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Preferential allocation of food by magpies *Pica pica* to great spotted cuckoo *Clamator glandarius* chicks

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Abstract Adult magpies *Pica pica* provide parasitic great spotted cuckoo *Clamator glandarius* nestlings with a diet very similar to that fed to their own chicks. In both naturally and experimentally parasitized nests, great spotted cuckoo chicks were fed at a higher rate than magpie chicks in the same nest. This preferential allocation of food by magpie parents to great spotted cuckoo chicks is consistent with the supernormal stimulus hypothesis, because this result implies that cuckoo chicks provide stronger stimuli for parental care than host chicks. Great spotted cuckoo chicks receive most of the food brought to the nest by the foster parents, because they exploit a series of stimuli which jointly (or sometimes individually) operate as a supernormal stimulus. This hypothesis predicts that if any stimulus is masked, the efficiency of the cuckoo in eliciting parental care will decrease. Here, we analyze experimentally the effects of two of these stimuli, preferential feeding of large nestlings and of nestlings with conspicuous palatal papillae. Firstly, when we experimentally introduced one medium-sized (7–9 days) cuckoo chick into an unparasitized magpie nest where the largest magpie chick was 12–15 days old, the cuckoo did not receive significantly more food than the average or the largest magpie chick. Secondly, when unparasitized nests were experimentally parasitized with a cuckoo chick that had its gape painted to mimic that of magpie chicks, the parasitic cuckoo received less food than the average magpie chick.

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Introduction

Altricial birds such as the hosts of parasitic cuckoos hatch in a helpless state with only the ability to gape for food; provisioning of adequate food for the young is clearly an important problem among breeding birds (Hussell 1991). Regulation of food provisioning involves supply to the brood and allocation among brood members (Hussell 1991). Brood parasitism is a form of reproduction in which certain individuals, the parasites, receive parental care from unrelated individuals, the hosts (Rothstein 1990). Few studies have analysed the parental behaviour of hosts, even though this behaviour has a critical and quantifiable influence on brood parasites (Mason 1986). Gill (1982) found that raising a shining bronze-cuckoo *Chrysococcyx lucidus* to fledging required less effort from the grey warbler *Gerygone igata* host in terms of feeding visits than raising a brood of several warblers. Brooke and Davies (1989) reported that reed warblers *Acrocephalus scirpaceus* fed nestling European cuckoos *Cuculus canorus* and broods of their own young at a similar rate and on a similar diet. When shining bronze-cuckoo and European cuckoo chicks hatch, they evict all other eggs and nestlings from the nest and are reared alone. Information about the parental behaviour of hosts is available for only one parasite species where the parasite chick is reared together with the host young (Mason 1986); this information is limited as Mason assessed only the quality of the nestling diet which different host species fed to parasitic shiny cowbird *Molothrus bonariensis* chicks.

The great spotted cuckoo *Clamator glandarius* is a specialist brood parasite, which, in contrast to most other cuckoos, parasitizes large-sized birds mainly members of the corvid family, and, in Europe, particularly the magpie *Pica pica* (Cramp 1985). Great spotted cuckoo eggs usually hatch earlier than those of the magpie host, but, unlike other cuckoos, the chick does not eject host eggs or nestlings. Instead, the fast-growing great spotted cuckoo chick readily outcompetes the smaller magpie nestlings for food and as a result drastically decreases the reproductive success of the host (Cramp 1985; Soler 1990; Soler et al. in press).

In our study area, magpies with unparasitized nests feed their young a diet based on imagines of Coleoptera, larvae, pupae and barley *Hordeum sativum* (Martinez et al. 1992). From the prey available, magpies select mainly larvae and spiders, showing a tendency to select larger prey among those available in the environment (Martinez et al. 1992).

