

## The increase in risk of predation with begging activity in broods of Magpies *Pica pica*

TOMAS REDONDO\* & FRANCISCA CASTRO†

\* Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain; † Departamento de Biología Animal, Facultad de Ciencias, Universidad de Córdoba, E-14071 Córdoba, Spain

Begging activity in broods of Magpies *Pica pica* was measured as the average total number of begging nestlings and the number of nestlings giving begging calls between 5 and 9 days since the first nestling hatched. There was considerable between-brood variation in begging activity relative to day-to-day variation within broods. Predation between 7 and 20 days of age was more frequent among those broods which had not previously suffered from brood reduction due to nestling starvation. Broods which were preyed upon showed significantly higher levels of begging activity than broods of a comparable size that were not preyed upon. In addition, the time elapsed from hatching to predation showed a negative correlation with the total number of begging nestlings. Within broods, those nestlings with the highest begging motivation (measured as the latency to respond when stimulated) seemed to be more readily taken by predators. These results confirm the existence of costs associated to begging in the form of an enhanced risk of being detected by predators.

During his classical study on nest predation in the neotropics, Skutch (1949) was "impressed by how much noisier the nest became at meal-time when it contained three nestlings than when it held two, and when it contained two than when it had a single occupant". He inferred that "by day nests are less likely to be betrayed by auditory than by visual clues—else natural selection would long ago have weeded out the noisy babies". However, the observable fact is that many altricial species of birds emit conspicuous begging sounds that reveal the location of the nest to non-intended receivers, including predators (Haartman 1953, Newton 1964, Perrins 1965, Kilham 1977, Gochfeld 1979, O'Brien & Dow 1979, Harris 1983).

Interspecific comparative studies also suggest that begging behaviour has evolved under the selection of predation. Assuming that at least some features of the begging display have an inherited component (see, for example, Webster & Hurnik 1987 for heritability measurements of calling rate in domestic hen chicks), species with safe nest sites should display a more conspicuous begging behaviour than species more vulnerable to nest predators. Birds nesting in protected sites, like holes, often emit louder (Kilham 1977, Fraga 1980), lower-pitched and more locatable calls (Redondo & Arias de Reyna 1988) than species which build open nests. For example, hummingbirds share several characteristics which predispose them to suffer from high predation pressures: they are small-sized birds which build open nests in tropical habitats. Most species of hummingbirds beg for food silently but the Violet-tailed Sylph *Agelaiocercus coelestis*, a species which nests in more protected sites, produces begging calls (Schuchmann 1983).

How is that natural selection has not eliminated a seemingly maladaptive trait like loud begging? A possible answer to this enigma has been offered by parent-offspring conflict theory (Trivers 1974), which states that nestlings will evolve conspicuous solicitation behaviour as a way of obtaining a larger fraction of resources than their parents have been selected to give (Harper 1986). Offspring will engage in costly solicitation activities whenever the benefit accrued (a larger sharing of food) more than compensates for the cost incurred. There is compelling evidence indicating that food provisioned by parents is a limiting resource for nestlings (e.g. Magrath 1989). Escalated begging by nestlings increases parental feeding rates (Haartman 1953, Hussell 1988, Stamps *et al.* 1989) and positively influences a nestling's probability of receiving food (Bengtsson & Rydén 1983; Gottlander 1987), hence nestlings are selected to increase begging activity when food is scarce (Hussell 1988, Smith & Montgomerie 1991, Redondo 1991). Since differential predation towards hungrier and presumably noisier broods exacerbates the cost of attempting to rear large broods, predation may be a limiting factor in the evolution of avian fecundity rates (Perrins 1977, Ricklefs 1977, Slagsvold 1982, 1984). In addition, theoretical treatments of parent-offspring conflict (MacNair & Parker 1979, Trivers 1985, Harper 1986) and the evolution of animal signals (Zahavi 1977) often assume the existence of a predation-related cost of conspicuous solicitation by nestlings. Regrettably, most of the above examples pointing to an association between begging activity and predation risk only give indirect evidence, and none has yet detected a positive relationship between both variables in quantitative terms.

This paper reports on the occurrence of an association between begging activity and predation risk in broods of the Magpie *Pica pica*. As in other altricial species which build nests in exposed sites (Ricklefs 1969), Magpies suffer from heavy nestling predation. Around 24% of all nestlings hatched are killed by predators (Baeyens 1981a, Reese & Kadlec 1985, Redondo unpubl.), the equivalent figure for complete broods being 26.1% (Alvarez & Arias de Reyna 1974, Högstedt 1980, Tatner 1982, Arias de Reyna *et al.* 1984, Balanca 1984). In most areas of their European range, Magpies are territorial during the breeding season and there is a large variability in reproductive success between pairs related to territory quality (Birkhead *et al.* 1986, Møller 1982). Both the incidence of predation and nestling starvation have been reported to be lower in high-quality territories (Högstedt 1980). Magpie nestlings give clearly audible begging calls (Linsdale 1937) and increase their begging rates in response to food deprivation (Redondo 1991), hence this association could be evidence of a higher predation risk incurred by hungrier nestlings in poor quality territories. However, the situation is complicated by the fact that experienced males obtain the best territories (Baeyens 1981b), and invest heavily in both feeding and protecting nestlings from predators (Goodburn 1991). Consequently, differences in parental quality and begging activity both predict the occurrence of differential predation towards broods in low-quality territories.

