 0–8 kHz.

The age of the magpie chicks was known to within ± 3 days as they hatch asynchronously, and consequently five age-classes of 3 days were established for the nestling period. For the two *Corvus* species, only three age-classes could be accurately determined (1–5, 8–12 and 15–19 days).

On each sonagram, we measured the frequency range and duration. Unlike the other corvid species, whose calls were more or less harsh, magpies have tonal calls. Energy was concentrated in several bands which included two independent fundamentals undergoing intense frequency modulation and their harmonics. Most of the energy accumulated in one fundamental band (usually the higher one) and we measured maximum and minimum frequency values of this band. The frequency range was then estimated as the difference between these two values. We also measured band-width of the more intense fundamental band during the onset, and the points of maximum and minimum frequency, as an estimate of sound amplitude at these points. In a sonagram obtained from a tonal call, both a higher level of darkness and a wider band at some point are indicative of higher amplitude values. When a recording is being analysed, total output intensity is adjusted, prior to paper-tracing, to a desired level (usually as high as possible without causing distortion). Consequently, band-width values cannot be compared between sonagrams but they provide us with a measure of the relative intensity at different points of the signal. For the remaining species, having harsh calls, the medium frequency value of a call was approximated to the intermediate point of its frequency range and no measurement of maximum and minimum frequency and band-width were taken as was done for the magpie.

Subsequently, we looked for sonagraphic material in the literature to take more families into account. For published sonagrams, measurements of frequency range and signal duration were taken by using a gauge (accuracy 0.01 mm), and medium frequency values obtained as above. When signals consisted of a series of repeated elements, duration was considered to be that of one element (with the exception of *Pardalotus xanthopygus*, in which elements were not clearly differentiated). Whenever signals belonging to nestlings of several ages were available, those nearest to half of the nestling period were chosen. In those calls that contained

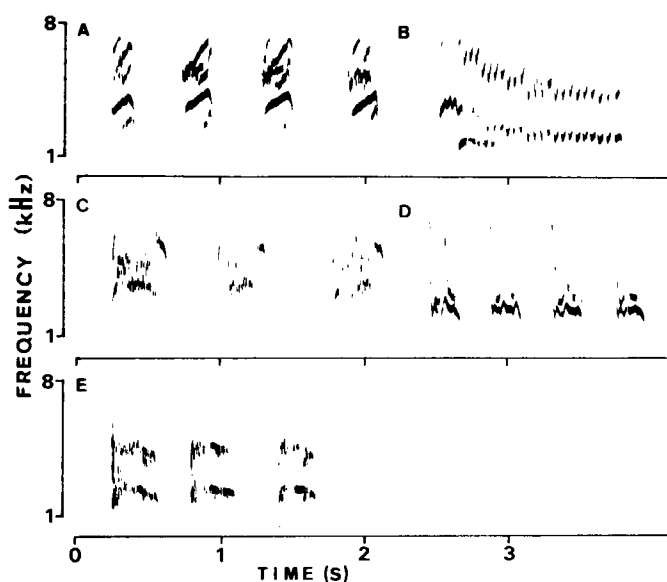


Figure 1. Begging calls of several altricial bird species. (A) Azure-winged magpie, *Cyanopica cyana*, 7 days old; (B) magpie, *Pica pica*, 10 days old (the short, low pitched call at the bottom-left of the sonogram is not a begging one); (C) jackdaw, *Corvus monedula*, 8 days old; (D) blackbird, *Turdus merula*, 7 days old; (E) carrion crow, *Corvus corone*, 9 days old.

several, well-differentiated harmonic-like bands, frequency values were referred to those of the fundamental band.

Data analyses were performed with the BMDP statistical programs package (Dixon 1981). Factor Discriminant Analysis followed the version of Foucart (1982).