The supernormal stimulus hypothesis (Dawkins and Krebs 1979) states that cuckoo nestlings provide hosts with a supernormal stimulus which ensures that they are fed preferentially. The idea of a supernormal stimulus implies that cuckoo chicks provide stronger stimuli for parental care than do host chicks. The cuckoo chick obtains more food because it exploits a series of stimuli which are very effective in eliciting parental care. The most important of these stimuli are: (1) larger body size, because the cuckoo chick hatches earlier, (2) a gape with well developed palatal papillae, and (3) greater intensity of begging in the cuckoo chick (unpublished work; Soler M, Soler J.J. and Martinez J.G.). These three stimuli, and perhaps others [e.g. faster growth (Soler and Soler 1991) and higher level of activity (personal observations)], alone or operating together, make the cuckoo chick a supernormal stimulus. This hypothesis predicts that if any of the stimuli are masked, the efficiency of the cuckoo in eliciting parental care will decrease.

Here we test whether magpies feed great spotted cuckoo nestlings and their own young a similar diet, and whether each parasitic chick receives more food than each magpie chick. Furthermore, we analyze experimentally the effects of two features (stimuli) which may govern the allocation of food by the host to parasitic offspring rather than host nestlings (1) body size and (2) the colour of the palatal papillae.

Methods

Study site

The field work was carried out in the Hoya de Guadix, southern Spain (37° 10′ N, 3°11′ W), a cereal-producing plain (especially barley) at approximately 1000 m a.s.l. The vegetation is sparse, with some holm oaks (*Quercus rotundifolia*) and many groves of almond trees (*Prunus dulcis*) in which magpies nest at high density.

Food samples

Feeding frequencies may not reflect the true consumption by nestlings, since the number or size of items delivered may vary (Royama 1966), and in the magpie it is difficult to assess load size visually because the food is carried in the throat pouch (Birkhead 1991). For these reasons, we decided to use the neck collar method in order to (1) study the nestling diet using the entire prey, facilitating prey identification and biomass calculation; and (2) analyse the exact quantity of food allocated to each nestling in a brood.

Magpie and great spotted cuckoo chicks have a similar capacity for food storage when provided with neck-collars. However, the oesophagus of magpie chicks is relatively long, while that of the great spotted cuckoos is relatively wide (personal observations). The food samples of magpie and great spotted cuckoo chicks were collected during the breeding seasons of 1989–1992 using the neck-collar method (Kluijver 1933). The ligature wire around the neck of the nestling is tight enough to hinder the swallowing of food and loose enough to avoid strangling the chicks. Though potential biases of the method have been recorded (Johnson et al. 1980), there is no evidence that the effect differs between cuckoos and magpies. In both naturally and experimentally parasitized nests we placed neck-collars on all chicks in the nest (including any cross-fostered chicks). After 3–4 h we checked the nests and collected the food. This duration was chosen because, according to our experience (Martinez et al. 1992), most chicks receive some food during this period, which is not long enough to cause the chicks to vomit. However, sometimes one or more boluses of food were found in the nest. When there was only one bolus of food in the nest and only one nestling had an empty gape, we assumed that the food originated from the nestling without food. If there was more than one bolus in the nest the test was not considered in the analyses. Each food sample (corresponding to each chick) was stored in 40% alcohol. The feeding rate of magpies during the nestling period ranges from 0.7 to 1.5 trips/young/hr (Buitron 1988). However, in our study area we observed that after neck-collars were placed on all chicks in a nest (the process lasted between 15 and 30 min), magpies did not start to feed nestlings until approximately 40–45 min later.

Nestling diet

Food samples were collected from 10 naturally and 16 experimentally parasitized nests, with great spotted cuckoo and magpie chicks present in the same nest. In both experimentally and naturally parasitized nests only one cuckoo chick (plus a number of magpie chicks) was present in each nest.