## METHODS

Data were collected during the 1990 breeding season at the Doñana Biological Reserve (southwestern Spain), where Magpies bred at high densities along a narrow area of marsh-scrub ecotone with a high productivity. Details of the study area can be found in Alvarez & Arias de Reyna (1974) and Rogers & Myers (1980). Birds selected meadow habitats with scattered bushes of heath *Erica scoparia* and blackberry *Rubus ulmifolius* for placing their nests. The study was restricted to the area (3 km × 0.5 km) with the highest nest density (42 nests/km<sup>2</sup>). Nests were located on a 1:25 000 map. All nests were placed in bushes, at heights above ground ranging from a few centimetres to 2 m. No nest placed below 0.5 m above ground was included in the sample. All nests were inspected daily from clutch initiation to clutch completion and from hatching until the chicks fledged. Brood-sizes were adjusted to 4–6 nestlings the day after the last nestling hatched. Most broods were not manipulated in this way but we enlarged eight broods containing three nestlings by adding a single nestling of the same age, collected from nests in which more than five hatched. Nestlings were individually marked with non-toxic waterproof ink when younger than 12 days and ringed with numbered PVC rings when older. They were weighed daily.

Careful daily inspection of nestlings allowed us to identify three major causes of mortality. Nestlings which disappeared after at least two consecutive days of zero or negative growth with no visible symptom of illness were assumed to have died

from starvation. Nestlings which showed evident signs of organic dysfunction (dull body colouration, generalized asthenia or inflammation) were assumed to have died from disease, irrespective of their body-mass changes. Predation was assumed to occur whenever an entire brood disappeared. In addition, we considered that partial within-brood losses of healthy nestlings (i.e. nestlings which were growing at a similar rate to their nestmates and which did not show symptoms of illness prior to their disappearance) were the result of partial predation. Out of 14 instances of suspected partial predation, surviving nestlings showed injuries in four cases and blood remains could be detected in another two instances. It is unlikely that accidental falling from the nest could have been responsible for the disappearance of nestlings in the remaining eight cases because of the deep cup and dense stick walls typical of a Magpie domed nest.

Between 5 and 10 days after the first nestling hatched, we recorded the begging activity of a brood by gently putting nestlings on a cloth, then stimulating them to beg with a single human vocalization. Both the absolute number of begging (gaping with or without calling) nestlings and the number of nestlings giving begging calls were recorded, as well as the sequential order in which nestlings begged (see Redondo 1991, for a description of the calls). In addition, we recorded the mass gain of nestlings during 1 h interval periods in early morning, coinciding with the daily peak in parental feeding rate (Buitron 1988). We computed relative mass increment per hour (as a percentage of initial nestling mass) as an estimate of food provisioning. Daily measures of begging activity and mass gain were obtained for as long as brood-size was not reduced due to partial mortality. Only those broods with at least two measurements were taken into account. Average values per brood were calculated to be included as separate data points for statistical purposes.

In order to test whether begging activity affected predation risk, we used a subsample of nests in which predation occurred between 7 and 20 days after the first nestling hatched. As nestlings older than 20 days were able to escape from the nest in response to disturbances (Redondo & Carranza 1989), we assumed that predation occurring in broods older than 20 days was independent of begging estimates obtained for chicks younger than 10 days. In addition to whether a nest was preyed upon, we used the number of days a brood remained safe from predation (time of brood survival, whereby Day 1 = date of first nestling hatched) as a measure of predation risk. In doing so, it is assumed that more vulnerable nests are destroyed more quickly (Ricklefs 1969), hence time of brood survival becomes a measure of the predation risk faced by a nest. Only one out of six enlarged broods in which brood reduction occurred was preyed upon, and consequently such reduced broods were included in the analyzed sample. This overestimates the begging activity of predation-free broods, which in turn makes statistical analyses conservative.

Statistical analyses were performed according to Zar (1984). Since the main hypothesis was that noisier broods attract more predators, all test probabilities are one-tailed, unless otherwise stated. Nonparametric partial correlation

coefficients (Siegel & Castellan 1988) were used to measure the association between two variables after controlling for the effects of a third one.

## RESULTS

Predation was an important source of nesting mortality in Doñana. Out of 66 completed clutches, 17 (25.7%) were destroyed by predators and 23 (50%) out of 46 successfully hatched broods were totally or partially preyed upon. Identified predators of nestlings included large Montpellier snakes *Malpolon monspessulanus*, kites *Milvus* spp., rodents *Eliomys quercinus* and *Rattus norvegicus*, a medium-sized carnivore (most likely genet *Genetta genetta* or polecat *Putorius putorius*) and Iberian lynx *Felis pardina*. Additional causes of within-brood mortality were starvation (21/46) and disease (14/46).

