

THE EVOLUTION OF

BEGGING

COMPETITION, COOPERATION & COMMUNICATION



EDITED BY
JONATHAN WRIGHT & MARTY L. LEONARD

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DISHONEST BEGGING AND HOST MANIPULATION BY *CLAMATOR* CUCKOOS

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ABSTRACT

Brood parasites may be favoured over host nestlings due to variation in the honesty of their begging signals. Begging behaviour of great spotted cuckoo nestlings and their host magpie nestlings was recorded when controlling food need. Cuckoo begging effort was dishonest as an indicator of nutritional need, whilst magpie begging was not. Cuckoos begged for longer and emitted more calls at a higher rate irrespective of the degree of food deprivation, although in contrast to magpies, cuckoos ate food in relation to their need. Energetic and predation costs are unlikely to account for these differences. Differences in indirect inclusive fitness costs can explain the more intensive begging by cuckoos. Magpie parents given a choice favoured larger nestlings and those begging more intensively. Cuckoos obtained more food and a larger share than magpies of a similar size. Magpies therefore received less food in the presence of a cuckoo, and cuckoos received a similar share irrespective of their size. Lack of relatedness to their magpie hosts therefore allows cuckoos to exploit a set of adaptive rules in the host parents and manipulate them into providing the latter with preferential care.

INTRODUCTION

The great spotted cuckoo (*Clamator glandarius*) is an obligate brood parasite that uses magpies (*Pica pica*) as its major host. Unlike the European cuckoo (*Cuculus canorus*), great spotted cuckoo nestlings do not evict host

eggs or nestlings after hatching, but severely depress the reproductive success of magpies by outcompeting host nestlings, which often starve to death. Magpie nestlings may occasionally survive (ca. 17% of successful parasitized nests), but they fledge at low masses and thus contribute little, if any, to their parents' reproductive output. Adult great spotted cuckoos are slightly smaller than magpies but grow faster and hatch two to three days earlier on average than magpies (Soler & Soler 1991). Field observations revealed that young cuckoos were not aggressive towards magpie nestlings. Instead, they appeared to monopolize the incoming food, and then precipitated the death of their emaciated nestmates by trampling and crowding them (Alvarez & Arias de Reyna 1974).

This chapter explores this apparent favouritism toward cuckoo nestlings by magpie parents, which may be confounded by factors that suggest alternative explanations. For instance, because cuckoos hatch earlier than magpie nestlings, and because across species nestlings beg more as they get older, more intense begging behaviour by cuckoos could simply be a side-effect of their older age (Redondo & Exposito 1990). Cuckoo nestlings may also have higher food requirements because of their larger size, faster growth (Soler & Soler 1991) or lower quality diet (Brooke & Davies 1989).

Differences in feeding success between cuckoos and magpies could simply be the result of competition, or due to traits other than begging, such as nestling number or gape morphology (Soler et al. 1995a,b). Previous experiments on broods containing a single cuckoo and several magpie nestlings have revealed that magpie parents feed cuckoo nestlings preferentially over magpie nestlings (Soler et al. 1995b). The distinctive appearance of cuckoo nestlings that are in the minority might allow them to receive more food, either because parents alternate between the type of nestling fed on successive visits, or because cuckoos provide a stronger stimulus following habituation to host young (Rothstein 1978).

In this chapter, we avoid these complications by comparing the begging behaviour of nestlings under controlled conditions and with similar nutritional need. We also tried to overcome the confounds of nestling number by giving magpie parents a choice between one nestling of each species, whilst controlling for growth, need and size, and studying nestlings at an early age when competitive interference between nestlings is poorly developed.

METHODS

Cuckoos and magpies were studied in Santa Fe (Granada, Spain), a population with remarkably high levels of parasitism (ca. 65%). Details of the study area can be found elsewhere (Zuñiga & Redondo 1992). Field data collected from this population between 1990 and 1998 were used to compute several parameters (e.g. survival and predation rates). Nests were inspected every other day during building and laying until clutch completion, and every day around hatching time, to determine nestling age precisely. Once broods had hatched, they were monitored every two days and matched to the treatments required for each experiment.