Each food sample was viewed under a binocular microscope (4 × 10 magnification), and the different prey items were identified (each cereal grain was considered one prey in the analyses). For the biomass estimates (mg dry weight), food samples were placed in an oven at 60°C for 48 h (to constant mass) and later all items of each prey type were weighed on a precision balance (0.0001 g). To analyse the diet, we used each nest as an independent observation. We calculated (1) the total number of items carried to the nest, (2) the percentage corresponding to each item, (3) how these percentages were distributed among the chicks present in the nest and the mean percentage of each item for every species in every nest. The last parameters were used in a Wilcoxon matched-pairs signed-ranks test to determine whether the number of different prey items provided by adult magpies to the cuckoo and magpie chicks were significantly different. A *G*-test was used to compare the frequency of each item in the diet of magpie and cuckoo chicks.

To avoid giving too much weight to the rare taxa in the species comparisons, we considered only the most important groups (as in number as in biomass), grouping the rest under "other items".

Quantification of food received by each chick

Here we have studied the same food samples as in the nestling diet analysis (10 naturally and 16 experimentally parasitized nests), and additionally those collected in 28 unparasitized magpie nests and 7 naturally parasitized nests containing only one great spotted cuckoo chick. Food samples were collected in nests where the oldest chick was 5–15 days old. Originally, we analyzed two different groups according to chick age (5–10 and 11–15 days old), but since the differences were not significant we pooled all data.

The quantity of food was consistently measured as biomass (dry weight) in order to avoid errors in the different drying levels of the food samples. Each food sample was weighed on a precision balance (0.0001 g), and mass was expressed as mg/h. To avoid giving too much weight to unfed magpie chicks (since the brood consisted of some magpies and only one cuckoo chick, there would be greater possibilities of one magpie chick remaining unfed), the average quantity of food received by magpie chicks was calculated disregarding chicks which were not fed.

Experimental procedure

In the experimental parasitism, a great spotted cuckoo chick was taken from its nest and immediately cross-fostered to an unparasitized magpie nest (in some cases it was taken in the afternoon and cross-fostered very early the next morning). The cuckoo chick was usually about 3 days older than the larger magpie chick (3.24 ± 1.18 days, $n = 17$). In the naturally parasitized nests, the age difference was less (0.38 ± 0.71 days, $n = 8$), but not significantly different from the age difference in experimentally parasitized nests (Mann-Whitney *U*-test, $U = 44$, $P = 0.16$). Each magpie nest was tested only once.

To test the importance of body size in the experiments, the great spotted cuckoo chick was approximately 5 days younger (cuckoo 8.20 ± 0.42, magpie 13.9 ± 0.55, $n = 10$; Wilcoxon matched-pairs test, $P = 0.005$) and significantly smaller (cuckoo 68.3 ± 3.36 g, magpie 127.1 ± 5.76 g, $n = 10$; Wilcoxon matched-pairs test, $P = 0.005$) than the oldest magpie chick in the brood. Each magpie nest was tested only once.

A second experiment was designed to test the importance of the colour of the palatal papillae. This experiment was conducted by experimentally parasitizing unparasitized magpie nests having 6–12 days old magpie chicks using a cuckoo chick of the same developmental stage. The cuckoo chicks were similar in age and mass to the larger magpie chicks (age: cuckoo 8.4 ± 0.6, magpie 8.1 ± 0.6, $n = 15$; mass: cuckoo 69.0 ± 8.1, magpie 64.3 ± 8.0, $n = 13$; in both cases, differences were not significant, Wilcoxon matched-pairs test, NS). The same magpie nest was tested twice on 2 consecutive days, one nest (randomly chosen) with the cuckoo's gape painted to mimic that of the magpie chick (red colour with the white palatal papillae masked) and the other with the cuckoo's gape unpainted. On the 2nd day the test was performed at the same time as on the 1st day. The gape of the cuckoo was painted with red food colour just before the chick was placed in the magpie nest. Tests in which magpies did not deliver food were excluded from the analyses. A control of the experimental treatment was performed by introducing a magpie chick in an unparasitized magpie nest with its gape either painted red to match a normal magpie gape or unpainted following exactly the same procedure as described above. The experimental magpie chick and the larger magpie chick were similar in age and mass (age: experimental magpie 10.00 ± 0.94, larger magpie 9.25 ± 0.98; mass: experimental magpie 77.87 ± 10.31, $n = 8$; mass: experimental magpie 77.87 ± 10.31, larger magpie 70.5 ± 9.85, $n = 8$. In both cases differences were not significant, Wilcoxon matched-pairs test, NS).