RESULTS AND DISCUSSION

Figure 1 shows a selection of sonograms which reveal easily locatable structures in the begging calls of several altricial species. All of them include abrupt transients and range over a wide frequency spectrum: some are harsh (as in *Corvus* spp. and *Cyanopica cyana*) or have multi-band frequency modulation (as in *Pica pica*). The blackbird's wide frequency range is mainly due to an initial portion of the signal that resembles an extremely wide onset, making the call quite heterogeneous. We felt that to consider frequency range values of this initial portion or the final one could bias the actual frequency range of the call and, consequently, did not include this species in certain comparisons (see below).

For the magpie, broad frequency range is a

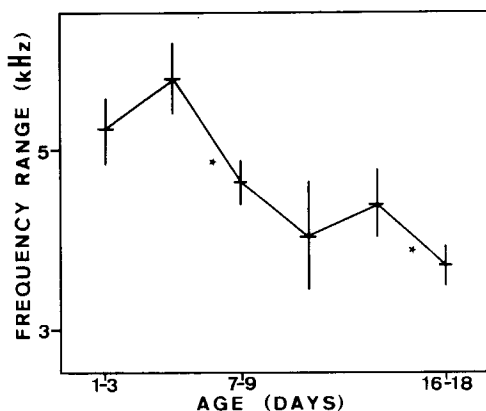


Figure 2. Mean values of frequency range in *Pica pica* begging calls during the nestling period. Vertical bars are 99% confidence intervals. Asterisks denote significant differences between means of adjacent classes as shown by a posteriori Bonferroni *t*-tests ($P < 0.05$) after performing a pooled one-way ANOVA (Welch test, $F = 34.7$, $df = 6$, 121 , $P < 0.001$).

feature common to the whole developmental period (Fig. 2). In all the age-classes, band-width in the onset of the signal remains wider than at the point of maximum frequency (Wilcoxon's test, $P < 0.0001$ in each of the five classes) or minimum

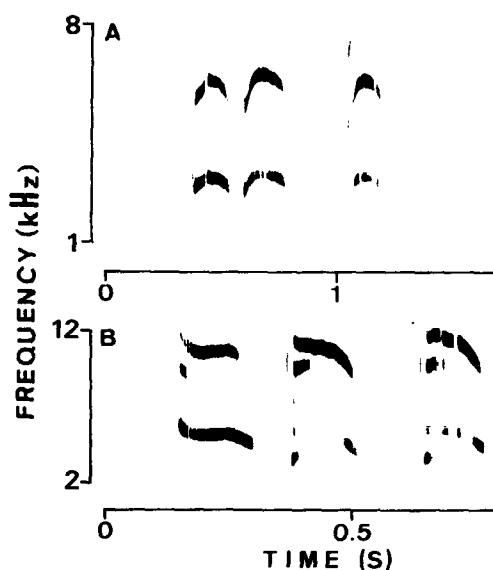


Figure 3. Abrupt onsets in tonal begging calls of newly hatched corvids. (A) *Corvus corone*, 3 days old; (B) *Pica pica*, 2 days old, at half speed.

frequency (Wilcoxon's test, $P < 0.0001$ in each of the five classes). In certain cases (Fig. 3) calls of very young birds are preceded by a 'click'-like structure, which is an extreme case of broad onset. These signals, however, have not been included in the analysed sample.

Wide frequency range is a trait common to the majority of species reviewed. Table I shows values of frequency range, duration and medium frequency of begging calls of 24 species of altricial birds. The frequency range values usually exceed those of passerine 'hawk' calls (Marler 1955; Klump & Shalter 1984). Values shown in Table I do not reflect call shape but most calls broadly came in one of the following four types. In certain species (*Hirundo rustica*, *Manorina melanocephala*, *Pardalotus xanthopygus*, *Philetarius socius*, *Picoides minor*, *Turdus merula* and *T. rufopalliat*), the structure of the call consists of a series of brief elements ranging over a wide frequency spectrum that resembles the shape of passerine mobbing calls. In *Corvus brachyrhynchos*, *Parus atricapillus*, *Parus hudsonicus* and *Poephila acuticauda*, begging calls comprise a series of energy bands very near each other in the frequency scale which creates a wide frequency range, while the same is true for another group of species in which calls are clearly

harsh (*Cissilopha yucatanica*, *Corvus corone*, *Corvus monedula*, *Cyanopica cyana*, *Progne subis*, *Sturnus vulgaris* and *Vireo gilvus*). Finally, a last group of species has calls that are tonal in quality but composed of several, harmonically related energy bands which undergo intense frequency modulation (*Fringilla coelebs*, *Merops apiaster*, *Passerina amoena* and *Pica pica*).

