

Estación Biológica de Doñana, C.S.I.C., Sevilla

Structural Variations in the Begging Calls of Nestling Magpies *Pica pica* and their Role in the Development of Adult Voice

TOMAS REDONDO & FRANCISCO EXPOSITO

REDONDO, T. & EXPOSITO, F. 1990: Structural variations in the begging calls of nestling magpies *Pica pica* and their role in the development of adult voice. *Ethology* 84, 307—318.

Abstract

Like most corvids, adult magpies (*Pica pica*) have harsh vocal repertoires characterized by a wide distribution of energy over the frequency scale. Shortly after hatching, begging calls of magpie nestlings have a tonal quality but become increasingly noisier as they develop. The appearance of harsh structures in the calls is closely related to a process of frequency modulation which ends at about 16—18 days. At this age, nestlings suddenly develop genuine harsh calls, typical of fledglings and adult birds. During development, similarities can be observed between frequency modulation and noise production, suggesting that nestlings acquire the ability to produce adult harsh vocalizations by modulating their begging calls. This hypothesis does not explain, however, why genuine harsh calls develop without transitional forms being evident in the preceding begging calls. Also, intra- and interspecific differences in modulation rates do not cause differences in noise production in the way that this hypothesis would at first suggest. Frequency modulation and noise production do not seem to be involved in the ontogeny of the adult voice. It is suggested that both features contribute to call degradation in the environment, in order to compensate for the increasing risks of nests being detected by predators due to the more detectable calls of older nestlings.

Corresponding author: T. REDONDO, Estación Biológica de Doñana, C.S.I.C., Apdo. 1056, E-41080 Sevilla.

Introduction

Birds of the family *Corvidae* differ from other passerines in that they have, among other characteristics, adult vocal repertoires composed primarily of harsh elements (AMADON 1944), in which energy is widely spread over a continuous frequency range at any moment of the call. Only tentative explanations from a causal viewpoint (HOPE 1980) have been attempted with regard to this phenomenon, whilst its functional significance and ontogeny are aspects which remain

virtually unexplored. The study of early vocal development in corvids, and its comparison with other passerine species, may help us develop new ideas about the evolution of harsh vocal repertoires in this family, as long as interesting parallelisms between ontogeny and phylogeny can be found for related traits, like the oscine song (IRWIN 1988). A former study (REDONDO et al. 1986) revealed that begging calls of nestling magpies *Pica pica* and two *Corvus* species (*C. corone* and *C. monedula*) showed species-specific features which followed von Baer's law (GOULD 1977), becoming increasingly differentiated with age in a way that mirrored taxonomic relationships between species. Begging calls of very young magpie nestlings have a tonal quality similar to many other passerines, but become increasingly noisier as they grow up (REDONDO et al. 1986). This could be evidence in support of a process of terminal addition (IRWIN 1988) in the evolutionary history of the species, providing that structural modifications, leading to a higher degree of harsh quality in the calls, were actually involved in the development of harsh adult calls.

Begging calls of magpie nestlings consist of two independent harmonic series which undergo a noticeable increase in frequency modulation during the growing period. Intense modulation affects the distribution of energy along the frequency scale in a peculiar way. Since a harmonic series is composed of bands whose frequency values are integer multiples of the fundamental band, the difference d (in frequency units) between the fundamental F and its n th harmonic can be put as: $d = (n + 1)F - F = nF$, i.e., the lower F , the closer the bands will remain. For instance, a change in frequency from 1 to 2 kHz in the fundamental band will lead to frequency changes in its 1st and 2nd harmonics of, respectively, 2 (2 to 4) and 3 (3 to 6) kHz in the same time interval. Such an increase in modulation rate with increasing frequency tends to "verticalize" the structure of an otherwise "horizontal" harmonic series, with many frequency values being produced at about the same time. This structure is referred to as a harsh or noisy one. Magpie begging calls have two simultaneous harmonic series. Slight differences in frequency between the two fundamentals become enlarged at the harmonics level and so contribute to the dispersion of energy over a wide frequency spectrum. Genuine harsh vocalizations are likely to be produced by rapid, irregular and asynchronous vibration of both halves in the syrinx (HOPE 1980). It is possible that, by intense frequency modulation of tonal begging calls, nestlings become trained to produce adult harsh calls.

Many studies dealing with the vocal ontogeny of altricial birds have concluded that adult repertoires have their origin in the begging call of nestlings (MESSMER & MESSMER 1956; LANYON 1960; HARTBY 1969; THOMPSON & RICE 1970; ZANN 1975; THIELCKE 1976; GEBAUER 1984; HOWES-JONES 1984). In fact, it has been suggested that the high structural plasticity shown by begging calls could be functional as it allows such calls to serve as the basis from which adult vocalizations can develop (MARLER & MUNDINGER 1975). This is very similar to that function proposed for the plastic phase of song development in songbirds (MARLER & PETERS 1982).