Experiment 1

To test whether cuckoos begged more than magpie nestlings for a comparable level of need, a laboratory experiment was performed with ten nestlings of each species of known age coming from different nests. In order to control for growth effects, nestling age was restricted to the day of maximum growth (8 days for cuckoos and 11 days for magpies), when daily mass gain (10-12g) and development for both species were most similar. Nestlings were collected near dusk the day before the experiment and not fed until the next morning in the laboratory. They were kept in individual nestboxes at 27°C. The feeding schedule involved transporting each nestling inside its box into a feeding chamber containing a stuffed adult magpie and a black glove that could be manipulated from behind a screen, and the recording equipment. Nestlings were stimulated to beg by moving the stuffed magpie and a hand inside the glove holding forceps to deliver the food. Nestlings were allowed to ingest *ad libitum* amounts of food (minced beef heart muscle) once every hour during 14 hours of artificial daylight. The amount of food consumed in each feeding session was measured by weighing food before and after feeding with an electronic precision balance (accuracy 0.01g). Nestlings were returned to their nests the following morning (ca. 36 hours being spent in the laboratory).

The degree of food deprivation was manipulated by modifying the above schedule with two short (0.5 hour) and two long (2.5 hour) intervals between feedings at randomly established times of the day. In this way we obtained three periods of food deprivation (0.5, 1 and 2.5 hours). Begging behaviour was recorded during the two feeding sessions following short and long deprivation intervals, plus two 1-hour sessions randomly chosen from the regular feeding schedule. During a feeding session, food was delivered

to nestlings whenever they gaped and made begging movements and/or calls. However, we had to consider slightly different satiation criteria for the two species, which were: failing to beg or stopping begging in magpies; and failing to swallow two consecutive meals or throwing the food away in cuckoos (see Results). Nestlings were visually stimulated to beg without feeding for a minute or until they stopped begging. Immediately afterwards, they were again stimulated to beg, using a sound stimulus (voice) and fed *ad libitum* as usual until they met the satiation criteria (three consecutive begging failures, see below). The complete begging bout (the total amount of time begging without feeding plus time spent begging until satiation) was recorded. This measure combines both nestling willingness to be fed, plus their ability to maintain begging behaviour following a feeding event. It should also compensate for individual differences in nestling responses to begging rewards as a result of previous experience. Means per nestling were computed using two begging samples per inter-feed interval duration.

Begging calls were recorded through a condenser microphone (AKG 568 EB) attached to a Sony cassette recorder (WM D6C), and analysed in a real-time sound spectrograph (KAY 5500, Kay Elemetrics Corporation) with a transform size of 300 Hz. We examined the total duration of begging bouts, the duration and number of calls per bout and the total time spent calling. During the second half of the begging bout, we defined begging failures as a lack of begging response following a vocal stimulus before satiation (magpies especially had to be stimulated several times before receiving the first meal, then they often responded by begging again). Measurements of the acoustic intensity of calls (in dB SPL) were taken during 0.5 hour and 2.5 hour trials using a Brüel & Kjaer 2235 sonometer at a distance of 0.5m. Records consisted of peak values of sound intensity per call resulting from an automatic averaging of the whole frequency range (A setting). This procedure was chosen because background noise (which showed 11% variation between recording sessions) could be filtered from high frequency begging calls. The body posture of nestlings during begging was estimated as the highest score displayed during a begging record. Rank scores were as follows: (1) fails to beg, (2) resting on belly, tarsi flexed, (3) body stretched, tarsi extended, and (4) the same as (3) plus wing flapping (see Redondo & Castro 1992a). We assumed that a begging parameter (e.g. calling rate) varied 'honestly' with deprivation time if it both (i) correlated with increasing deprivation and (ii) at least two adjacent mean values (e.g. those corresponding to 0.5 and 1.0 hour, or 1.0 and 2.5 hours) were significantly different in that particular direction (Paired Wilcoxon test). Parameter values for cuckoos and magpies were compared using Mann-Whitney U tests.