Such structures suggest that selection has favoured traits in the begging calls that make them easy to locate, contrary to Marler's (1955) views. This phenomenon seems, at first sight, maladaptive. There is some evidence to support the view that nest predators can use acoustical cues for gaining access to occupied nests (Dunn 1977; Gochfeld 1979), so we would expect cryptic strategies to be selected in the acoustic behaviour of prey. If we take for granted that altricial nestlings are well-adapted, it follows that locatable begging calls must benefit their senders in order to be maintained by natural selection.

The Costs and Benefits of Calling

In altricial species, the chances of survival of nestlings largely depend on two major factors: food supply and predation. The amount of food delivered by the parents to the nest is a limited resource for which nestlings can compete. Trivers (1974) first pointed out the existence of a conflict of interests between parents and offspring about the allocation of investment in the nestlings. The optimal amount for a nestling may not be optimal for the parents and for the other offspring.

For a developing nestling, an increased food supply implies that a faster growth rate will be achieved (Ricklefs 1983) which, in turn, shortens its nest dependence period and consequently its high risks of being predated (Clark & Wilson 1981). From the time the eyes open, there is sibling competition for those advantageous positions in the nest to which adults deliver most of the food and, again, the bigger nestlings are fed more frequently because of their greater competitive advantage (Ryden & Bengtsson 1980). However, during the earlier stages of development, most species lack the motor coordination at least to display oriented-gaping responses (Smith 1983) and the degree of growth that nestlings will show later in the nestling period largely depends on an adequate food supply when younger. Presumably, at an early age, acoustic signals may help a nestling

Table 1. Acoustic parameters of begging calls in altricial species divided into two groups according to their nesting habits

Species	Frequency range (kHz)	Mean duration (s)	Medium frequency (kHz)	Reference
Hole-nesters				
Order Coraciiformes				
Meropidae				
<i>Picoides minor</i>	7.18	0.12	4.28	Winkler & Short 1978
Order Coraciformes				
Meropidae				
<i>Merops apiaster</i>	2.24	0.24	2.33	Jilka & Ursprung 1980
Order Passeriformes				
Hirundinidae				
<i>Hirundo pyrrhonota</i>	6.00	0.11	5.00	Brown 1985
<i>Hirundo rustica</i>	4.42	0.08	3.38	Samuel 1971
<i>Progne subis</i>	3.97	0.14	2.98	Brown 1984
Paridae				
<i>Parus atricapillus</i>	3.22	0.35	5.58	Ficken et al. 1978
<i>Parus hudsonicus</i>	5.41	0.45	5.00	McLaren 1976
Dicaeidae				
<i>Pardalotus xanthopygus</i>	5.95	1.02	5.98	Short et al. 1983
Sturnidae				
<i>Sturnus vulgaris</i>	3.26	0.31	3.36	Hartby 1969
Corvidae				
<i>Corvus monedula</i>	4.50	0.28	3.03	This study†
Mean (\pm SD)‡	4.61 \pm 1.40 (4.62 \pm 1.50)	0.31 \pm 0.26 (0.31 \pm 0.27)	4.1 \pm 1.2 (4.2 \pm 1.2)	
Open-nesters				
Order Passeriformes				
Turdidae				
<i>Turdus merula</i>	§	0.23	4.40	This study
<i>Turdus rufopalliatus</i>	3.20††	0.06††	2.80††	Grabowsky 1979
Meliphagidae				
<i>Manorina melanocephala</i>	2.48	0.05	3.55	O'Brien & Dow 1979
Emberizidae				
<i>Passerina amoena</i>	1.04	0.12††	6.75††	Thompson 1976
Vireonidae				
<i>Vireo gilvus</i>	5.10††	0.33††	5.68††	Howes-Jones 1984
Fringillidae				
<i>Acanthus flavirostris</i>	1.77	0.15	6.49	Marler & Mundinger 1975
<i>Fringilla coelebs</i>	3.67	0.13	7.87	Wilkinson 1980
Estrildidae				
<i>Poephila acuticauda</i>	2.88	0.06	6.65	Zann 1975
Ploceidae				
<i>Philetarius socius</i>	2.50‡‡	0.20††	6.20††	Channing & Maclean 1976
Corvidae				
<i>Cissilopha yucatanica</i>	2.92	0.26	3.57	Hardy 1979
<i>Corvus brachyrhynchos</i>	0.98	0.42	1.96	Chamberlain & Cornwell 1971
<i>Corvus corone</i>	3.50	0.16	2.63	This study†
<i>Cyanopica cyana</i>	6.00	0.27	4.33	This study
<i>Pica pica</i>	4.60	0.52	4.46	This study†
Mean (\pm SD)‡	3.12 \pm 1.4 (2.83 \pm 1.5)	0.20 \pm 0.12 (0.13 \pm 0.08)	4.8 \pm 1.8 (5.7 \pm 1.6)	
F-value§§†	5.56* (6.55)*	1.42 (2.57)	1.18 (4.51)	