In this paper, we describe the structural changes that occur in the begging calls of magpie nestlings from hatching until shortly after fledging, in an attempt

to relate the observed modifications in call structure to a hypothetical way of production of harsh calls starting from tonal ones. The vocal repertoire of adult magpies has been described elsewhere (GOODWIN 1952; BAEYENS 1979), but published sonagrams are only available for begging calls of newly-hatched birds (KORBUT 1977) and adult alarm (rattle) calls (BUITRON 1983). Observations of adult vocalizations come from our own, unpublished material.

Material and Methods

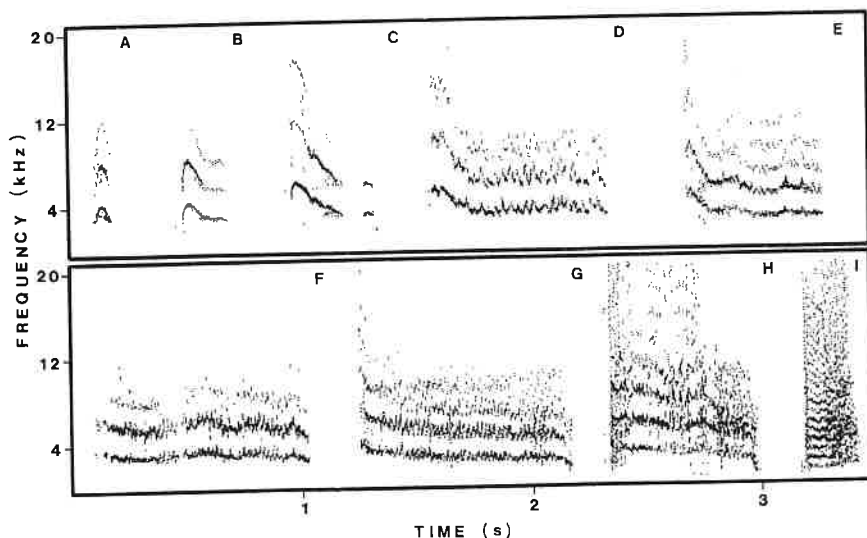
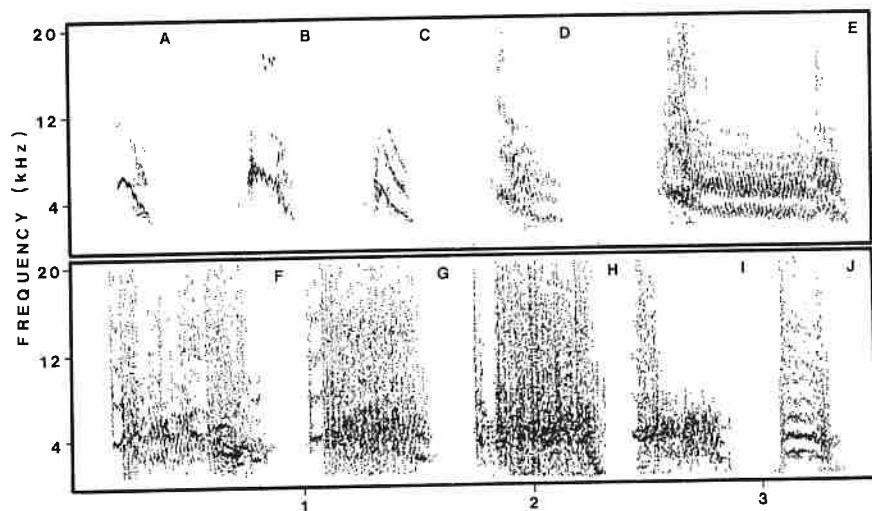
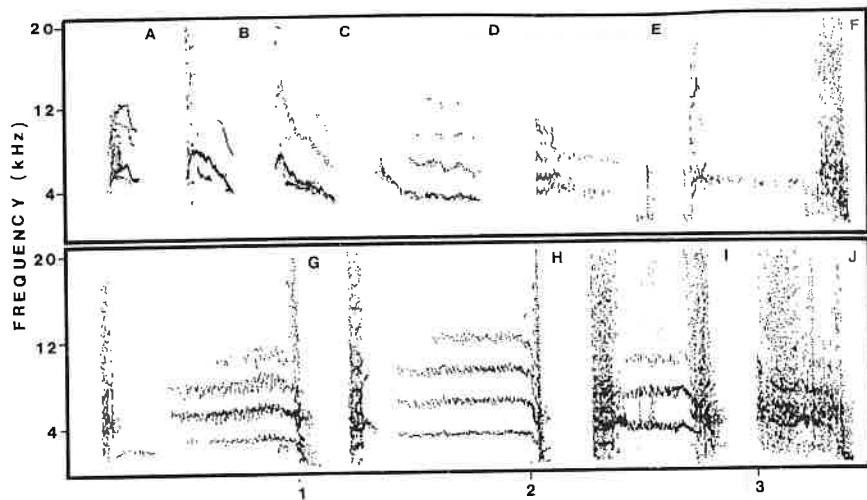
Field recordings of nestling calls were carried out during the spring of 1985, in a cleared oakwood near Espiel, Córdoba. Nestling age was determined by periodically inspecting the nests, with a margin error of ± 1 day due to asynchronous hatching. Consequently, 7 age-classes of 3 days were established for covering the whole nestling period (24 days ± 2.6 SD). Begging calls were recorded in the absence of the parents, using an Uher 4200 Report Monitor through a condenser microphone AKG 568 EB, at 9.5 cm/s speed. Calls were analysed at half speed in a Voice Identification 700 sonagraph (wide band setting) in the frequency range 0—12 kHz. Most begging calls showed two non-harmonically related energy bands (fundamentals), and their harmonics. Measurements of call duration were taken at the dominant fundamental. Resolution between the fundamentals was possible whenever they showed differences in frequency greater than 400 Hz. Frequency modulation in tonal calls appeared as a series of V-like structures (Frequency Modulation Units or FMUs). We looked for the sharpest FMU in each call (that which had the most sloping limbs), and measured the maximum rate of frequency modulation as the slope (in Hz/ms) of its initial limb. The number of FMUs in a call includes only those whose frequency-range was at least half of that of the sharpest FMU. Calls of nestlings older than 7—9 days usually contained one or more segments in which energy dispersed over a continuous range of frequency values. Such segments were most commonly (but not always) associated with FMUs (see Fig. 2). We estimated the noisy quality of a call by measuring the duration of its longest harsh segment. Finally, we also measured the relative amplitude of both fundamentals at the points of maximum and minimum frequency of the dominant one by using a FFT digital sonagraph UNISCAN II 4600.

