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RULES OF FOOD ALLOCATION BETWEEN NESTLINGS OF THE BLACK-BILLED MAGPIE *PICA PICA*, A SPECIES SHOWING BROOD REDUCTION

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SUMMARY.—*Rules of food allocation between nestlings of the black-billed magpie Pica pica, a species showing brood reduction.*

Aims: The existence of a size hierarchy of nestlings in a brood facilitates a secondary readjustment of brood size to resource availability, through the death of the smaller chicks when food is scarce. A mechanism to facilitate brood reduction would be for parents preferentially to feed the biggest nestlings in the nest. Therefore, feeding rules employed by adults are important because they predetermine the extent of brood reduction when food is scarce. In this study, feeding rules are studied in a species with habitual brood reduction, the black-billed magpie (*Pica pica*).

Location: Hoya de Guadix, southeastern Spain.

Methods: Nests were filmed using a micro-camera.

Results: Parents preferentially fed the bigger nestlings, and those with higher begging levels, i.e. those which came closer to parents, responded most quickly, had higher begging intensity and adopted a higher posture when begging. Moreover, the preference by parents for the biggest nestlings was independent of the level of begging and the position in the nest. The process of multiple feeding (when more than one nestling was fed during one feeding event) was also analysed, in relation to nestling age and size: such events were more frequent with younger chicks in the nest, and when the first chick fed was relatively small.

Conclusions: Results are congruent with the adaptive brood reduction hypothesis.

Key words: begging behaviour, black-billed magpie, brood reduction, food allocation, parental investment, *Pica pica*, reproductive strategies.

RESUMEN.—*Reglas de reparto del alimento entre los pollos en la Urraca* Pica pica*, una especie con reducción de nidada.*

Objetivos: La existencia de una jerarquía en el tamaño de los pollos de una nidada facilitaría un reajuste secundario del número de pollos a la disponibilidad de alimento, muriendo, en caso de escasez, los pollos más pequeños. Un mecanismo que facilitaría esta reducción de nidada consistiría en que los padres alimentaran preferentemente a los pollos de mayor tamaño en la nidada. Por tanto, las reglas de reparto de alimento que siguen los adultos son importantes ya que pueden predecir el nivel de reducción de nidada en caso de escasez de alimento. En este estudio se analiza el comportamiento de reparto del alimento en una especie en la que normalmente se produce reducción de nidada, la urraca (*Pica pica*).

Localidad: Hoya de Guadix, sudeste de España.

Métodos: Los nidos fueron filmados con una micro-cámara.

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Resultados: Los padres cebaron preferentemente a los pollos de mayor tamaño y que solicitaron alimento a mayor nivel (más cerca de los padres, con mayor rapidez, más intensidad y alcanzando mayor altura al pedir). Además, la preferencia por los pollos de mayor tamaño era independiente del nivel de petición y de la posición en el nido. Se analizó también el proceso de ceba múltiple (cuando se alimentó a más de un pollo en un mismo evento de ceba) en relación al tamaño y edad de los pollos. Estos eventos fueron más frecuentes cuando los pollos fueron de corta edad, y cuando el primer pollo en ser alimentado fue relativamente pequeño.

Conclusiones: Los resultados son congruentes con la hipótesis de la reducción de nidada adaptativa.

Palabras clave: comportamiento petitorio, estrategias reproductivas, inversión parental, *Pica pica*, reducción de nidada, reparto del alimento, urraca.

INTRODUCTION

The begging behaviour by which nestlings seek food from their parents, and the parental responses to such demands, comprise a model for studying the parent-offspring conflict (Trivers, 1974). The family unit comprises an entity in which the interests of parents and offspring, as well as those of siblings, do not coincide (Mock and Parker, 1997; Parker *et al.*, 2002b). The resolution of such conflicts may be mediated by the emission of honest begging signals, which parents may interpret without risk of deception. This possibility has been demonstrated theoretically (Godfray, 1995a; Godfray and Johnstone, 2000), and its empirical proof has generated great interest (e.g., Kilner and Johnstone, 1997; Wright and Leonard, 2002).