Predation in broods older than a week ( $n=44$ ) was especially frequent among those broods which had not previously suffered from within-brood mortality. Of broods free from mortality due to starvation or diseases, 65% ( $n=13$ ) were attacked by predators, while the comparable figure for broods with partial losses was 29% ( $n=7$ ) (Fisher's exact test,  $P=0.019$ ). Starvation accounted for most of the above difference. When broods in which within-brood mortality could not be attributed to starvation were removed from the analysis, the proportion of broods subject to predation remained fairly low (Fig. 1). Four out of eight enlarged broods were preyed upon. Those broods which remained safe from predators had in fact experienced a larger reduction in size ( $36.1 \pm 7.7\%$  s.e.,  $n=24$ ) than broods which were subsequently preyed upon ( $18 \pm 6.2\%$  s.e.,  $n=20$ ) (Mann-Whitney  $U$ -test,  $Z=2.01$ ,  $P<0.05$ ). Among these, the time elapsed from hatching to predation was positively correlated with the percentage of dead nestlings due to causes other than predation, after controlling for the effect of brood-size (Kendall's partial  $r=0.49$ ,  $P<0.05$ ,  $n=19$ ). This suggests that the extent of brood reduction affected the timing of nest predation, so that broods with a higher partial mortality remained safe for longer. The spatial distribution of nests did not reveal a clear pattern concerning the association of brood reduction or predation with certain areas (Fig. 2).

The relative gain in mass of nestlings was dependent upon brood-size (Table 1) so that nestlings in smaller broods gained more weight (Spearman's  $r=-0.22$ , two-tailed  $P<0.01$ ,  $n=178$ ) but no significant effects were detected associated with the occurrence of brood reduction and predation (Table 1). However, when only zero or negative increments were considered (due to nestlings which failed to obtain food), a significant interaction appeared between the occurrence of brood reduction and predation, whereby relative mass losses were higher for nestlings in non-reduced broods which were subsequently preyed upon (Table 1, Fig. 3).

There was considerable variation in the number of begging nestlings per nest. The average number of nestlings giving begging calls was usually lower than the average number of begging nestlings (Table 2), although the two measures were

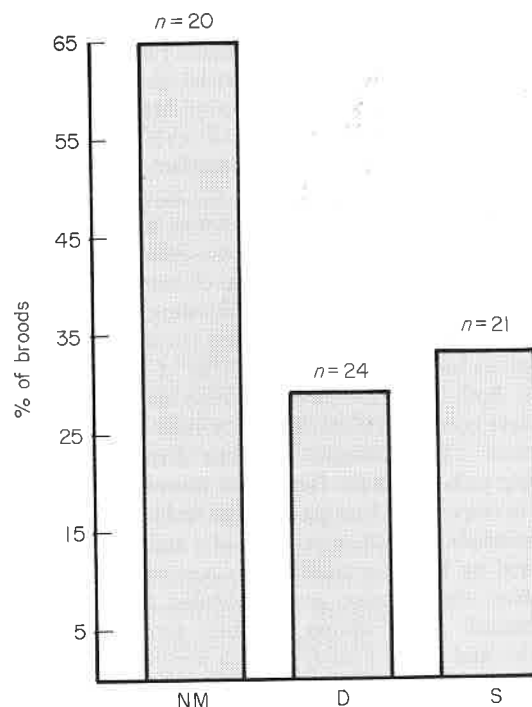
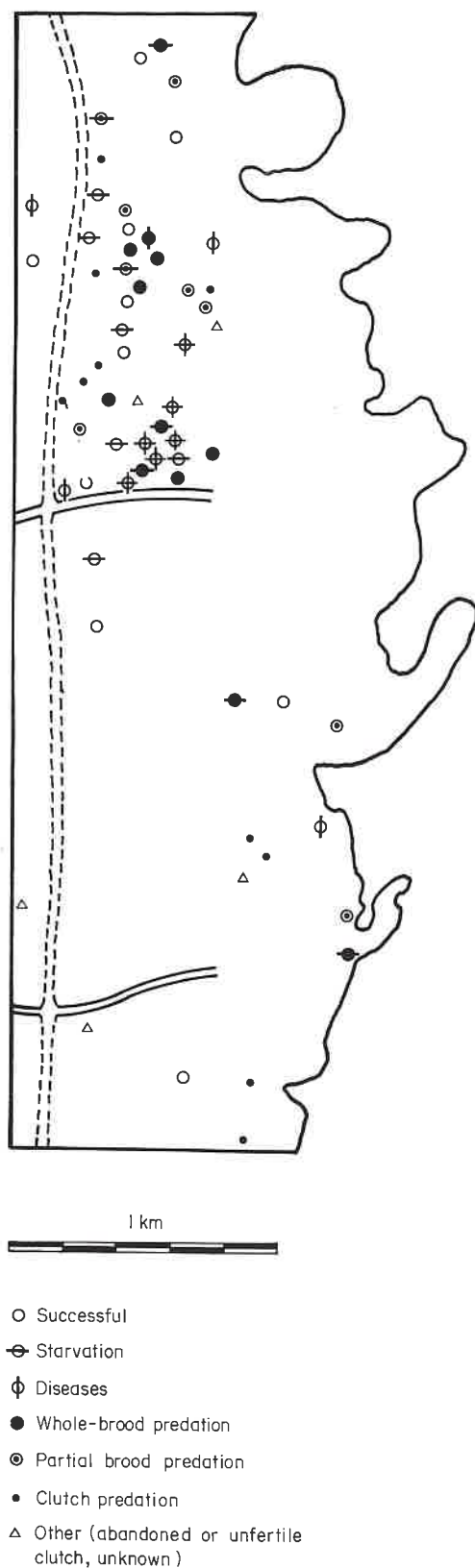