Recordings were made from 81 different nestlings at 26 nests. 22 nests were recorded only once and 4 nests were recorded on two occasions with at least one week between each. For each nestling at a given age, we selected a sample of 4 to 7 calls, then computed average values to be included as separate data points in statistical analyses. Sample sizes of analyzed calls and individuals for the 7 age classes are shown in Table 1.

In the spring of 1988, we also hand-reared 28 nestlings from the moment of hatching in order to control variations in the structure of calls due to varying degrees of hunger motivation and as a mean of mapping individual developmental patterns. In the laboratory, nestlings were kept in artificial (plaster) magpie nests, each containing three to seven nestlings of the same age, in boxes with controlled humidity and temperature. Nestlings were fed every h from 08.00 to 20.00 h when 1—15 days old and every 2 h when older. Food supplied to nestlings was a modification of LANYON's (1979) recipe, finely homogenized so as to flow through a 4-mm canula attached to a syringe. Further details of protocols can be found in REDONDO (1989). 19 out of the 28 nestlings developed successfully and were kept in the laboratory until fledgling vocal repertoire was completed. This included the uttering

Table 1: Sample sizes of analyzed calls, individuals and nests

	Nestling age (days)						
	1—3	4—6	7—9	10—12	13—15	16—18	19—21
Calls	76	86	108	62	84	98	40
Nestlings	16	17	20	10	16	19	6
Nests	4	5	5	3	4	6	3



of 'Alarm Calls' and 'Brief Contact Notes'. Juveniles were released when they were capable of feeding by themselves in an outdoor aviary. Daily recording sessions for these nestlings provided us with samples of calls of different birds with similar degrees of food deprivation, estimated as the ratio: cumulative food weight consumed in a day/fast body weight. Recording equipment in the laboratory was the same as above. Individual vocal histories shown in this paper were assembled by using UNISCAN II sonagrams obtained from nestlings with a similar degree of food deprivation, both within- and between individuals.

Results

I. Vocal Repertoire

Nestlings were able to give soft 'Begging Peeps' for the first time when 1—2 days old. These calls had a tonal quality and a characteristic shape of inverted 'U' (Fig. 1). 23 out of 52 (44.2 %) 'Peeps' analyzed revealed the existence of two independent fundamentals and/or vertical striations indicative of rapid amplitude modulations caused by interference between both fundamentals (WILKINSON 1980). 'Begging Peeps' gradually changed to 'Begging Trills' within the first days of life. Throughout the nestling period, 'Trills' became longer and more complex as a result of strong frequency modulation of both fundamentals and their associated harmonics (Fig. 1) but they still maintained their tonal quality (Fig. 2). To the ear, they also gained in amplitude, though no intensity measurement was made. Energy dispersion also increased with age but was most commonly restricted to certain points of the 'Trills', namely the valleys of FMUs (Fig. 2). This process of enlargement and frequency modulation of the calls became suddenly disrupted, by the transition from 'Begging Trills' to 'Begging Screams' just when nestlings were about to leave the nest (Figs. 1 and 3). The 'Scream' is the begging call of fledglings. It is much shorter than the preceding Begging 'Trills' and lacks their characteristic frequency modulation and energy dispersion.

Begging calls from hand-reared nestlings could be differentiated between individuals. Call structure was consistent both within and between begging bouts in the same day, and some of its characteristic elements were retained throughout the whole nestling period. For example, individual Y9G produced vocalizations which showed amplitude modulation and contained harsh segments at the end and the onset of the call. Calls of B6W started with an intense, unmodulated portion and were extremely noisy while those of G4R were highly tonal (Fig. 1).