† Values corresponding to half of the nestling period.

‡ Figures in parentheses after removing corvid species.

§ See text for explanation.

†† Directly taken from the author.

‡‡ Estimated from adult calls.

§§ One-way ANOVA, $df=1, 21(15)$; * $P < 0.05$.

to compete efficiently. In the magpie, the frequency range of begging calls is significantly higher in the first two age-classes, before the eyes open at 7–9 days (Fig. 2).

MacNair & Parker (1979) developed a model of intra-brood conflict in which the fitness of a young individual increases asymptotically as a function of the intensity of begging from its parents. Begging offspring also incur costs, a factor that reduces their fitness function and that is, in turn, a monotonic decreasing function of the level of begging. When costs are shared by the individual that begs the most and by its siblings (as in the case of predation), the model clearly shows that begging can become intense. The model also predicts that the intensity of begging which is expected to be evolutionarily stable becomes greater as the slope of the cost function decreases (MacNair & Parker 1979).

During the earliest stages of development, nestlings may be able to induce the parent to feed the nestling broadcasting the most locatable calls. Locatability of the signal then becomes a factor on which nestling fitness depends. According to MacNair & Parker, when the costs of highly locatable calls are shared by the whole brood, genes associated with more locatable calls will spread through the population and, once fixed, they cannot be displaced by genes that make their carriers vocalize less-locatable signals. As a result, we would find that most species have locatable calls. Fixation of such a strategy would be favoured if predation costs could be somehow reduced. We will briefly consider some options.

Alternative Cryptic Strategies for Calling Young Birds

Natural selection may have rewarded design features other than non-locatability of begging calls that reduce chances of predation.

(1) Locatable calls may attract few predators providing that such calls cannot be detected beyond the vicinity of a nest. A low sound pressure at the sound source and directional broadcasting can help to attain a low signal-to-noise ratio at the receiver. Several physical properties of a signal may promote excess attenuation in the environment, leading to similar results. High frequencies suffer greater attenuation in heterogeneous environments due to scattering and reflections from obstacles (Morton 1975; Wiley & Richards 1978). Begging calls usually have higher frequencies than other

Table II. Correlation between frequency range and extreme frequency values of the calls during the first 2 weeks of life in magpie chicks

	Age (days)				
	1–3	4–6	7–9	10–12	13–15
Maximum frequency					
<i>r</i>	0.98	0.98	0.97	0.99	0.99
<i>P</i>	0.01	0.01	0.01	0.01	0.01
RMS (%)	4.05	3.1	5.5	0.66	1.47
Minimum frequency					
<i>r</i>	0.73	0.69	0.16	0.24	0.15
<i>P</i>	0.01	0.01	NS	NS	NS
RMS (%)	47.26	51.98	98.4	96.1	98.9

r: correlation coefficient; *P*: level of significance for the correlation; RMS: residual mean squares of the regression as a percentage of total variance.