Values given are means ± SE.

Results

Do great spotted cuckoo and magpie chicks receive a similar diet?

In naturally parasitized nests, adult magpies provided cuckoo chicks with a diet similar to that fed to their own offspring (Table 1, percentage of nest with every type of prey, $G = 1.43$, $df = 7$, $P > 0.95$). The main difference was Coleoptera (sub-optimal prey with a high percentage of chitin), which were more numerous in the diet of the cuckoo chick (Wilcoxon matched-pairs test, $z = 2.0$, $n = 10$, $P = 0.04$, Table 1). This result may be the consequence of small sample size, because in experimentally parasitized nests the difference between the diet of great spotted cuckoo and magpie chicks was not significant for any item (see Table 1), although a similar trend was observed, more chitinous prey (Orthoptera and Coleoptera) being preferentially given to cuckoo chicks (Table 1).

Do great spotted cuckoo chicks receive a greater amount of food than magpie chicks?

The amount of food carried to the nest by magpie parents in unparasitized nests was positively and significantly correlated with the age of the chicks ($r = 0.51$, $n = 28$, $P = 0.006$) and, in every age class, the quantity of food was significantly correlated with the number of chicks per nest ($r_s = 0.75$, $n = 13$, $P = 0.003$ and $r_s = 0.55$, $n = 15$, $P = 0.03$, for nests in which the older chick is between 5–10 days old and between 11–15 days old, respectively).

In both naturally and experimentally parasitized nests, the great spotted cuckoo chicks received more food (biomass/h) than magpie chicks in the same nest (Table 2 ; Wilcoxon matched-pairs test, $T = 4$, $n = 8$, $P = 0.001$ and $T = 7$, $n = 17$, $P = 0.05$, respectively, for naturally and experimentally parasitized nests). In naturally parasitized nests the great spotted cuckoo chicks obtained a higher percentage (74.4 ± 11.1, $n = 8$) of the food brought by the magpie parents than in experimentally parasitized nests (50.0 ± 6.9, $n = 17$; Mann-Whitney *U*-test, $U = 34.5$, $P = 0.05$). This difference may be because old cuckoo nestlings, artificially introduced into magpie nests at the beginning, sometimes remained quiet without begging (personal observations).

The total amount of food carried per hour by magpie parents to unparasitized nests (142.5 ± 31.0 mg/h, $n = 28$) was not significantly different from that carried to parasitized nests (107.8 ± 22.7 mg/h, $n = 25$, naturally and experimentally parasitized nests pooled; Mann-Whitney *U*-test, $U = 313$, $P = 0.51$). Actually, the average amount of food was almost one-third higher in unparasitized as compared to parasitized nests. The number of chicks per nest in unparasitized nests (4.1 ± 0.3) was very similar to that found in parasitized (natural plus experimental) nests (4.0 ± 0.3). The average amount of food received by each chick in unparasitized nests tended to be greater than that received in parasitized nests, both when all chicks present in the nest were considered (36.8 ± 7.1 mg/h, $n = 28$ and 21.80 ± 4.5 mg/h, $n = 25$, respectively, $t = 1.73$, $P = 0.09$), and when only those which received

Table 1 Diet of great spotted cuckoo and magpie chicks in naturally and experimentally parasitized nests