The parent-offspring conflict predicts that each offspring will demand a greater parental investment than is optimal for the parents to deliver (Trivers, 1974). In the case of intersibling conflict (Macnair and Parker, 1979; Mock and Parker, 1997), the prediction would be that, when the parents need to distribute food between brood members, each nestling will demand more than its fair share. The parents may derive greater fitness via passive food distribution behaviour, which is by feeding the hungriest and most assertive nestling (Bonabeau *et al.*, 1998; Rodríguez-Gironés *et al.*, 2001a; Parker *et al.*, 2002a). Whether or not a nestling gets food from the adults does not solely depend on its relative size but also on its investment in costly begging behaviours. Given the costs of such signalling, and that their relative benefit depends on the requirement for food (i.e. hunger), their intensity will depend on the nestlings' needs (Rodríguez-Gironés *et al.*, 2001a; Parker *et al.*, 2002a). Thus, irrespective of whether or not the parents distribute food passively, begging intensity is an honest reflection of the nestlings' needs (Royle *et al.*, 2002).

Avian broods frequently show a size hierarchy, the result of asynchronous hatching (Magrath, 1990; Stenning, 1996; Mock and Parker, 1997). Since larger nestlings are more likely to survive to breed such a size hierarchy brings about a gradient in the reproductive fitness of the offspring (Winkler, 1987; Mock and Parker, 1997). The existence of a size hierarchy may be an adaptation (on the part of the parents) to the uncertainty of food availability while the young are growing, given that it facilitates brood reduction when food is short, permitting the fittest offspring to survive in good condition. (Lack, 1968; Magrath, 1989; Forbes *et al.*, 2001). Hence, since larger nestlings have greater reproductive fitness, in species in which brood reduction exists the parents should feed preferentially those nestlings which have the greatest chance of success (Soler, 2001).

Here we have studied food distribution by adults between brood members and examined whether this is related to begging behaviour and relative nestling sizes. The magpie (*Pica pica*) is a species which displays brood reduction (Birkhead, 1991; Soler *et al.*, 1996). The mean clutch size of the study population was 6.9, with 74.4 % fledging success (Soler *et al.*, 1996). We studied behaviour both in nests with small young (little developed, unfeathered and with eyes shut) and large young (feathered and with eyes open). Basically, we attempted (1) to examine the effect of relative nestling size on parental food distribution behaviour, and (2) to analyse the circumstances which give rise to multiple feeding, in which several nestlings are fed during one parental visit.

MATERIALS AND METHODS

Study area and filming procedure

The study was conducted between 1993 and 1997 in the Hoya de Guadix in southeast Spain (37º 10' N, 03º 11' O). This is an area of cereal and almond (*Prunus dulcis*) cultivation, with some Iberian holm oaks (*Quercus rotundifolia*). The magpies nest in both tree species.

A Toshiba® model CCD microcamera was hidden within the nest structure to film the nests. The filmed images were recorded on a VHS video recorder which was linked to the camera by a 20m-long cable and was contained within a camouflaged hide. A monitor within the hide allowed events within the nests to be seen. An hour was allowed for the parents to accept the microcamera and to begin feeding the nestlings as normal. If they failed to do so within this time, the equipment was withdrawn and the site abandoned so as not to compromise the breeding pair. Those nests where the magpies successfully accepted the camera were filmed for approximately two hours.

Many magpie pairs (about 90 %) were alarmed by the camera and cable and pecked at them, or did not enter the nest within the stipulated period, which made data collection very difficult. In addition, the necessary data could not be obtained from some of the nests filmed, for various reasons, which reduced the sample size. Ultimately, we were able to analyse adequately the feeding in four nests with small, naked nestlings (mean mass ± SD: 53.08 ± 18.45 g: brood sizes being four in one nest, six in another and five in two other nests) We also obtained data from seven nests with larger, feathered young (mean mass ± SD: 123.22 ± 30.90 g), these having their eyes open, better thermoregulatory ability (Choi and Bakken, 1990) and showing greater locomotory activity (Bengtsson and Rydén, 1981). The brood sizes in these seven nests were one of three nestlings, one of four, three of five, one of six and one of eight. The high rate of rejection of the camera might suggest that our sample was biased, but we do not have motives to think that filmed nests were not a representative sample of the population for the behaviour studied.

Before filming began the nestlings were weighed to the nearest gram with a Pesola spring balance and their beaks or heads were marked with non-toxic paint, to permit individual identification and to test the effect of body mass and begging behaviour on the probability of being fed.