Experiment 2

The differential response of magpie parents towards cuckoo and magpie nestlings was determined *via* choice experiments: one cuckoo-magpie set plus a control set containing two magpie nestlings in comparable size combinations. To create experimental two-nestling broods, we temporarily removed all brood contents from magpie nests containing nestlings of three to eight days old and replaced them with two experimental nestlings of two to six days old from a different nest. We chose this age range because differences in development (e.g. eyes opening) are less pronounced and nestlings show limited physical activity, which minimizes direct physical interference. Nestlings were weighed using an electronic precision balance (accuracy 0.01g), they were then left in the nest for three hours before being weighed again. On each occasion, we recorded the behaviour and position of nestlings. Relative Food Intake (RFI) was defined as mass gain by each nestling expressed as a percentage of initial body mass. Differences in RFI between nestlings were plotted as a function of relative mass asymmetry between nestlings, allowing detection of variation in RFI with regard to relative nestling size. An index of relative mass asymmetry was calculated as the difference in mass between nestlings divided by their average mass. This variable controls for existing biases in asymmetry caused by variation in absolute body mass. In addition, we computed food share (the percentage of total mass gain) and nestling mass ratios (dividing the mass of a focal nestling by the mass of its broodmate) as estimates of feeding success and relative size, respectively. We were careful to choose adequate combinations of nestling sizes to represent the whole range of values of relative mass asymmetry within the age span considered. Tests in which parents failed to deliver any food (i.e. negative or zero RFI) were excluded from analyses. Neither nestlings nor parents were tested more than once. There were no overall differences in the initial mass of cuckoos (mean \pm SE: 24.2 ± 2.4 g) and magpies (26.8 ± 3.7 g) in the cuckoo-magpie set (Wilcoxon test, $P > 0.5$, $n = 29$ broods). The initial mass of cuckoos in those tests where the cuckoo was the larger nestling (35.4 ± 5.4 g, $n = 17$) did not differ significantly from that of the larger magpie nestling in controls (29.6 ± 2.9 g, $n = 16$; Mann-Whitney U test, $P > 0.6$). The initial mass of cuckoos in those tests where the cuckoo was the smaller nestling (14.6 ± 1.8 g, $n = 12$) did not differ significantly from that of the smaller magpie nestling in controls (14.1 ± 1.2 g, $n = 16$; Mann-Whitney U test, $P > 0.9$).

We chose nestlings with an average level of nutritional condition, i.e. those coming from broods containing between three and five nestlings (with two cuckoos at the most) and avoiding the smallest nestling in a brood.

However, six of the cuckoo-magpie tests involving nestlings of equal size deliberately included cuckoo nestlings showing extreme begging behaviour. Three such tests included a cuckoo nestling that was reared alone and another three included a cuckoo that was the smallest nestling in a brood containing at least three more cuckoos. Singleton cuckoo nestlings often failed to beg in the hand, while small cuckoo nestlings from multiply-parasitized broods begged most intensively. If begging was the main factor influencing food intake then such cases should make it especially clear.

Nonparametric statistical analyses were selected whenever possible, the main exception being analyses of covariance for comparisons of feeding success (food share, RFI and absolute mass gain) of experimental categories of nestlings (cuckoo plus magpie, magpie plus cuckoo and magpie plus magpie), after controlling for the effects of the covariate nestling size (body mass, size asymmetry and mass ratio). Requirements of normality (central distribution) and homogeneity of variance were not violated for both raw data and residuals in every case.

RESULTS

Experiment 1

In the laboratory, cuckoo nestlings begged for much longer and emitted more vocalizations, both in absolute terms and per unit time, than magpie nestlings irrespective of their degree of food deprivation. Time since the last feeding predictably affected the duration of begging bouts, the amount of calling per bout, the calling rate and the total number of begging calls emitted by magpie nestlings, while cuckoos showed no predictable variation in any of these parameters (Table 1). Postural scores followed a similar pattern. Cuckoos usually begged fully stretched and very seldom in resting postures. A conspicuous difference between the two species was the temporal pattern of calling (i.e. gaping). Magpie begging was discrete and well separated in time, with pauses during which nestlings neither gaped nor called. In contrast, cuckoos emitted a continuous quivering flow of calls with persistent gaping, accompanied by head-bowing movements. Acoustic intensity of calls was similar for both species and showed little variation in relation to need (although the high frequencies involved and the limited sensitivity of the apparatus may mask differences detectable with a more sensitive device).

Begging bouts of cuckoos were much longer than magpie begging bouts, and the former required less stimulation to complete a full bout before the

behaviour ceased, suggesting a higher motivation for begging in cuckoos independent of need. This is depicted in Table 1, as the number of begging failures. Similarly, cuckoos accepted food on almost every occasion it was offered to them (97.3%, with the exceptions being only two instances by two different nestlings, $n = 110$ tests), while magpies were three times more likely to fail to eat any food (8.2% of 110 tests, five nestlings). At this and older ages, cuckoo nestlings begged for food in postures that evidently would have interfered with begging of a nestmate (had nestlings in the lab not been isolated), both by spreading their wings to full extension and pushing themselves forward. In natural nests this behaviour is likely to prevent magpies from placing themselves in nest locations closest to the parents, adding to the effect of the intensive begging behaviour of cuckoos.