Genuine harsh calls could be recorded in the wild when nestlings were 16—18 days old, and were identified as 'Distress Calls' uttered by nestlings while being handled. Mean age of occurrence of 'Distress Calling' was 21 days \pm 2.6 SD ($n = 9$). In addition 'Alarm Calls' were given by almost-fledged nestlings (23 days \pm 2.2 SD, $n = 23$) which prematurely abandoned the nest in response to disturbances. These calls were emitted in short bouts of 1—4 syllables. A third type of harsh call, the 'Brief Contact Note', was emitted by fledglings during

Fig. 1: Three individual histories of begging call development in laboratory-reared nestlings. First (A) calls in each series are 'Begging Peeps' recorded when 1 day old, last calls are 'Begging Screams' of fledglings. Time between subsequent calls is 3 days. Above: nestling Y9G, middle: nestling B6W, below: nestling G4R

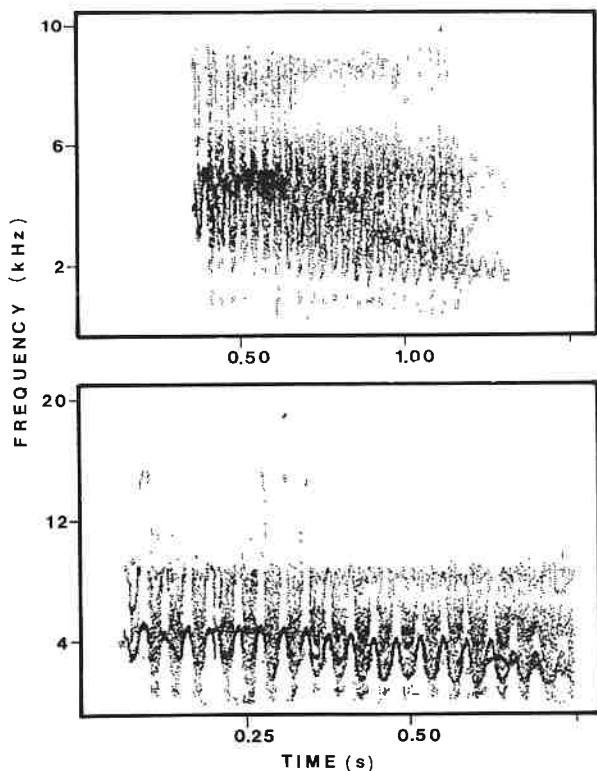


Fig. 2: Begging Call of a nestling 14 days old analyzed at normal (above) and half speed (below)

exploration and play episodes (Fig. 4). These three calls appear *de novo*: they do not show transitional forms with earlier (begging) calls nor is there evidence of a period of gradual modification of their structure, except, perhaps, for 'Distress Calls', which appear with a more tonal quality in nestlings younger than 18 days. All hand-reared nestlings gave 'Alarm Calls' and 'Brief Contact Notes' when at least 21 days old. No 'Distress Calls' were recorded in the laboratory.

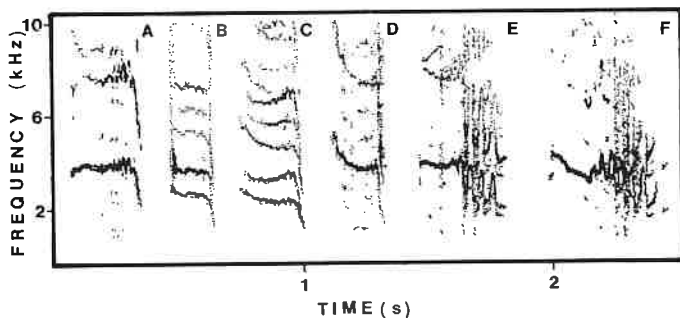


Fig. 3: A—D: 'Begging Screams' of fledglings. E, F: transitional forms between 'Begging Trills' and 'Begging Screams'

II. Changes in the Structure of Begging Calls

Begging calls ('Trills' and 'Screams') consist of two independent fundamentals and their accompanying harmonics. The two fundamentals were clearly discernible during the whole nestling period. The most intense fundamental was invariably the higher-pitched one (Wilcoxon test, $p < 0.001$ in all age classes, for tests involving relative amplitude of the bands at both points of maximum and minimum frequency value).