Analysis of the recordings

The recordings were analysed using a VHS editing unit which allowed images to be examined frame by frame. Recordings were run until a feeding event was detected. An instance of multiple feeding was recorded when an adult fed several young successively during the same feeding occasion. In all these cases the datas were assigned to one of three categories: (1) a simple feed, when only one nestling was fed, (2) the identity of the first nestling fed during a multiple feed, and (3) the identity of a nestling fed subsequently during a multiple feed. The identity of the nestling being fed was recorded whenever possible. The feeding events were analysed frame by frame to assign a score to each nestling which demanded food, under each of the following variables:

1) Order. The latency, or relative begging sequence. The order in which each nestling begged for food following a parent's arrival or made a food-soliciting call. Thus, the nestling whose latency was '1' was the first one to beg.

2) Position. Relative position in the nest with respect to the adult. The distance from a nestling's beak to its parent's body. Thus, the nestling whose position score was '1' was the closest to its parent at the moment of begging for food.

3) Intensity. Relative begging intensity within the brood. This was scored according to increasing begging intensity, as described by Redondo and Castro (1992), from begging with the beak open and legs flexed to begging with the neck and legs completely extended, while calling and wing flapping. A continuum of begging intensity was assumed for ranking purposes. When two or more nestlings begged with similar vigour the recordings were examined carefully to establish which of them did so with greater intensity (for example, which beat its wings most strongly or extended its body more), or the most active nestling was considered to be the most intense begger (Rydén and Bengtsson, 1980). Thus, the nestling with Intensity '1' was the one which sought food most actively.

4) Height. Relative height when begging: considering the height order of the nestlings' heads. The nestling with Height '1' was the one whose head was higher up than those of its nest companions.

Since brood sizes differed, both the size order within a brood and the various orders of begging intensity were standardised according to the formula: (value – 1) / (brood size – 1) (Smith and Montgomerie, 1991). This formula admits values between 0 and 1, so that values closest to 0 correspond to nestlings of relatively greatest size, lowest relative latency, closest to the parents, showing greatest relative begging intensity and having the head highest, according to the variable under consideration. It must be borne in mind that all the variables are expressed in the form of relative orders and not as absolute values, so that a value for one nestling in one nest during one feeding event is not independent of the scores of its siblings.

The recordings from five nests were examined by two separate investigators. Both of them gave the same scores to begging activities on 97.5 % of occasions (n = 163 feeds examined), indicating a high level of between-investigator repeatability.

A principal component analysis (PCA) was used to generate a correlation index with the four variables of nestling behaviour measured. The first transformation (PC1) explained 61.3 % of the variance in nestling begging behaviour and showed a negative relationship with the four variables of $-0.61 < r < -0.90$. This index, termed the 'total begging level' is used in later analyses instead of the four separate variables, to simplify data presentation.

Statistical analysis

The data relating to feeding is normally distributed and hence allowed parametric statistics, following Sokal and Rohlf (1995). The Fisher Exact test (2-tailed) was used to compare frequencies in 2 x 2 contingency tables. The mean value for each nest was used for comparisons between nestlings fed and not fed, or fed in a simple or a multiple feed, to avoid pseudoreplication problems (Hurlbert, 1984). In these cases we used Student's t-test for paired comparisons or an ANOVA for repeated measurements.

RESULTS

Feed distribution according to age

In the four nests with small nestlings filmed, a total of 123 feeds were recorded

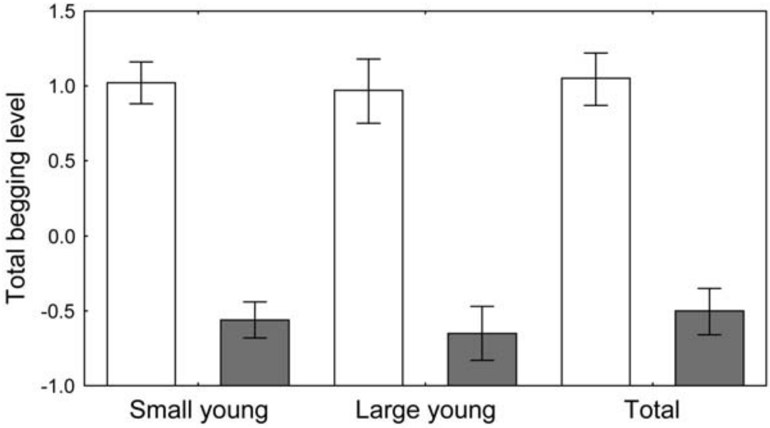

FIG. 1.—Total begging level by fed nestlings (white) and unfed nestling (grey) ($n = 11$ nests), in nests with young broods ($n = 4$ nests), and with older broods ($n = 7$ nests). Bars indicate standard deviations.
*[Valores de nivel total de petición de los pollos que recibieron ceba (blanco) y los que no (gris) en el total (*n *= 11), en nidos de pollos pequeños (n = 4 nidos) y en nidos de pollos grandes (*n *= 7 nidos). Las barras indican la desviación típica.]*