	Naturally parasitized nests					
	Mean ± SE of the average percentage of each item received per nest					
	Cuckoo chicks	Magpie chicks	Wilcoxon matched-pairs test		Percentage of nests with each type of prey	
Type of prey	Mean SE	Mean SE	z	$P =$	Cuckoo chicks	Magpie chicks
Araneidae	0.7 ± 0.7	0.3 ± 0.48	0.0	1	10.0% (1/10)	10.0% (1/10)
Orthoptera	25.4 ± 12.9	2.7 ± 0.34	1.5	0.13	50.0% (5/10)	40.0% (4/10)
Hymenoptera	6.4 ± 4.9	0.2 ± 0.32	1.6	0.11	30.0% (3/10)	10.0% (1/10)
Coleoptera	21.3 ± 10.0	1.2 ± 0.63	2.0	0.04	50.0% (5/10)	20.0% (2/10)
Larvae (Lepidopt.)	6.4 ± 4.9	3.8 ± 0.31	0.0	1	30.0% (3/10)	20.0% (2/10)
Other items	5.0 ± 5.0	–	0.0	1	10.0% (1/10)	0% (0/10)
Carrion	11.4 ± 6.4	2.0 ± 1.43	1.2	0.23	40.0% (4/10)	20.0% (2/10)
Cereal (Barley)	0.2 ± 0.2	0.9 ± 0.16	1.1	0.29	10.0% (1/10)	20.0% (2/10)
Number of nests	10	10			$G = 1.43$, $df = 7$, $P > 0.95$	
	Experimentally parasitized nests					
Isopoda	4.1 ± 3.7	0.8 ± 0.6	0.4	0.72	12.5% (2/16)	18.8% (3/16)
Araneidae	4.6 ± 1.4	2.5 ± 0.7	0.9	0.40	56.3% (9/16)	68.8% (11/16)
Orthoptera	5.6 ± 2.2	4.1 ± 2.4	0.5	0.60	37.5% (6/16)	68.8% (11/16)
Dermaptera	2.2 ± 1.8	0.3 ± 0.3	0.7	0.47	12.5% (2/16)	12.5% (2/16)
Hymenoptera	1.8 ± 1.4	2.3 ± 1.3	0.3	0.74	12.5% (2/16)	31.3% (5/16)
Coleoptera	14.6 ± 5.1	4.4 ± 0.9	0.5	0.12	50.0% (8/16)	68.8% (11/16)
Larvae (Lepidopt.)	0.4 ± 0.4	1.3 ± 0.6	1.4	0.18	6.3% (1/16)	37.5% (6/16)
Others items	7.3 ± 3.1	3.1 ± 1.8	0.7	0.47	56.3% (9/16)	50.0% (8/16)
Carrion	–	0.4 ± 0.2	0.8	0.07	0% (0/16)	31.3% (5/16)
Cereal (Barley)	1.9 ± 1.2	1.3 ± 1.3	0.4	0.72	18.8% (3/16)	6.3% (1/16)
Number of nests	16	16			$G = 12.40$, $df = 9$, $P > 0.19$	

food were considered (42.5 ± 7.3 mg/h, $n = 28$ and 25.6 ± 4.6 mg/h, $n = 25$ respectively, $t = 1.89$, $P = 0.06$). The quantity of food carried per hour to unparasitized nests (142.5 ± 31.0 mg/h, $n = 28$) was much higher than that carried to parasitized nests with a cuckoo chick alone (20.6 ± 8.1 mg/h, $n = 7$; Mann-Whitney *U*-test, $U = 2.91$, $P < 0.005$). Cuckoos reared alone received less food than those reared together with magpies (in naturally and experimentally parasitized nests, Table 2). This disparity is probably caused by the fact that before we fitted chicks with neck-collars (usually 1 or 2 h after sunrise), each single cuckoo chick had received all the food which the parents were able to carry to the nest. Single cuckoos may have been more satiated than cuckoo chicks accompanied by magpie chicks if the same quantity of food had been distributed among all chicks in the nest. Thus, cuckoos which share the nest with magpie chicks may usually be hungrier early in the morning than those reared alone.

Why did great spotted cuckoo chicks receive more food than magpie chicks?