Figure 1. The percentage of successfully hatched Magpie broods which were preyed upon in broods showing no mortality due to other causes (NM), broods in which at least one nestling died from starvation (S) and broods in which at least one nestling died from starvation or disease (D). A larger proportion of broods preyed upon occurred among NM broods compared with S broods (Fisher's exact test,  $P=0.042$ ).

positively correlated (Spearman's  $r=0.67$ ,  $P<0.001$ ,  $n=38$ ). Such a difference arises as a result of a gradual increase in the intensity of the begging display as nestlings become hungrier (i.e. nestlings with a low hunger motivation refrain from uttering begging calls while begging). Despite such variability in the intensity of the display related to short-term changes in nestling motivation, our estimates of begging activity showed the existence of a large between-brood variation across several days relative to within-brood variation (Table 2). No differences were observed between reduced ( $n=20$ ) vs non-reduced broods ( $n=13$ ) in the average proportion of begging nestlings (Mann-Whitney  $U$ -test,  $z=1.15$ , n.s.) or the proportion of nestlings giving begging calls ( $z=1.05$ , n.s.).

Despite the fact that larger broods were noisier (Spearman's  $r=0.69$ ,  $P<0.001$  for the absolute number of begging nestlings;  $r=0.63$ ,  $P<0.001$ , for the number of nestlings giving calls;  $n=38$ ), they were not at a higher risk of being taken by predators than smaller ones. On the contrary, the proportion of 4-chick broods subject to predation (6/12) was slightly higher than the proportion of 5 (5/13) and 6-chick broods (3/7). In addition, small broods tended to be preyed upon at an earlier age than larger ones (Spearman's  $r=0.46$ , two-tailed  $P<0.05$ ,  $n=19$ ).



If noisier broods stand a higher predation risk, we should expect those broods subject to predation to have displayed a higher level of vocal activity. Both the absolute number of begging nestlings and the number of nestlings giving begging calls were higher in broods which subsequently were preyed upon than in non-preyed upon broods of a comparable size (Fig. 4). However, this is probably a rather crude way of testing the hypothesis because there are some factors (like a safe nest situation or efficient parental defence) which could prevent very noisy broods from being taken by predators. A more sensitive test is to focus on those nests actually encountered by predators, then to ask whether noisier broods were destroyed at a more rapid rate than comparable quieter ones. Survival time from hatching to predation showed a significant partial correlation with the number of begging nestlings (Kendall's partial  $r = -0.46$ ,  $P < 0.01$ ), though not with the number of nestlings giving begging calls ( $r = -0.26$ , n.s.,  $n = 15$ ) when the effect of brood size was controlled for.

In a small subsample of nests ( $n = 11$ ), predators took one or two nestlings. The victimized chicks tended to be those coming from late-hatched eggs but none of them was starving at the time the nest was attacked. In fact, their average body-mass ranked above their position in the hatching sequence (Fig. 5). However, they showed a clear trend to be among the nestlings with the shortest latency to beg when stimulated during the two days before they disappeared.

## DISCUSSION

The hypothesis that noisy broods attract predators to the nest makes several predictions concerning the pattern of nest predation. First, hungrier (and noisier) broods should stand a higher predation risk, other things being equal, than well-fed broods; second, larger broods should attract more predators; and, third, older broods should be at a higher risk if begging calls become louder as nestlings grow up.

This study provides suggestive evidence that noisy broods attract predators to the nest. Since sampling was restricted to the area of maximum density of breeding pairs, where the proportion of experienced breeders is highest (Reese & Kadlec 1985), it is unlikely that differences in parental quality could account for the observed association between begging activity and predation risk. The possibility that the reduced predation rate on brood-reduced nests could be because poorer birds are displaced to sub-optimal nesting areas, where nests have higher starvation rates, and that these areas are ignored by predators because of their low profitability, is not supported by the rather uniform distribution of nests in space, independently of their fate. We might speculate that partial predation within a brood may be influenced by individual differences in begging behaviour;

**Figure 2.** Map of the study area showing the spatial distribution of Magpie nests according to causes of mortality. Those broods in which nestlings died from several different causes are indicated by a combination of symbols.

Source	Sum of Squares	d.f.	F	P
<i>All nestlings</i>				
Main effects	30.050	4	2.087	n.s.
Size	25.497	2	3.541	<0.04
Reduction	0.045	1	0.013	n.s.
Predation	6.323	1	1.757	n.s.
2-factor interactions	17.226	5	0.957	n.s.
S × R	3.198	2	0.444	n.s.
S × P	12.352	2	1.716	n.s.
R × P	0.116	1	0.032	n.s.
Residual	590.364	164		
Total	637.643	173		
<i>Nestlings with negative gain</i>				
Main effects	1.802	4	0.725	n.s.
Size	0.092	2	0.074	n.s.
Reduction	0.323	1	0.519	n.s.
Predation	1.090	1	1.754	n.s.
2-factor interactions	12.548	5	4.040	<0.02
S × R	4.774	2	3.842	<0.05
S × P	2.244	2	1.806	n.s.
R × P	4.361	1	7.020	<0.02
Residual	10.561	17		
Total	24.911	26		