Table 1. Begging in relation to nutritional need by cuckoo and magpie nestlings (means and SE in brackets).

	Time since the last feeding (hours)			
	0.5	1.0	2.5	P*
Magpies:				
Begging duration (s)	21.80 (2.37)	19.80 (1.51)	26.80 (1.94)	<0.01
Time calling (s)	5.50 (0.55)	8.10 (0.83)	9.60 (0.99)	<0.05
Begging calls /bout	9.50 (1.33)	12.80 (0.36)	16.00 (1.20)	<0.001
Calling rate (calls/s)	0.43 (0.05)	0.67 (0.04)	0.60 (0.03)	<0.05
Call intensity (dB SPL)	97.30 (1.81)	--	97.10 (1.29)	NS
Postural score	2.30 (0.17)	2.61 (0.14)	3.02 (0.11)	<0.05
No. of begging failures	8.00 (0.82)	6.20 (0.63)	6.00 (1.11)	NS
No. of meals eaten	2.60 (0.14)	2.59 (0.13)	3.76 (0.11)	NS
Cuckoos:				
Begging duration (s)	68.00 (9.67)	99.60 (17.08)	79.20 (9.56)	NS
Time calling (s)	34.90 (6.17)	46.70 (10.28)	35.20 (5.42)	NS
Begging calls /bout	114.30 (18.70)	169.30 (40.50)	139.30 (22.10)	NS
Calling rate (calls/s)	1.65 (0.09)	1.64 (0.18)	1.71 (0.11)	NS
Call intensity (dB SPL)	93.94 (2.34)	--	100.52 (1.85)	NS
Postural score	3.24 (0.07)	3.27 (0.11)	3.31 (0.06)	NS
No. of begging failures	0.30 (0.21)	0.40 (0.22)	0.20 (0.13)	NS
No. of meals eaten	3.02 (0.12)	4.05 (0.10)	9.50 (0.40)	<0.05

* Minimum tail probabilities (after Bonferroni corrections) in the comparison between deprivation intervals within species (Wilcoxon test). For all begging parameters except call intensity, cuckoos differ significantly from magpies at any level of food deprivation (Mann-Whitney U test, $P < 0.05$).

Despite cuckoos being much smaller than magpies (cuckoos: $62.2 \pm 3.95\text{g}$; magpies: $106.0 \pm 2.85\text{g}$; Mann-Whitney U test, $P < 0.001$), nestlings of both species consumed similar cumulative amounts of food over the 14 hours (cuckoos: $43.1 \pm 1.12\text{g}$; magpies: $40.4 \pm 1.68\text{g}$; Mann-Whitney U test, $P > 0.9$). As a result, the cumulative relative food intake of cuckoos (62.0% of body mass $\pm 2.5\text{g}$) was much higher than that of magpies ($40.8\% \pm 1.1\text{g}$; Mann-Whitney U test, $P < 0.001$). Cuckoos unexpectedly ate food in proportion to deprivation time, whilst magpies did not. This apparently anomalous result may be a consequence of honest begging (see below).

Compared to magpies, cuckoo nestlings never failed to beg when first stimulated, even if recently fed. Most between-interval variation in magpie begging (i.e. the key requirement for honesty) occurred within the first minute of each begging trial and before nestlings ate any food. Unlike cuckoos, which kept begging during and after being fed, the number of begging displays by magpies during the second minute was equivalent to the number of meals eaten (with minor errors due to feeding failures). Magpies terminated begging bouts almost independently of deprivation and after receiving a mean of 3.0 meals. The experimental protocol involved feeding nestlings in response to gaping, and so cuckoos were often fed without completely swallowing the food (80% of trials). Magpies seldom begged again before swallowing the previous meal (5%), but 8/10 cuckoos threw away mouthfuls of food after being fed several times just to beg again!

Experiment 2

When given a choice, magpie parents favoured the cuckoo. This occurred both in those tests where the cuckoo was the larger nestling (cuckoo: 14.1% RFI ± 1.76 ; magpie: $6.9\% \pm 1.86$; Wilcoxon test, $P < 0.001$) and when the cuckoo was the smaller nestling (cuckoo: $10.9\% \pm 1.17$; magpie: $7.8\% \pm 1.27$; Wilcoxon test, $P < 0.001$). Overall, cuckoos had higher RFI than magpies in 86% of tests. Considering all the data, the two control magpie nestlings had similar RFI (Wilcoxon test, $P > 0.9$), although, the interaction between nestling size and RFI proved more complex, as follows.