(mean ± SD, 30.8 ± 11.3 feeds per nest), which took place during 68 feeding events (17.0. ± 3.9 events per nest). Multiple feeds occurred on 28 of these events (41.2 %, 43.0 ± 25.2 %). Multiple feeds were more frequent than simple feeds in two nests (63.9 ± 3.9 % were multiple feeds), whereas simple feeds were more frequent than multiple ones in the other two nests (77.8 ± 12.1 % of feeding events). Between 2 and 6 nestlings were fed during multiple feeds (3.0 ± 1.2 nestlings fed per multiple feed).

In the seven nests with large nestlings, a total of 186 feeds were recorded (26.6 ± 11.5 feeds per nest), during 157 feeding events (22.4 ± 10.9 events per nest). Multiple feeds occurred in 24 (15.3 %) of these events. Multiple feeds were significantly more frequent in nests with small nestlings (Fisher Exact test, $P < 0.001$). Simple feeds were significantly more frequent in nests with large young (Binomial test, 2-tailed, $P < 0.02$, Siegel and Castellan, 1988), and in those nests two or three nestlings were fed during multiple feeds (2.2 ± 0.4).

The effect of begging behaviour and nestling size on feeding

Nestlings which were fed had a higher begging level than those which were not fed ($t_{10} = 11.52$, $P < 0.001$, Fig. 1). The difference remains when nests of each age-class are analysed separately, both for nests with small young ($t_3 = 5.99$, $P < 0.01$) and those with older ones ($t_6 = 9.25$, $P < 0.001$). There was no interaction between brood age and differences between fed and not-fed nestlings (ANOVA for repeated measurements; age x feed interaction: $F_{1,9} = 0.02$, $P = 0.90$; fed *vs.* not-fed: $F_{1,9} = 111.54$, $P < 0.001$; Fig. 1). The mean values of the standardised orders for the four begging variables (position, order, intensity and height) of the fed nestlings in the nests with small young did not differ from those obtained from the nests with large young (*t*-test, $t_9 < 2.0$, $P > 0.10$; Fig. 2). Together, these results suggest that the fed nestlings begged closer to the feeding parent, sooner than the non-fed young, with greater

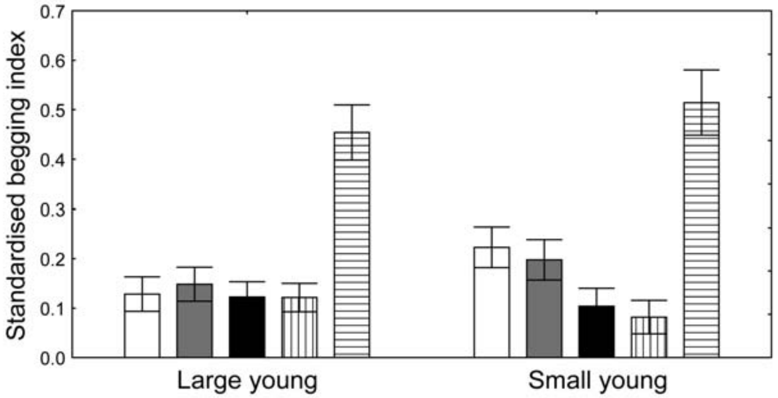

FIG. 2.—Mean standard begging indices and relative nestling masses of nestlings that were fed in nests with young broods ($n = 4$) and in nests with older broods ($n = 7$). Bars indicate standard deviations. White: relative proximity to parents, grey: order of begging or relative latency, black: relative begging intensity, vertical hatching: relative head height reached during begging, horizontal hatching: relative mass.
*[Orden estandarizado medio de los valores de petición y del peso relativo de los pollos que fueron cebados en nidos con pollos pequeños (*n *= 4) y en nidos con pollos grandes (*n *= 7). Las barras indican la desviación típica. Blanco: proximidad relativa a los padres, gris: orden relativo de petición, negro: intensidad relativa de petición, rayado vertical: altura relativa al pedir, rayado horizontal: peso relativo.]*