The most remarkable changes that begging calls undergo during the nestling period involve an increase in duration and frequency modulation. 'Trills' of nestlings 16–18 days old may last for up to 1.4 s (mean 736.9 ms \pm 135.8 SE), which implies a mean rate of increase of 40.5 ms/day. The pattern of increase in call duration is closely matched to the corresponding curve of increase in the number of FMUs per call (Fig. 5a, b), both variables being positively correlated

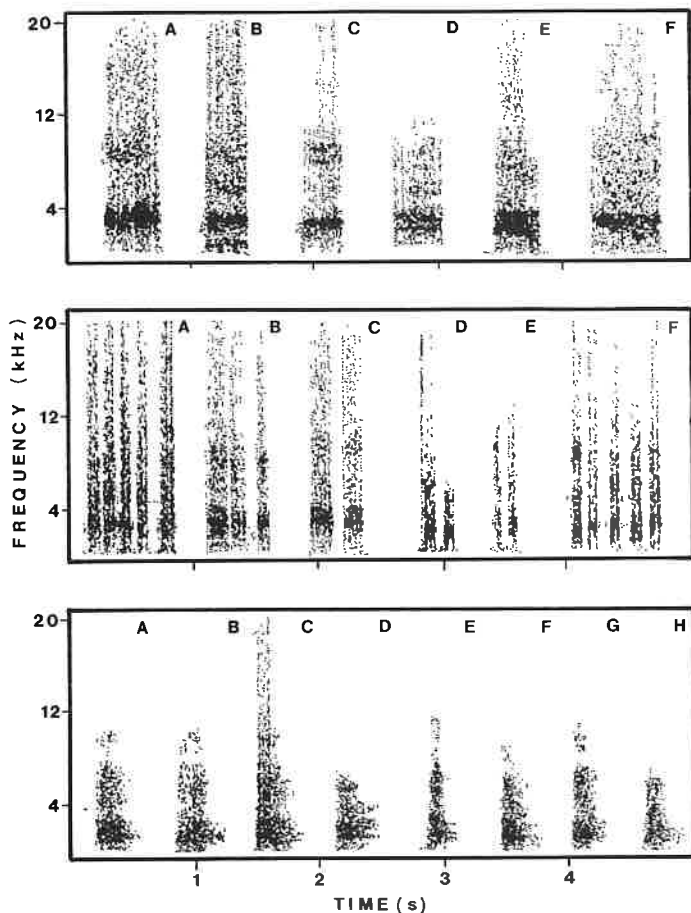


Fig. 4: Harsh calls of fledglings. Above: 'Distress Calls', middle: 'Alarm Calls', below: 'Brief Contact Notes'. Calls F, G, H, correspond to nestlings Y9G, B6W and G4R, respectively

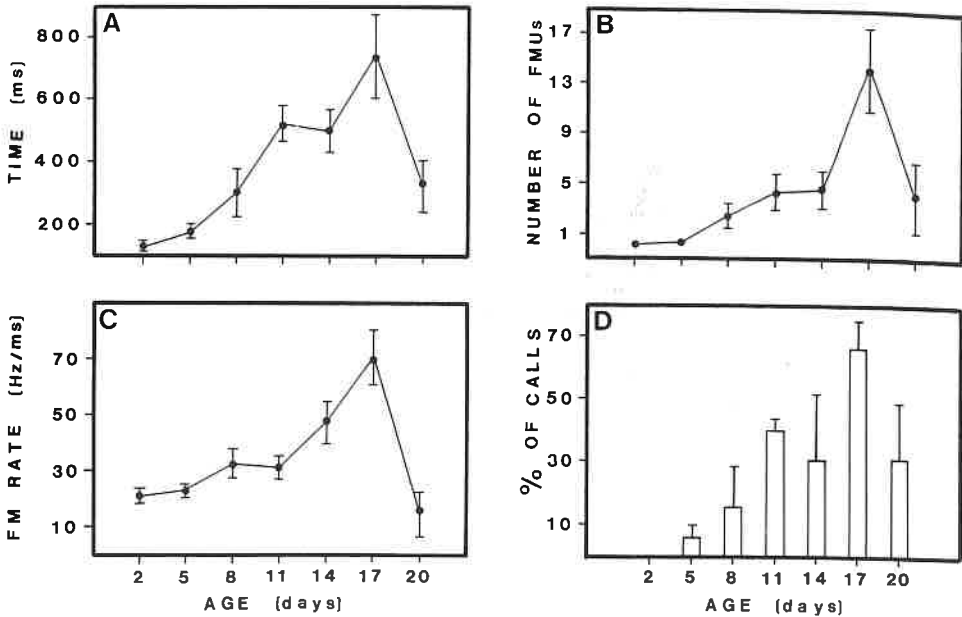
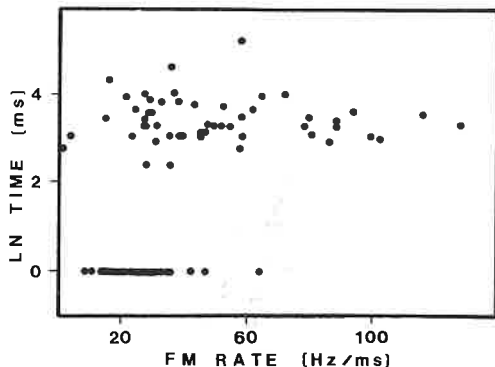


Fig. 5: A: Duration of begging calls during the nestling period. B: Changes in the number of FMUs per call. C: Changes in the maximum rate of frequency modulation. D: Proportion of individuals in a given age which uttered begging calls containing harsh segments. Bars: SE around means

(Pearson's correlation coefficient, $r = 0.36$, d.f. = 103, $p < 0.001$). FMUs not only became more numerous with age but also gained in modulation rate between 1 and 18 days, showing a sharp decrease during the age class 19—21 days (Fig. 5c) which mirrors that of the above variables. The abrupt descent in call duration and frequency modulation during this age-class reflects the transition from 'Trills' to 'Screams' which occurs at this moment. Modulation rate also correlated positively with the number of FMUs ($r = 0.24$, d.f. = 103, $p < 0.02$).