calls of a species' repertoire. This is partly a consequence of the inverse relationship which exists between signal frequency and body size of the sender (Wallschläger 1979), since young birds are smaller than adults of the same species. Nevertheless, begging calls often emphasize higher frequencies (see Fig. 3). In *Parus hudsonicus*, the more intense band of the call is the sixth. In *Cissilophya yucatanica*, the second band of the signal (about 5 kHz) is the dominant one. In *Pica pica*, band-width in the maximum frequency point of the signal remains significantly larger than in the minimum frequency point in all the age classes considered (Wilcoxon's test, $P < 0.001$). Moreover, calls of magpie chicks have a higher pitch as their frequency range widens. Such a positive correlation mainly involves the maximum frequency value of the calls although, during the time before the eyes open, just when signals are more easily locatable, both the maximum and the minimum frequency of the call rises when frequency range increases (Table II; Fig. 2).

(2) As a sound travels through a medium it becomes not only attenuated but also degraded due to reverberations and amplitude fluctuations which disperse energy over the frequency-time plane, eliminating clear distinctions between separate elements of the call (Richards & Wiley 1980). The amount of degradation of a signal in a given environment is proportional to the sender's distance from the receiver. An economic predator would enhance its hunting efficiency by not res-

ponding to signals coming from distant or already alerted prey (Smythe 1970). In at least three species of bird, receivers can adjust their level of responsiveness to the amount of degradation perceived in the song of conspecifics (McGregor & Krebs 1984). Begging calls have a complex structure which includes dispersion of energy over a wide frequency range, and this sometimes gives them a harsh quality. If such signals are perceived by predators as coming from a distant source, this mechanism may be an additional way of reducing predatory attempts. Brosset & Chappuis (1968) analysed the responses of carnivores to playbacks of adult and young passerine calls. They found that calls of young birds were easily perceived by the subjects under study but, unlike adult calls, those of young birds did not trigger a predatory response in them, a phenomenon which they attributed to 'some cortical filtering mechanism'.

Locatability and Predation Risk

We have suggested that begging calls of altricial species are, as a rule, easily locatable, because of vocal competition between siblings for food items, providing that additional predation costs caused by more locatable calls could be overcome by mechanisms that diminish the predators' responses.

The model proposed by MacNair & Parker (1979) provides us with a set of predictions concerning the expected intensity of begging relative to the level of costs associated with increased locatability. Those species that suffer a greater predation risk are expected to have less locatable signals. We have also been concerned with detectability of the calls and we predict that species submitted to higher predation rates should promote attenuation and/or degradation of their calls to a greater degree.

Nest accessibility is a key factor on which predation risk depends. Those species that nest in safe places, like holes, are much less prone to predation than species that build open nests (Lack 1968). The same is true for individuals within a species that show different nesting habits (Roëll 1978). It has been said that hole-nesting species beg louder than open-nest builders (Armstrong 1975).

When comparing the hole- versus open-nesters listed in Table I, a Factor Discriminant Analysis correctly classified 74% of species (Fig. 4). This figure can be improved (82.3%) by removing corvid