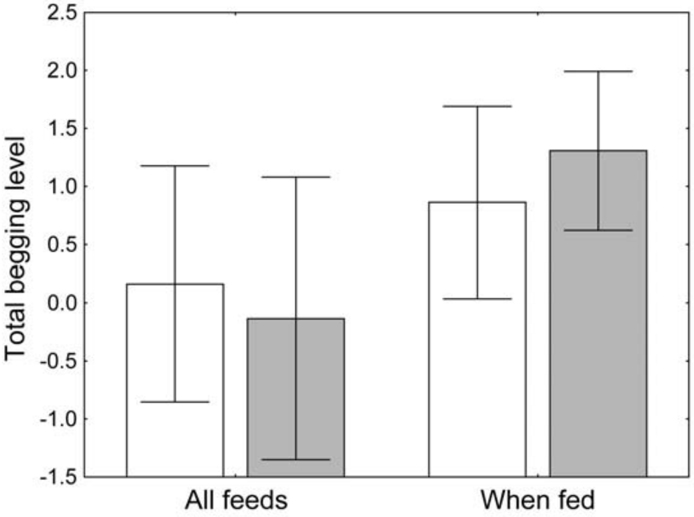

FIG. 3.—Total begging levels of the largest (white) and the smallest (grey) nestlings in each nest, at each feeding event and only when fed. Bars indicate standard deviations.
[Valores de nivel total de petición del pollo más grande (blanco) y más pequeño (gris) en cada nidada en los eventos de ceba en los que pidieron y sólo en los que fueron alimentados. Las barras indican la desviación típica.]

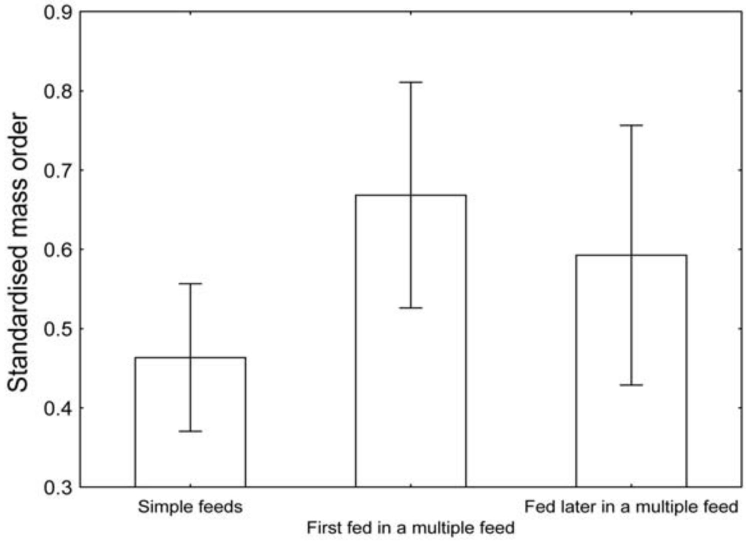

FIG. 4.—Relative standardised masses of nestlings fed during simple feeds, as the first fed in multiple feeds, and as those fed subsequently during multiple feeds. Bars indicate standard deviations. *[Peso relativo estandarizado de los pollos cebados en cebas simples, los primeros de cebas múltiples y después de los primeros en cebas múltiples. Las líneas indican la desviación típica.]*

intensity and reached higher up than their non-fed siblings. These findings did not alter with nestling age.

With respect to nestling size, fed nestlings were larger than non-fed ones (standardised size order of fed nestlings: 0.48 ± 0.08; of non-fed nestlings: 0.57 ± 0.11; $t_{10} = 3.89$, $P < 0.02$). There was no difference between the number of feeds demanded by the largest and the smallest nestlings within a nest (largest nestling: 14 ± 6.86; smallest nestling: 17 ± 5.88; $t_{10} = 1.13$, $P = 0.29$). Possibly the largest nestling, when it begged, exhibited greater begging scores than the smallest nestling, but there was no significant difference between the mean begging scores of the largest and smallest young ($t_{10} = 1.06$, $P < 0.31$; Fig. 3). Nevertheless, when the largest nestling was fed it exhibited a lower total begging score than the smallest nestling, when the latter was fed ($t_{10} = 2.43$, $P < 0.05$; Fig. 3).