The proportion of begging calls containing harsh segments increases between 1 and 18 days (Fig. 5d). It shows a decrease during the 19—21 days age-class which reflects the tonal quality which characterizes Begging 'Screams'. The ontogenetic course of this variable closely resembles that of frequency modulation, suggesting a relationship between them. Calls containing harsh segments ($n = 52$) had a significantly higher modulation rate ($49.36 \text{ Hz/ms} \pm 3.87 \text{ SE}$) and number of FMUs (mean $1.49 \pm 0.16 \text{ SE}$) than those with no harsh structure at all ($24.48 \text{ Hz/ms} \pm 1.39 \text{ SE}$ and $0.69 \text{ FMUs} \pm 0.24 \text{ SE}$, respectively; Mann-Whitney test, $Z = 5.68$, $p < 0.001$ for modulation rate; $Z = 5.07$, $p < 0.001$ for the number of FMUs), thus supporting the idea that harsh segments are most commonly found within the series of FMUs, although 31 out of 149 harsh begging calls recorded (20.8 %) did not contain any FMU at all. The existence of harsh structures when intense frequency modulation is absent, suggests that the latter may not be a necessary condition for the former to occur. On the other hand, if noise production occurs as a consequence of frequency modulation, we

Fig. 6: Average individual values of duration of the longest harsh segment in a call (in naperian logarithms) plotted against the maximum rate of frequency modulation. Those individuals for which no call containing harsh structures was found, are scored zero in the vertical axis



would therefore expect an abundance of harsh vocalizations beyond a certain modulation threshold. However, the occurrence of harsh segments is not necessarily associated with the highest values of modulation rate recorded (Fig. 6).

Discussion

Magpies can, on average, produce harsh vocalizations from day 20 onwards. Fledgling calls can be truly considered as part of the adult repertoire, for they can also be found in adult birds with the exception of 'Alarm Calls'. Fledgling begging 'Screams' ('Appeal Note', "Cheeuch!" Call) [GOODWIN 1952]; 'Begging Call' [BAEYENS 1979]) and 'Distress Calls' ('Screaming' [GOODWIN 1952]; 'Squawk' [BAEYENS 1979]) are almost identical to those of adult birds. 'Alarm Calls' become progressively longer, adding a higher number of elements, to produce the characteristic 'rattles' of adults ('Chattering' [GOODWIN 1952; BAEYENS 1979]). This process lasts for about 3—4 weeks after leaving the nest (BUIRON 1983). Calls very similar in structure to fledgling 'Brief Contact Notes' are uttered by adult birds during pair interactions and aggressive encounters ("Tchurch" note (peaceable form) [GOODWIN 1952]; 'Soft note' [BAEYENS 1979]).

Below the age 19—21 days, begging calls have a series of brief harsh segments associated with FMUs. Occurrence of harsh segments and frequency modulation are closely associated, both in the structure of the calls and during the ontogeny. Also, the appearance of genuine harsh calls coincides with the end of the period of increase in frequency modulation. These findings support the hypothesis that frequency modulation and its associated noise production is a mechanism involved in the development of adult calls. However, the same hypothesis fails to provide a satisfactory explanation for the following facts:

1) In some individuals (like Y9G in Fig. 1), energy dispersion only occurs at the onset and the end of the call, at the very points where modulation is less intense. Also, about 21 % of harsh begging calls occur in the absence of frequency modulation.

2) Individuals with very different ontogenetic histories of frequency modulation and noise production (like B6W and G4R), are equally capable of producing genuine harsh calls as fledglings (see Fig. 4).

3) Other corvid species show a clear independence between frequency modulation and noise production during ontogeny. Carrion crow *Corvus corone* and jackdaw *C. monedula* nestlings have much noisier begging calls than magpie nestlings of a similar age but frequency modulation in their calls is very slight (crow) or even absent (jackdaw) (REDONDO et al. 1986).

4) If frequency modulation is a mechanism adapted to produce harsh structures, we should expect noisy begging calls to be associated with the highest values of modulation rate. However, Fig. 6 suggests that this is not the case. High frequency modulation often results in energy dispersion but is not a necessary condition for its occurrence.

5) Genuine harsh calls appear de novo during ontogeny and there is no evidence to support the hypothesis that they develop from begging 'Trills'. The sudden appearance of calls without evident transitional forms in preceding calls appears to be the rule, rather than the exception, in the early vocal ontogeny of birds (HOWES-JONES 1984). This casts doubt on whether begging calls play as important a role in the development of adult vocalizations as is generally thought.