Figure 1 shows the results from the control set of choice experiments concerning differential feeding success in relation to relative nestling size. When magpie nestlings were similar in size, parents fed them equally, but heavier magpie nestlings were preferentially fed over smaller ones when the asymmetry in nestling body mass exceeded a threshold value close to 0.7 (i.e. the large nestling was about 2.5 times larger than the small one).

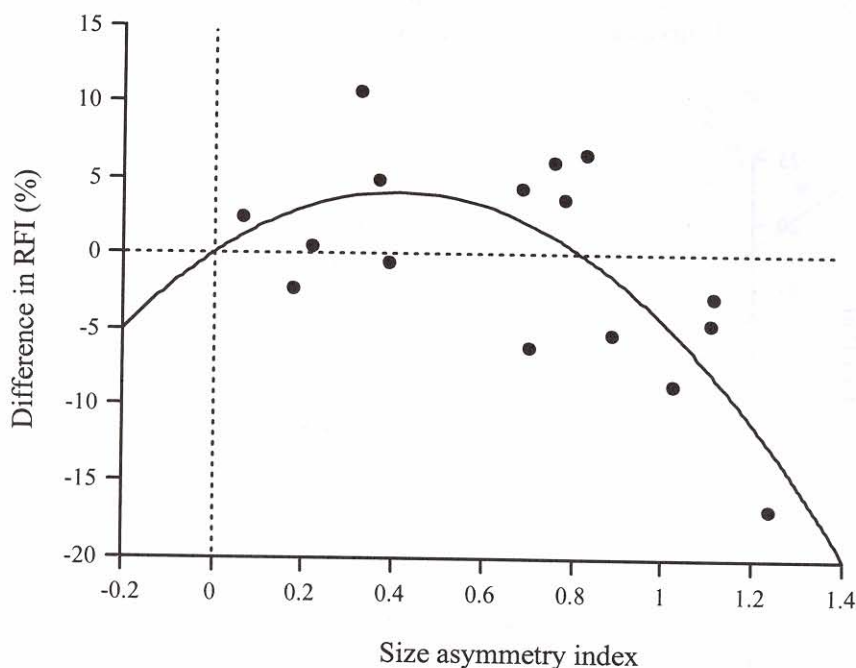


Figure 1. Results of the control set of experiments. Differences in RFI between magpie nestlings (small minus large) are plotted against the size asymmetry index (difference in mass between large minus small nestlings, divided by average mass). The data points have been fitted to a non-linear polynomial regression model ($y = 10.73x - 15.79x^3$; ANOVA, $P < 0.01$) subject to the following realistic restrictions: $y = 0$ when $x = 0$ (i.e. nestlings of equal size are fed the same); if so, y must be positive for small values of x (because parents must be allowed to feed both nestlings equal absolute amounts of food, hence the larger RFI for smaller nestlings, but y is continuous so that this must occur for values of x near zero).

Figure 2 shows an analogous result for the cuckoo-magpie set of choice experiments. Magpie parents always favoured cuckoo nestlings when they were larger or equal to magpie nestlings; the greater the mass asymmetry in favour of the cuckoo, the larger its food share. When smaller, cuckoo nestlings did better than a comparable magpie nestling by never being consistently disfavoured. Of the six magpie nestlings 2.5-3.0 times smaller than their magpie broodmate (Figure 1), five were not fed at all, while cuckoo nestlings in a similar situation never failed to be fed. There were no significant differences in RFI depending on whether magpie parents were caring for magpie nestlings, cuckoo nestlings, or both, prior to the test (ANCOVA, $P > 0.2$). Both in Figure 1 and 2, abscissa values outside the

range shown are unrealistic under natural field conditions, so it does not matter if model curves approach infinity when x is much larger than zero.