Table 1. Results from a three-factor ANOVA assessing the effects of brood-size (S), brood reduction (R), and predation (P) upon the average mass increments of nestlings Magpie obtained during 1 h periods in early morning, expressed as percentage of initial nestling mass

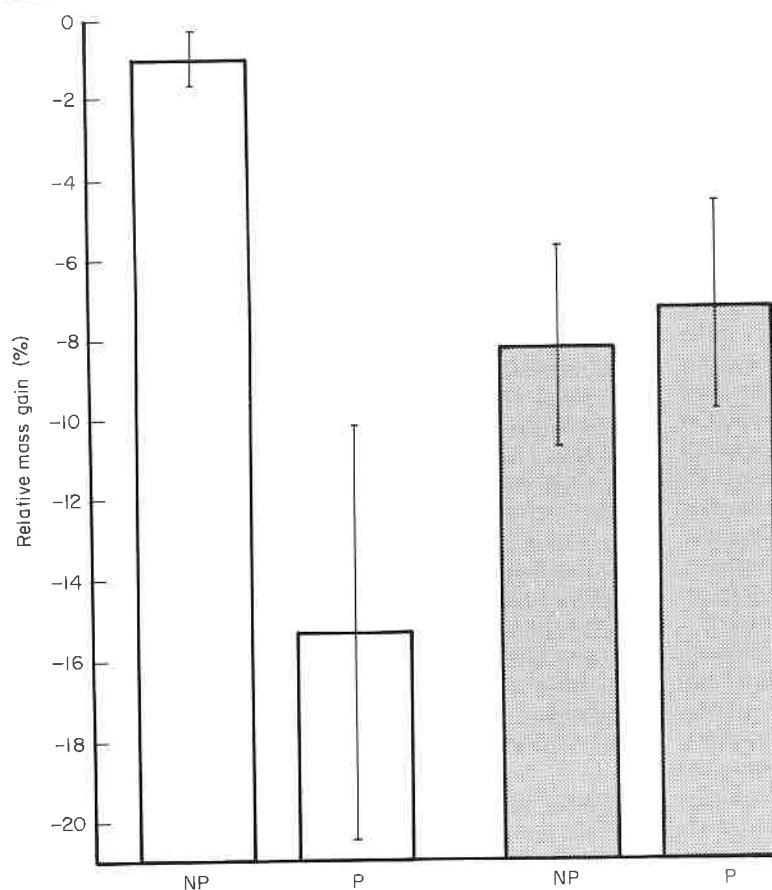


Figure 3. Average ( $\pm$ s.e.) negative mass increments (expressed as percentage of initial nestling mass) obtained during 1 h periods in early morning for Magpie broods according to causes of mortality. White bars: nests in which no nestling died from starvation; Black bars: brood-reduced nests; P: preyed-upon broods; NP: broods not preyed upon.

**Table 2.** Numbers of begging Magpie nestlings and nestlings giving begging calls in relation to brood-size

	Brood-size		
	4	5	6
<i>Total number of begging nestlings</i>			
Average	3.45	4.09	5.12
s.e.	0.62	0.77	0.65
Range	2.0-4.0	2.2-5.0	4.0-6.0
H	28.67	22.82	15.35
P	0.004	0.029	0.032
<i>Number of nestlings giving calls</i>			
Average	1.52	2.32	3.81
s.e.	0.87	0.69	1.42
Range	0.0-3.0	1.0-3.5	1.3-6.0
H	23.81	8.93	14.48
P	0.022	0.709	0.043
Number of nests	13	13	8
Number of observations	61	61	40

H: Kruskal-Wallis' nonparametric ANOVA between nests.

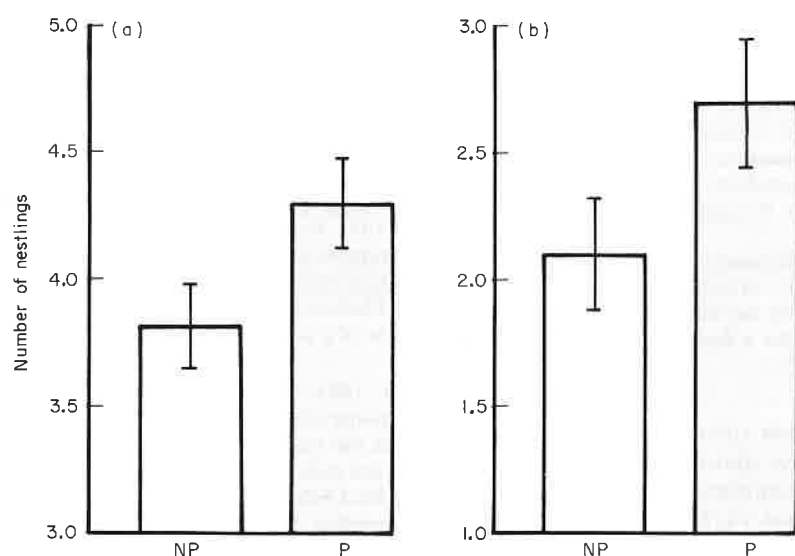
highly motivated nestlings might be more conspicuous to a predator which strikes at a single chick.