In short, the development of begging calls includes an increase in energy dispersion at some points of the call caused by intense frequency modulation, but the hypothesis that such a process is involved in the acquisition of adult voice can hardly be supported. At least two alternative explanations can be proposed for these results. First, energy dispersion is an epiphenomenon of frequency modulation. Second, both energy dispersion and frequency modulation share a function other than their involvement in the production of the adult voice.

Energy dispersion in begging calls is not an exclusive feature of corvids. RYDEN (1978) pointed out that nestling begging calls have, as a rule, a very dispersive structure. As in the magpie, begging calls of a wide range of species from grassfinches to crows show an increase in spectral complexity with nestling age caused by energy dispersion and/or frequency modulation (HARTBY 1969; HORWICH 1969; CHAMBERLAIN & CORNWELL 1971; ZANN 1975; McLAREN 1976; THIELCKE 1976; THOMPSON 1976; FICKEN et al. 1978; MULLER & SMITH 1978; O'BRIEN & DOW 1979; WILKINSON 1980; HOWES-JONES 1984; see GRABOWSKY 1979 for an exception). Such a structure is likely to facilitate call degradation in the environment, hence reducing the possibility of call detection by potential nest predators (REDONDO & ARIAS DE REYNA 1988).

Calls of older nestlings are of a longer duration (THOMPSON 1976; WILKINSON 1980) and a lower pitch than younger nestlings' calls. These two features increase the risk of call detection by predators because longer calls convey a larger amount of information, and low frequencies are resistant to environmental attenuation. Also, older nestlings have much louder calls than young ones (COLLIAS 1952; MESSMER & MESSMER 1956; HARTBY 1969; HORWICH 1969; ARMSTRONG 1975; MARLER & MUNDINGER 1975; ZANN 1975; THIELCKE 1976; THOMPSON 1976; MULLER & SMITH 1978; WINKLER & SHORT 1978; WILKINSON 1980; STAMPS et al. 1985; EARLE 1986). The increase in call loudness (and, perhaps, duration) is probably a consequence of the increase in solicitation intensity with offspring age predicted by theoretical models of parent-offspring conflict (HARPER 1986; LAZARUS & INGLIS 1986), in spite of its associated costs due to an enhancement in

nest detectability by predators. Louder calls of older nestlings may overcome such a cost by dispersing energy in order to promote call degradation. This hypothesis leads to several testable predictions. First, we could expect a positive correlation between loudness and harshness of calls, both within a single bout of begging and throughout the period of development. Second, it is expected for species which develop in safer nest sites, like holes, to have calls with a less dispersive structure than species nesting in more exposed sites, other things being equal (i.e. hole-nesting species seem to have louder (ARMSTRONG [1975] and lower-pitched calls (REDONDO & ARIAS DE REYNA [1988] than open-nesting ones).

Acknowledgements

Thanks go to Dr. L. ARIAS DE REYNA and coworkers for their invaluable assistance with field work, Mr. A. PACHE and Mrs. B. PASCUAL for solving lots of problems at the laboratory, and two anonymous referees for greatly improving the manuscript. Mrs. S. ELDER revised the English. Research funds from Cátedra de Biología y Etología, Fac. Veterinaria, Cáceres, provided partial financial support.

Literature Cited

- AMADON, D. 1944: The genera of Corvidae and its relationships. *Am. Mus. Novit.* **1251**, 1—20.
- ARMSTRONG, E. A. 1975: *Discovering Bird Song*. Shire Publ., Aylesbury.
- BAEYENS, G. 1979: Description of the social behaviour of the magpie (*Pica pica*). *Ardea* **67**, 28—41.
- BUITRON, D. 1983: Variability in the responses of black-billed magpies to natural predators. *Behaviour* **78**, 209—236.
- CHAMBERLAIN, D. R. & CORNWELL, G. W. 1971: Selected vocalizations of the common crow. *Auk* **88**, 613—634.
- COLLIAS, N. E. 1952: The development of social behaviour in birds. *Auk* **69**, 127—159.
- EARLE, R. A. 1986: Vocalizations of the South African cliff swallow *Hirundo spilodera*. *S. Afr. J. Zool.* **21**, 229—232.
- FICKEN, M. S., FICKEN, R. W. & WITKIN, S. 1978: Vocal repertoire of the black-capped chickadee. *Auk* **95**, 34—48.
- GEBAUER, A. 1984: Die Lautentwicklung beim Buntspecht, *Dendrocopos major*. *Ann. Orn.* **8**, 107—127.
- GOODWIN, D. 1952: Notes and display of the magpie. *Brit. Birds* **45**, 113—122.
- GOULD, S. J. 1977: *Ontogeny and Phylogeny*. Harvard Univ. Press, Cambridge.
- GRABOWSKY, G. L. 1979: Vocalizations of the rufous-backed thrush (*Turdus rufopalliatu*s) in Guerrero, Mexico. *Condor* **81**, 409—416.
- HARPER, A. B. 1986: The evolution of begging: sibling competition and parent-offspring conflict. *Am. Nat.* **128**, 99—114.
- HARTBY, E. 1969: The calls of the starling (*Sturnus vulgaris*). *Dansk. Orn. Foren. Tidsskr.* **62**, 205—230.
- HOPE, S. 1980: Call form in relation to function in the Steller's jay. *Am. Nat.* **116**, 788—820.
- HORWICH, R. H. 1969: Behavioural ontogeny of the mockingbird. *Wilson Bull.* **81**, 87—93.
- HOWES-JONES, D. 1984: The vocal behaviour of young warbling vireos. *Can. J. Zool.* **62**, 1714—1719.
- IRWIN, R. E. 1988: The evolutionary importance of behavioural development: the ontogeny and phylogeny of bird song. *Anim. Behav.* **36**, 814—824.
- KORBUT, V. V. 1977: Early phases of the development of acoustic signalization in birds of the family corvidae. *Zool. Zh.* **56**, 1357—1365.