Great spotted cuckoo chicks may receive more food for various reasons, of which two are: they are usually considerably larger than magpie chicks and their gape has conspicuous spurred papillae.

To test these two hypotheses, we performed two experiments.

1. Importance of body size. We found no evidence of a size effect. When we experimentally introduced one cuckoo chick 6–8 days old into an unparasitized nest

Table 2 Quantity of food carried to the nest and received by host and parasite chicks in naturally and experimentally parasitized nests. For magpies (second row) numbers are the mean of the means

	Quantity of food received (mg/h) mean ± SE (sample size)	
	Naturally parasitized nests	Experimentally parasitized nests
Great spotted cuckoo	87.2 ± 39.0 (8)	49.7 ± 11.4 (17)
Magpie (mean)	9.1 ± 4.7 (8)	19.3 ± 5.3 (17)
Largest magpie chick in the brood	11.5 ± 8.0 (8)	29.7 ± 10.3 (17)
Total quantity of food carried to the nest	105.6 ± 36.7 (8)	108.9 ± 29.4 (17)
Total quantity of food carried to parasitized nests with only one cuckoo chick	20.6 ± 8.1 (7)	

where the largest magpie chick was 12–15 days old, the cuckoo received more food than the average magpie chick (cuckoo chick: 76.4 ± 19.2 mg/h, $n = 10$, average magpie chick: 43.3 ± 7.2 mg/h, $n = 10$), and than the largest magpie chick in each brood (59.4 ± 12.9 mg/h, $n = 10$). But in this case differences were not significant (Wilcoxon matched-pairs test, $t = 13$, $n = 10$, $P = 0.14$ and $T = 20$, $n = 10$, $P = 0.44$ respectively). Another piece of information which supports the importance of body size is that large cuckoo chicks were preferred over than smaller cuckoo chicks (personal observations).

2. Importance of the papillae. When unparasitized nests were experimentally parasitized with a cuckoo chick (of a similar size as the larger magpie chick, see Methods) with its gape painted to mimic that of the magpie chicks, the parasitic cuckoo did not receive more food than the average magpie chick or than the largest magpie chick in the nest. In fact, the trend was the opposite (Table 3). The cuckoo chick with its gape painted received significantly less food than when unpainted (Table 3, Wilcoxon matched-pairs test, $t = 12$, $n = 15$, $P = 0.006$). When unpainted, the great spotted cuckoo chick received more food in 13 of 15 tests and monopolized a significantly higher percentage of the total food carried to the nest by the magpie parents (44.0 ± 7.5%) than when painted (25.7 ± 7.9%; Wilcoxon matched-pairs test, $T = 18$, $n = 15$, $P = 0.03$). The total amount of food carried to the nest was significantly higher when the cuckoo gape remained unpainted (Table 3, Wilcoxon matched-pairs test, $T = 16$, $n = 15$, $P = 0.01$).

The experimental treatment (the red food colour) did not affect the results, since an alien magpie chick that was experimentally introduced into an unparasitized magpie nest received similar quantities of food when its gape was painted (76.5 ± 28.1 mg/h, $n = 8$) as when its gape was unpainted (87.8 ± 33.8 mg/h, $n = 8$; Wilcoxon matched-pairs test, $T = 12$, $P = 0.40$), and the total amount of food carried to the nest was also very similar (247.1 ± 85.7 mg/h, and 248.4 ± 49.9 mg/h, respectively; Wilcoxon matched-pairs test, $T = 17$, $n = 8$, $P = 0.88$).

Table 3 Quantity of food received by host and parasite chicks or carried to the nest when the cuckoo chick had a painted gape mimicking that of magpie chicks, with the white palatal papillae masked and when the cuckoo chick had an unpainted gape. For magpies (second row) numbers are the mean of the means.