It is unclear whether noisier broods were also hungrier. The disproportionate risk of predation incurred by broods with no partial mortality provides equivocal evidence in this sense. It may be that surviving nestlings in reduced broods received more food, and hence begged less noisily. Evidence in support of this possibility is provided by the fact that nestlings in smaller broods obtained more food, and that nestlings in non-reduced broods which were preyed upon had been less likely to be fed during 1 h sampling intervals. Alternatively, brood-reduced nests could have been visited at a lower rate

(because a lower provisioning rate is the cause, or effect, of brood reduction), and predators are less likely to detect a nest via the parents' nest visitation. In any case, neither begging activity, nor food provisioned to nestlings, showed significant differences between reduced and non-reduced broods. A third possibility is that there may be a great deal of between-brood variation in begging activity which is unrelated to differences in the amount of food provisioned to a nest, as it has been found for other species (Hussell 1988, Stamps *et al.* 1989).

Perrins (1965) reported that large broods of Great Tits *Parus major* were more readily encountered by sound-guided predators (weasels, squirrels and woodpeckers). On the other hand, Högstädt (1980) found that whereas artificially enlarged broods of Magpies suffered from heavier predation losses, no such effect was apparent when considering natural-sized broods. The main conclusion from Högstädt's study was that parents adjusted clutch-and brood-size to an individual optimum, so that mortality factors were evenly distributed among the various brood-size classes. We found, however, that smaller broods experienced a slightly higher risk of predation. Although sample sizes were too small to allow comparisons between brood-size classes, the effect obscured a trend for broods subject to predation to display higher absolute levels of vocal activity during the days preceding predator attack. Only after controlling for the effect of brood-size did such a trend become evident.

Magpie begging calls become increasingly louder as nestlings grow older (Redondo 1991). This effect could increase the risk of predation for older broods but, in fact, daily mortality rates due to predation reach a peak around the middle of the nestling period (Redondo & Carranza 1989). Evidence obtained from other species also point to a lack of a relationship between age-related variations in the intensity of begging calls and the likelihood of predation (Young 1963, Holcomb 1969, Greig-Smith 1980, Knight & Temple 1986). The first likely reason why predation should not be more prevalent among older broods is that predators quickly



**Figure 4.** Average ( $\pm$ s.e.) values of the total number of begging Magpie nestlings (a) and the number of nestlings giving begging calls (b) adjusted for brood size in preyed-upon broods (P) and broods not preyed upon (NP). Comparison between adjusted means (analysis of covariance): (a)  $t_{28} = 1.88$ ,  $P < 0.05$ ; (b)  $t_{28} = 1.76$ ,  $P < 0.05$ . Broods that were preyed upon ( $n = 14$ ) had a significantly higher proportion of begging nestlings (Mann-Whitney U-test,  $z = 1.89$ ,  $P < 0.05$ ) and of nestlings giving begging calls ( $z = 2.02$ ,  $P < 0.05$ ) than broods that were not preyed upon ( $n = 18$ ).



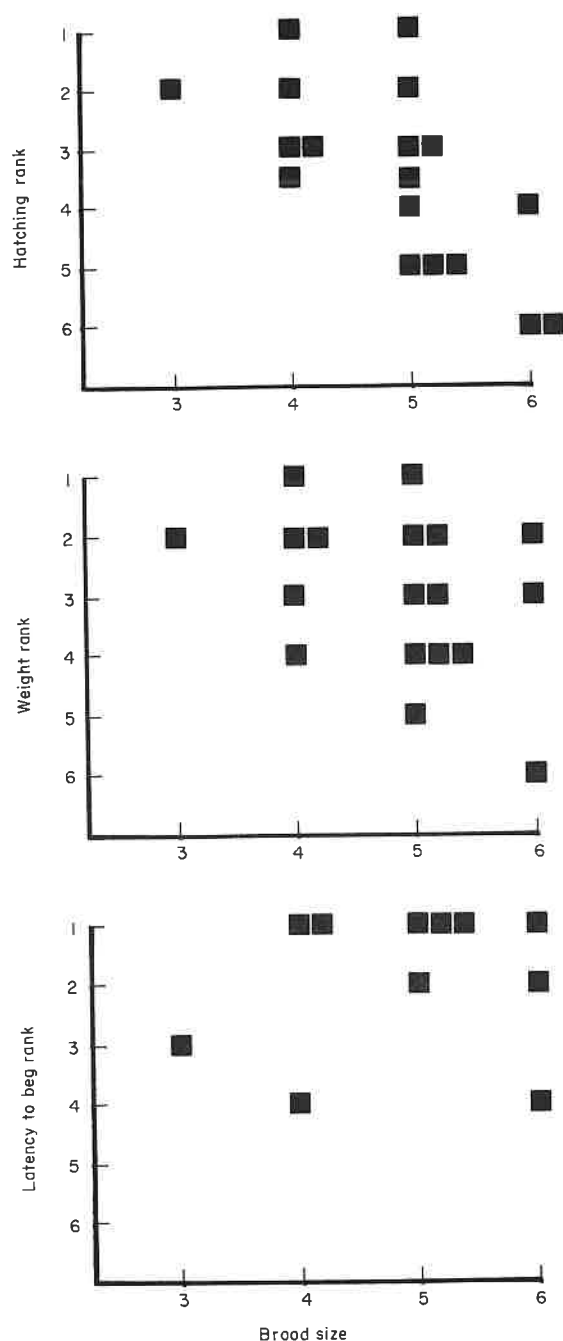


Figure 5. The identity of victimized Magpie nestlings in cases of partial predation according to hatching (1 = first hatched) and body mass rank (1 = heaviest) on the day before they disappeared, and the latency-to-beg rank (1 = shortest latency) averaged for the 2 days preceding their disappearance.