- LANYON, W. E. 1960: The ontogeny of vocalizations in birds. In: *Animal Sounds and Communication*. (LANYON, W. E. & TAVOLGA, W. N., eds.) Am. Inst. Biol. Sci. Publ. No. 7, Washington, pp. 321—347.
- — 1979: Development of song in the wood thrush (*Hylocichla mustelina*), with notes on a technique for hand-rearing passerines from the egg. *Am. Mus. Novit.* 2666, 1—27.
- LAZARUS, J. & INGLIS, I. R. 1986: Shared and unshared parental investment, parent-offspring conflict and brood size. *Anim. Behav.* 34, 1791—1804.
- MARLER, P. & MUNDINGER, P. C. 1975: Vocalizations, social organization and breeding biology of the twite (*Acanthus flavivestris*). *Ibis* 117, 1—17.
- — & PETERS, S. 1982: Subsong and plastic song: their role in the vocal learning process. In: *Acoustic Communication in Birds*. Vol. 2. (KROODSMA, D. E. & MILLER, E. H., eds.) Acad. Press, New York, pp. 25—50.
- MCLAREN, M. A. 1976: Vocalizations of the boreal chickadee. *Auk* 93, 451—463.
- MESSMER, I. & MESSMER, E. 1956: Die Entwicklung der Lautäußerungen und einiger Verhaltensweisen der Amsel (*Turdus merula merula* L.) unter natürlichen Bedingungen und nach Einzelaufzucht in schalldichten Räumen. *Z. Tierpsychol.* 13, 341—441.
- MULLER, R. E. & SMITH, D. G. 1978: Parent-offspring interactions in zebra finches. *Auk* 95, 485—495.
- O'BRIEN, P. H. & DOW, D. D. 1979: Vocalizations of nestling noisy miners *Manorina melanocephala*. *Emu* 79, 63—70.
- REDONDO, T. 1989: El sistema de comunicación acústica de crias de urraca (*Pica pica* L.). Ph. D. Thesis, Univ. of Córdoba, Córdoba.
- — & ARIAS DE REYNA, L. 1988: Locatability of begging calls in nestling altricial birds. *Anim. Behav.* 36, 653—661.
- —, — —, GONZALEZ-ARENAS, J., RECUERDA, P. & ZUÑIGA, J. M. 1986: Diferenciación de la llamada de petición de alimento durante el desarrollo de tres especies de córvidos. *Misc. Zool.* 10, 287—297.
- RYDEN, O. 1978: Differential responsiveness of great tit nestlings, *Parus major*, to natural auditory stimuli. *Z. Tierpsychol.* 47, 236—253.
- STAMPS, J. A., CLARK, A., ARROWOOD, P. & KUS, B. 1985: Parent-offspring conflict in budgerigars. *Behaviour* 94, 1—39.
- THIELCKE, G. 1976: *Bird Sounds*. Michigan Univ. Press, Ann Arbor.
- THOMPSON, W. L. 1976: Vocalizations of the lazuli bunting. *Condor* 78, 195—207.
- — & RICE, J. O'H. 1970: Calls of the indigo bunting (*Passerina cyanea*). *Z. Tierpsychol.* 27, 35—46.
- WILKINSON, R. 1980: Calls of nestling chaffinches *Fringilla coelebs*: the use of two sound sources. *Z. Tierpsychol.* 54, 346—356.
- WINKLER, H. & SHORT, L. L. 1978: A comparative analysis of acoustical signals in pied woodpeckers (Aves, Picoidea). *Bull. Am. Mus. Nat. Hist.* 160, 1—110.
- ZANN, R. 1975: Inter- and intraspecific variation in the calls of three species of grassfinches of the subgenus *Poephila* (Gould) (Estrildidae). *Z. Tierpsychol.* 39, 85—125.

Received: October 23, 1989

Accepted: February 5, 1990 (H.-U. Reyer)