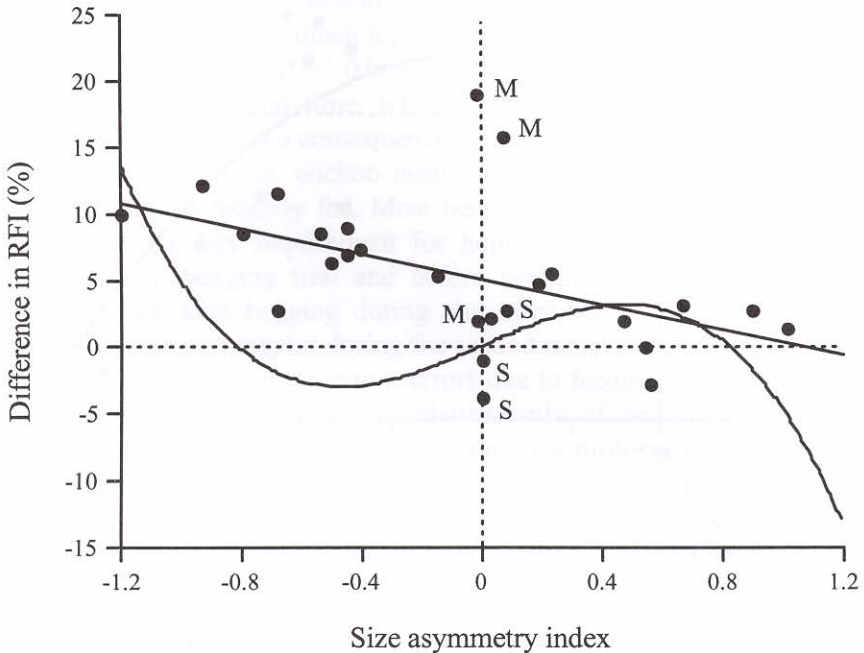


Figure 2. Results of the cuckoo-magpie set of choice experiments. Differences in RFI (cuckoo minus magpie) are plotted against the size asymmetry index (magpie minus cuckoo divided by their average), as in Figure 1. The non-linear regression function in the magpie test (see Figure 1) is shown for comparison. The data shown here fitted an exponential model ($y = 4.22e^{-1.031x}$, ANOVA, $P < 0.01$) better than a linear one. When cuckoos were smaller than magpies they were equivalent to the smaller magpie nestling in Figure 1 and x values are positive as in the control set. Conversely, negative values of x correspond to those tests where cuckoos were larger than magpies. Points marked with S refer to singleton cuckoo nestlings, and M to last-hatched cuckoo nestlings in multiply-parasitized broods.

As predicted, cuckoos showing extreme begging levels prior to the test showed the largest variation in feeding success for a given asymmetry. Two of the three cuckoos reared singly showed lower RFI than magpies, while two of the three small cuckoos coming from multiply-parasitized broods showed the highest RFI values (Figure 2).

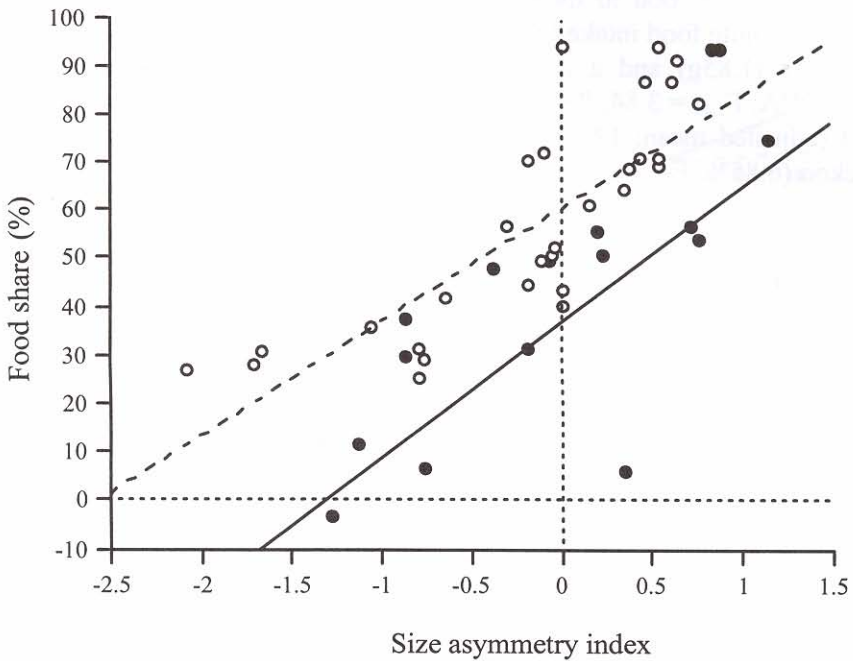


Figure 3. A comparison of linear regression lines for food share in relation to size asymmetry between cuckoo nestlings (open dots, dotted line) and comparable magpie nestlings (black dots, continuous line), when both are paired with a second magpie nestling of similar characteristics.