remove the broods which are easier to find (Ricklefs 1969, Willis 1973). Experiments with artificial nests have shown that the rate of nest destruction as a function of exposure time is higher at the initial stages (Gottfried & Thompson 1978, Martin 1987). This may partly compensate for the improved

detectability of older broods. Second, developmental changes in the acoustic structure of begging calls show a general pattern across different species which suggests that older nestlings emit calls which are more easily degraded into the environment (Redondo & Exposito 1990), thus reducing the chances of being accurately detected and/or decoded by an acoustically-guided predator. Third, nestlings respond to external situations presumably associated with the occurrence of predation, like parental alarm calls or novel stimuli, by ceasing to beg (Rydén 1978, Bischof & Lassek 1985) or by means of self-defensive behaviours, and such abilities improve with age (Khayutin 1985, Redondo & Carranza 1989).

Altogether, the above considerations show that complex interactions may exist between begging activity, predation risk and other variables. As a consequence, tests of the hypothesis looking for an association between predation risk and an indirect estimator of brood noise, such as brood size or nestling age, may be difficult to interpret.

Fieldwork at Coto Doñana was made possible by the excellent facilities provided by the Estación Biológica de Doñana (CSIC) and the Patronato (research project 107/89). We thank J. Aperribay and L. Arias de Reyna for their invaluable assistance with field work. This manuscript greatly benefited from the comments of E. Aguilera, F. Alvarez, J. Amat, R. Fraga, and two anonymous referees. Financial support was provided by C.I.C.Y.T. PB87-0316 research project, a grant from the Departamento de Biología Animal to F. C. and a post-doctoral M.E.C. grant (Perfeccionamiento de Doctores y Tecnólogos) to T.R.

## REFERENCES

- Alvarez, F. & Arias de Reyna, L. 1974. Reproducción de la Urraca (*Pica pica*) en Doñana. *Doñana Acta Vert.* 1: 77-95.
- Arias de Reyna, L., Recuerda, P., Corvillo, M. & Cruz, A. 1984. Reproducción de la Urraca (*Pica pica*) en Sierra Morena (Andalucía). *Doñana Acta Vert.* 11: 79-92.
- Baeyens, G. 1981a. Magpie breeding success and Carrion Crow interference. *Ardea* 69: 125-139.
- Baeyens, G. 1981b. The role of sexes in territory defence in the Magpie (*Pica pica*). *Ardea* 69: 69-82.
- Balanca, G. 1984. Le déterminisme du succès de la reproduction chez une population des pies bavardes (*Pica pica*). *Gibier Faune Sauvage* 4: 5-27.
- Bengtsson, H. & Rydén, O. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the Great Tit *Parus major*. *Behav. Ecol. Sociobiol.* 12: 243-251.
- Birkhead, T.R., Eden, S.F., Clarkson, K., Goodburn, S.F. & Pellatt, J. 1986. Social organization of a population of Magpies *Pica pica*. *Ardea* 74: 59-68.
- Bischof, H.-J. & Lassek, R. 1985. The gaping reaction and the development of fear in young Zebra Finches (*Taeniopygia guttata castanotis*). *Z. Tierpsychol.* 69: 55-65.
- Buitron, D. 1988. Female and male specialization in parental care and its consequences in Black-billed Magpies. *Condor* 90: 29-39.
- Fraga, R.M. 1980. The breeding of Rufous Horneros (*Furnarius rufus*). *Condor* 82: 58-68.