Multiple feeds

We compared the relative masses of the nestlings fed during a simple feed (1) with those of the first (2) and subsequent (3) nestlings fed during a multiple feed. The nestling which was chosen to be fed first during a multiple feed had a standardised relative mass greater than those selected during simple feeds (ANOVA for repeated measurements; $F_{2,18} = 3.82$, $P < 0.05$; Fig. 4). This suggests that multiple feeding events occurred when the nestling chosen for feeding was relatively small.

DISCUSSION

Begging behaviour and food distribution rules

The four begging behaviour variables measured in this study are well known to influence the probability of nestlings being fed by their parents. For example, in some species it has been shown that the nestlings nearest the parents get fed preferentially (Smith and Montgomerie, 1991; Kacelnik *et al.*, 1995; Whittingham *et al.*, 2003). In other studies the nestling which is most likely to be fed is the first one to beg when an adult arrives (Price and Ydenberg, 1995; Leonard and Horn, 1996; Dearborn, 1998) or the one which reaches highest above the others (Teather, 1992; Lichtenstein and Sealy, 1998; Lichtenstein, 2001). Redondo and Castro (1992) found that in magpies the begging intensity increases with nestling hunger. Furthermore, the hungriest nestlings were fed first, which suggests that the parents chose the young which begged most. The present study corroborates these authors' suggestion, showing that the probability of being fed is related to begging intensity.

The most probable advantage of these feeding rules to parents is that, where all nestlings are in conditions of equal reproductive value, they will feed the most needy, reducing their likelihood of starving to death and, hence, increasing their biological fitness (Harper, 1986). Nevertheless, our begging intensity index also included variables more related to competition between siblings (position within the nest) or associated with relative size (relative height reached when begging) as well as those which directly indicate need to the parents (neck extension, wing movements etc.) Thus it is possible that very needy nestlings may be unable to reach an ideal position in the nest or may be unable to compete successfully with larger siblings, leading to a reduction in brood size. In accordance with this scenario, Redondo (1993) found that the magpie feeds its larger nestlings preferentially, which could be due to parental preference for the larger young, or to the larger nestlings being able to gain privileged positions within the nest through their competitive advantage (e.g., Ostreiher, 2001), or that they beg with greater intensity. According to our results, the magpies fed the larger nestlings preferentially but this was not due to the bigger young begging at higher intensity than the smallest (proximity to parents included). Smaller nestlings have also less food requirements than larger chicks, but because larger nestlings were fed when begging at a lower level that when small nestlings were fed, findings suggest that parents took into account more the need of larger nestlings than the need of smaller chicks. Hence, when food is short, the food distribution rules detected in this study would produce brood reduction, through the death of the smallest and least competitive young. There is experimental evidence that begging behaviour in magpies is costly (Rodríguez-Gironés *et al.*, 2001b), so that begging intensity is an honest signal of need (Godfray, 1991, 1995b; Kilner and Johnstone, 1997). This, together with findings on between-sibling competition (Parker *et al.* 2002a, 2002b), explains the food distribution behaviour of adults of this species.

Nestlings which are largest at fledging are more likely to survive to breed (Husby and Slagsvold, 1992) and hence have greater reproductive fitness. From this standpoint, nestling size should be a characteristic used by parents when deciding which nestling to feed, when food is scarce, since this would increase parental biological efficiency (Clutton-Brock, 1991; Mock and Parker, 1997). Within-brood size differences may be due to age differences or to other factors such as gender (Teather, 1992). In general, such differences may be brought about or controlled by the parents. One of the most frequent ways of producing a size hierarchy within a brood is through asynchronous hatching (Magrath, 1990; Stenning, 1996). magpies show asynchronous hatching and, since they feed larger young preferentially, those lowest in the size hierarchy would starve to death when food is scarce. Such a situation would minimise the energy loss in a nest represented by the death of a nestling. For example, Soler (1990) found that in the Jackdaw (*Corvus monedula*) although only 36.1 % of the young survived to fledging, these represented 58.1 % of the biomass produced. It is also the case that brood reduction permits the larger nestlings to fledge in better physical condition (Magrath, 1989; Forbes *et al.*, 2001).

The function of multiple feeds

The parents used the same rules to distribute food independently of nestling age. Nevertheless, multiple feeds were more frequent when the young were smaller, no doubt because at this age the parents could bring more food in one than a single nestling could ingest. On the other hand, multiple feeds occurred when the first chick chosen for feeding by the parents was relatively small, suggesting once again that several young are fed during the same feeding event when the first nestling is too small to consume all the food delivered.

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