	Quantity of food received (mg/h) Mean ± SE (sample size)	
	Cuckoo chick with painted gape	Cuckoo chick with unpainted gape
Great spotted cuckoo	29.8 ± 11.2 (15)	87.9 ± 20.6 (15)
Magpie (mean)	32.3 ± 5.4 (15)	45.9 ± 11.8 (15)
Largest magpie chick in the brood	35.9 ± 9.0 (15)	45.5 ± 16.9 (15)
Total quantity of food carried to the nest	101.9 ± 18.6 (15)	204.2 ± 46.6 (15)

Discussion

The diet provided to parasite nestlings is a critical aspect of host quality. It would therefore be important to determine whether food items fed to cuckoos are as easy to collect as those fed to magpies. It has been suggested repeatedly that the diet of great spotted cuckoo young is comprised only of insects, because they refuse hosts offering other types of food, such as grain, carrion and vertebrate prey (Valverde 1953; Di Carlo 1971; Cramp 1985). However, our results show that young cuckoos accept grain and carrion. We found that suboptimal prey with high chitin contents were given preferentially to cuckoos (Table 1). Does the adult magpie choose to feed high-quality prey to its own young? This idea is unlikely because fledgling success of magpies in parasitized nests is very low (Soler 1990; Soler et al. in press a). Considering that Brooke and Davies (1989) reported a similar tendency in reed warblers feeding European cuckoos (82.6% of cuckoo faeces contained Coleoptera remains, while in unparasitized nests Coleoptera appeared in only 33.9% of the reed warbler faeces). Perhaps the host, in order to satisfy the voracious parasitic nestlings, might decrease the quality of the prey types and thereby decrease feeding effort.

Why did great spotted cuckoo chicks receive more food than magpie chicks?

It has been suggested that cuckoo nestlings provide hosts with a supernormal stimulus for parental care (Dawkins and Krebs 1979), ensuring that they are fed preferentially. Is this really the case? The quantity of food brought to an experimentally parasitized nest was not higher than that brought to an unparasitized nest; indeed, the tendency was the opposite. Therefore, raising the chicks in a parasitized nest to fledgling requires less effort than raising a brood of an unparasitized nest, mainly because in a naturally parasitized nest magpie nestlings only rarely survive to fledge (Soler 1990; Soler et al. in press b). Similar results have been found in other studies. Gill (1982) showed that raising a shining bronze-cuckoo to fledgling required less effort in terms of feeding-visits than raising a brood of several host chicks. Davies and Brooke (1988) found that reed warblers did not prefer to feed a cuckoo chick when given a simultaneous choice of a cuckoo chick and one or two young reed warblers.

However, great spotted cuckoo chicks received significantly more food than magpie chicks (Table 2), and it has also been reported that great spotted cuckoo nestlings grew faster than magpie nestlings in parasitized and unparasitized nests (Soler and Soler 1991). The supernormal stimulus hypothesis implies that cuckoo chicks provide stronger stimuli for parental care than host chicks, and the evidence for preferential feeding of cuckoo chicks by magpies is consistent with this idea. Why does the great spotted cuckoo chick receive most of the food brought to the nest by the foster parents? Great spotted cuckoo chicks exploit a series of stimuli which are very effective in eliciting parental care. According to parent-offspring conflict theory (Trivers 1974), young are selected to demand more food than their parents are selected to provide. When parents and young are closely related (this is usually the case in normal broods without parasitism), offspring selfishness is somewhat constrained (Trivers 1974; Nur 1984; Godfray 1991). A more intense demand of food by a cuckoo nestling is predicted because it has no genetic relationship with its host, and a cuckoo chick would not suffer a decrease in fitness even if it literally worked its hosts to death following independence (Brooke and Davies 1989).