- Gochfeld, M. 1979. Begging by nestling Shiny Cowbirds: adaptive or maladaptive. *Living Bird* 63: 41-50.
- Gottfried, B.M. & Thompson, C.F. 1978. Experimental analysis of nest predation in an old-field habitat. *Auk* 95: 304-312.
- Gottlander, K. 1987. Parental feeding behaviour and sibling competition in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* 18: 269-276.
- Goodburn, S.F. 1991. Territory quality or bird quality? Factors determining breeding success in the Magpie *Pica pica*. *Ibis* 133: 85-90.
- Greig-Smith, P.W. 1980. Parental investment in nest defence by Stonechats (*Saxicola torquata*). *Anim. Behav.* 28: 604-619.
- Haartman, L. von. 1953. Was reizt den Trauerfliegenschnäpper (*Muscicapa hypoleuca*) zu füttern? *Vogelwarte* 16: 157-164.
- Harper, A.B. 1986. The evolution of begging: sibling competition and parent-offspring conflict. *Am. Nat.* 128: 99-114.
- Harris, M.P. 1983. Parent-young communication in the Puffin *Fratercula arctica*. *Ibis* 125: 109-114.
- Högestedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* 210: 1148-1150.
- Holcomb, L.C. 1969. Age-specific mortality of American Goldfinch nestlings. *Auk* 86: 760-761.
- Hussell, D.J.T. 1988. Supply and demand in Tree Swallow broods: a model of parent-offspring food-provisioning interactions in birds. *Am. Nat.* 131: 175-202.
- Khayutin, S.N. 1985. Sensory factors in the behavioural ontogeny of altricial birds. *Adv. Stud. Behav.* 15: 105-151.
- Kilham, L. 1977. Nesting behaviour of Yellow-bellied Sapsuckers. *Wilson Bull.* 89: 310-324.
- Knight, R.L. & Temple, S.A. 1986. Nest defence in the American Goldfinch. *Anim. Behav.* 34: 887-897.
- Linsdale, J.M. 1937. The natural history of Magpies. *Pac. Coast Avif.* 25: 1-234.
- Macnair, M.R. & Parker, G.A. 1979. Models of parent-offspring conflict. III. Intra-brood conflict. *Anim. Behav.* 27: 1202-1209.
- Magrath, R.D. 1989. Hatching asynchrony and reproductive success in the Blackbird. *Nature* 339: 536-538.
- Martin, T.E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. *Condor* 89: 925-928.
- Møller, A.P. 1982. Characteristics of Magpie *Pica pica* territories of varying duration. *Ornis Scand.* 13: 94-100.
- Newton, I. 1964. The breeding biology of the Chaffinch. *Bird Study* 11: 47-68.
- O'Brien, P.H. & Dow, D.D. 1979. Vocalizations of nestling Noisy Miners *Manorina melanoccephala*. *Emu* 79: 63-70.
- Perrins, C.M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. *J. Anim. Ecol.* 34: 601-647.
- Perrins, C.M. 1977. The role of predation in the evolution of clutch size. In Stonehouse, B. & Perrins, C.M. (eds), *Evolutionary Ecology*: 181-191. Baltimore: University Park Press.
- Redondo, T. 1991. Early stages of vocal ontogeny in the Magpie (*Pica pica*). *J. Orn.* 132: 145-163.
- Redondo, T. & Arias de Reyna, L. 1988. Locatability of begging calls in nestling altricial birds. *Anim. Behav.* 36: 653-661.
- Redondo, T. & Carranza, J. 1989. Offspring reproductive value and nest defense in the Magpie (*Pica pica*). *Behav. Ecol. Sociobiol.* 25: 369-378.
- 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.
- Reese, K.P. & Kadlec, J.A. 1985. Influence of high density and parental age on the habitat selection and reproduction of Black-billed Magpies. *Condor* 87: 96-105.
- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9: 1-48.
- Ricklefs, R.E. 1977. A note on the evolution of clutch size in altricial birds. In Stonehouse, B. & Perrins, C.M. (eds), *Evolutionary Ecology*: 193-214. Baltimore: University Park Press.
- Rogers, P.M. & Myers, K. 1980. Animal distributions, landscape classification and wildlife management, Coto Doñana, Spain. *J. Appl. Ecol.* 17: 545-565.
- Rydén, O. 1978. Differential responsiveness of Great Tit nestlings, *Parus major*, to natural auditory stimuli. *Z. Tierpsychol.* 47: 236-253.
- Schuchmann, K.-L. 1983. Analyse und Ontogenese des Sperrverhaltens bei Trochiliden. *J. Orn.* 124: 65-74.
- Siegel, S. & Castellan, N. 1988. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.
- Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91: 430-455.
- Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54: 159-169.
- Slagsvold, T. 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *J. Anim. Ecol.* 53: 945-954.
- Smith, H.G. & Montgomerie, R. 1991. Nestling Robins compete with siblings by begging. *Behav. Ecol. Sociobiol.* 29: 307-312.
- Stamps, J.A., Clark, A., Arrowood, P. & Kus, B. 1989. Begging behaviour in Budgerigars. *Ethology* 81: 177-192.
- Tatner, P. 1982. The breeding biology of Magpies *Pica pica* in an urban environment. *J. Zool. Lond.* 197: 559-581.
- Trivers, R.L. 1974. Parent-offspring conflict. *Am. Zool.* 14: 249-264.
- Trivers, R.L. 1985. *Social Evolution*. Menlo Park: Benjamin Cummings.
- Webster, A.B. & Hurnik, J.F. 1987. Heritability of the peep vocalization in White Leghorn-type chicks. *Appl. Anim. Behav. Sci.* 19: 157-168.
- Willis, E.O. 1973. Survival rates for visited and unvisited nests of Bicolored Antbirds. *Auk* 90: 263-267.
- Young, H. 1963. Age-specific mortality in the eggs and nestlings of Blackbirds. *Auk* 80: 145-155.
- ZAHAVI, A. 1977. Reliability in communication systems and the evolution of altruism. In Stonehouse, B. & Perrins, C.M. (eds), *Evolutionary Ecology*: 253-259. Baltimore: University Park Press.
- ZAR, J.H. 1984. *Biostatistical Analysis*. New Jersey: Prentice-Hall.

Submitted 7 March 1991; revision accepted 24 July 1991