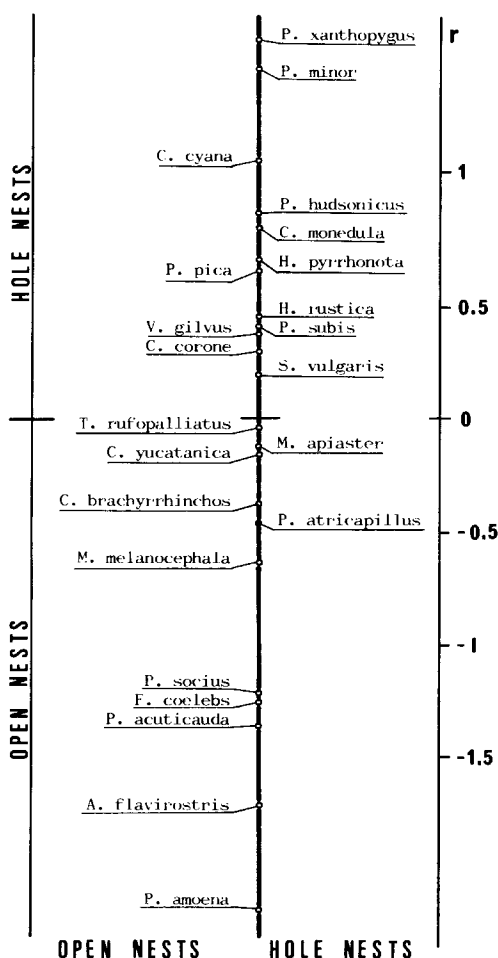


Figure 4. Factor Discriminant Analysis. Loadings (correlations) of cases (species) on the single discriminant factor. Species belonging to hole-nesting (on the right of the figure) or to the open-nesting group (on the left) are classified correctly if they show, respectively, positive and negative loadings on the axis.

species whose harsh repertoires constitute a special, family-specific trait. Accurate classification of species is due to a single variable, frequency range (Table I) whose mean values are greater for the hole-nesting group, a fact consistent with the model's predictions.

If we expect open-nesting species to have more attenuable signals, this group should show higher frequencies, on average, than hole-nesting ones. Since frequency of the call depends to a large extent on the caller's body size, we need to take this into account when comparing medium frequency values

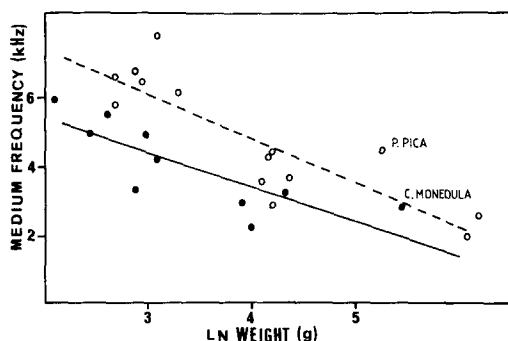


Figure 5. Medium frequency value of begging calls plotted against adult weight (in Naperian logarithms) of 24 species of altricial birds. Open circles: open-nesting species ($y = -1.3x + 10$). Closed circles: hole-nesting species ($y = -0.9x + 7.3$). Differences between adjusted means of both groups are significant at $P < 0.02$ level (analysis of covariance, $t = 2.61$, $df = 21$).

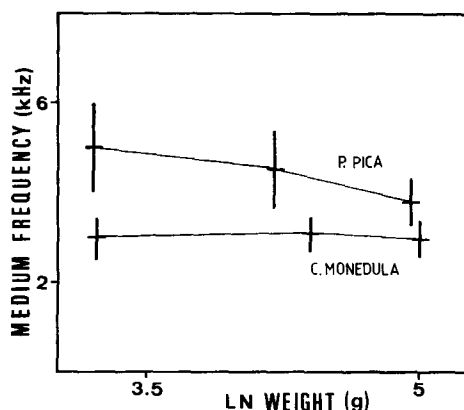


Figure 6. Mean (\pm SD) values of medium frequency of begging calls in two corvid species throughout the growing period plotted against body weight (in Naperian logarithms). Differences between species remain significant for the three age classes (one-way ANOVA, $P < 0.01$).

of the calls. Hole-nesting species tend to have lower frequency values, on average, than open-nesting ones of similar adult weight (Fig. 5).

A major problem underlying these findings is that begging calls are variable and age-dependent. However, we consider that general trends in the results are not strongly influenced by such drawbacks. Consider the case of *Pica pica*, a species whose vocal repertoire during the nestling phase undergoes almost dramatic changes. As can be

concluded from Fig. 6, variability in the medium frequency values of the calls in this species remains within tolerable limits for the scale employed in Fig. 5. *Corvus monedula*, a much more conservative species regarding its vocal development, does not suffer appreciable oscillations around the value occupied in the same figure.

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