There are some stimuli in unparasitized nests of altricial birds which generally govern parental allocation of food among nestlings. These together (or even alone) could operate as a supernormal stimulus that make the cuckoo chick successful in receiving a disproportionately large amount of parental care. Here, we have analyzed two of these stimuli:

First, great spotted cuckoo nestlings often enjoy a competitive advantage because they typically hatch earlier than magpie nestlings, and these nestlings being best placed, reacting first and stretching the highest are fed preferentially by the parents (Lockie 1955; Lohrl 1968; Rydén and Bengtsson 1980; Bengtsson and Rydén 1981). If the cuckoo chick is considerably larger than the magpie chicks, this will provide the cuckoo with a competitive advantage. In support of this argument, the parasitic chick did not receive significantly more food than the largest magpie chick or than the average magpie chick when smaller than the magpie chicks. However, it was preferentially fed because of other stimuli such as the palatal papillae, the intensity of begging, and the higher level of activity. Apparently, the size effect may help the cuckoo as it normally helps the larger sibling in a brood and not in a supernormal way.

Second, great spotted cuckoo chicks mimic host young, both visually (Lack 1968) (before feathers develop) and vocally (Mundy 1973; Redondo and Arias de Reyna 1988). However, the gape of the cuckoo and host differs markedly, that of magpies being wider and redder, while that of the cuckoo is lighter and with well developed palatal papillae, which are absent in magpie chicks (Mundy and Cook 1977; Cramp 1985). It has frequently been suggested that preferential feeding of great spotted cuckoos is stimulated by the conspicuous palatal papillae (Mundy and Cook 1977; Cramp 1985; Fry et al. 1988). Our results support this idea of the palatal papillae stimulating the foster parent to feed preferentially the cuckoo chick (Table 3). The fact that the total amount of food carried to the nest was significantly higher when the cuckoo gape remained unpainted implies that the conspicuous palatal papillae are effective in eliciting parental care. Therefore, the palatal papillae may be considered a supernormal stimulus.

The results of the painting experiment were much stronger than those of the body size experiment. This is because in the body size experiment, cuckoos were smaller than the magpies but still had their conspicuous palatal papillae and begged more intensively; that is, cuckoos enjoy two competitive advantages. In the painting experiment, cuckoos had their palatal papillae masked and they were no larger than the magpie chicks (see Methods), and thus the cuckoo chick had only one competitive advantage (more intense begging). These results provide additional evidence supporting the idea that as more competitive advantages are masked, more markedly decreases the efficiency of the cuckoo in eliciting parental care. Thus, the three stimuli operating together make the great spotted cuckoo chick a supernormal stimulus.

Dawkins and Krebs (1979) suggested that hosts may not be able to resist a cuckoo chick any more "than the junkie can resist his fix". As stated, this hypothesis implies a stable outcome of the cuckoo-host arms race (Dawkins and Krebs 1979). In this extreme sense we cannot conclude that the cuckoo chicks provide hosts with a supernormal stimulus, because magpies do not always show a preference for cuckoo chicks, given that in some nests magpie chicks were fed preferentially. Davies and Brooke (1988) found similar results, concluding that there was no supernormal stimulus that elicited host feeding. In another experimental study of chick recognition (Soler et al. in press b), we found that magpies showed some discriminatory capacity against cuckoo chicks and that cuckoo chicks when cross-fostered in an unparasitized magpie nest were neglected by magpies (not fed, ejected or attacked) at a higher frequency than a magpie chick fostered in a parasitized magpie nest. We concluded that the cuckoo chick does not provide its magpie host with a supernormal stimulus to avoid chick recognition.

The supernormal stimulus concept may be weaker than stated by Dawkins and Krebs (1979). Tinbergen (1951) considered supernormal stimuli simply to be those that are more effective than the normal ones. Thus, as stated above, the supernormal stimulus hypothesis implies that cuckoo chicks provide stronger stimuli for parental care than do host chicks, and our results support this hypothesis. Calculating data from Davies and Brooke (1988; Table XVIII), each European cuckoo chick received on average 4.5 feeds while each reed warbler chick received 3.5 feeds. Therefore, perhaps the European cuckoo chick also provides hosts with a supernormal stimulus ensuring that they are fed preferentially.

In conclusion, the evidence for preferential feeding by magpies of great spotted cuckoo chicks is consistent with the supernormal stimulus hypothesis.

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