The higher competitive ability of cuckoos is demonstrated more clearly in Figure 3, where it is shown that cuckoos received more food than a comparable magpie nestling in similar circumstances. Relative size played a major role in the fraction of food obtained (linear regression: $F_{1,44} = 76.4$, $P < 0.001$). After controlling for the effect of nestling size relative to its nestmate, an ANCOVA showed that a cuckoo paired with a magpie nestling obtained a larger food share (adjusted mean: 65.3%) than a magpie nestling under the same circumstances (45.4%; $F_{1,44} = 17.0$, $P < 0.001$; SNK post-hoc comparisons, $P < 0.005$). Congruently, magpie nestling feeding success was more severely affected by the presence of a cuckoo nestmate as compared with the presence of a second magpie nestling. When sharing the nest with a cuckoo, a nestling obtained a much smaller food share (adjusted mean: 33.6%) than when sharing it with another magpie of identical relative size (49.9%; $F_{1,44} = 11.3$, $P < 0.005$, SNK, $P < 0.05$). However, the higher

success of cuckoos relative to magpies was not merely a result of diverting a larger share of food to themselves, but actually because they received a larger absolute food intake (adjusted mean: 3.23g), as compared to a magpie nestmate (1.85g) and a control magpie nestling of similar size (2.17g; ANCOVA: $F_{1,44} = 3.84$, $P < 0.05$; Figure 4). As above, cuckoos had a higher RFI (adjusted mean: $12.32\% \pm 0.88$) than magpie nestlings paired with a cuckoo (6.85% ; $F_{2,73} = 8.1$, $P < 0.001$, SNK, $P < 0.010$).

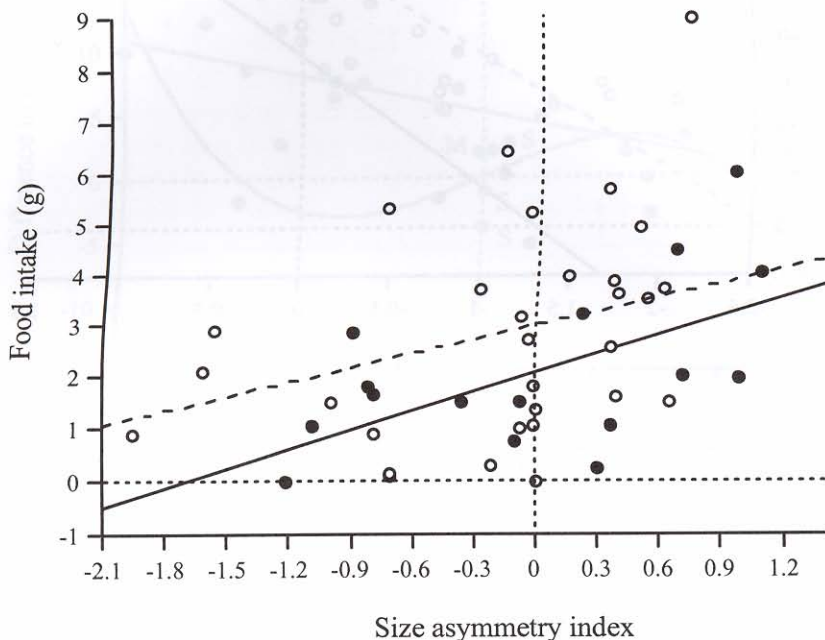


Figure 4. Regression lines for absolute food intake in relation to the size asymmetry of cuckoo nestlings (open dots, dotted line) and magpie nestlings (black dots, continuous line), when both are paired with a second magpie nestling of similar characteristics.

Considering absolute body mass of nestlings instead of relative size-asymmetry introduces a source of error into any comparisons. Despite this, cuckoos obtained a larger food share (adjusted mean: 63.3%) than both magpies of a similar size sharing the nest with them (34.8%; SNK, $P < 0.001$), and similar control-set magpies (49.0%; ANCOVA: $F_{2,73} = 11.2$, $P < 0.001$, SNK, $P < 0.050$; Figure 5).

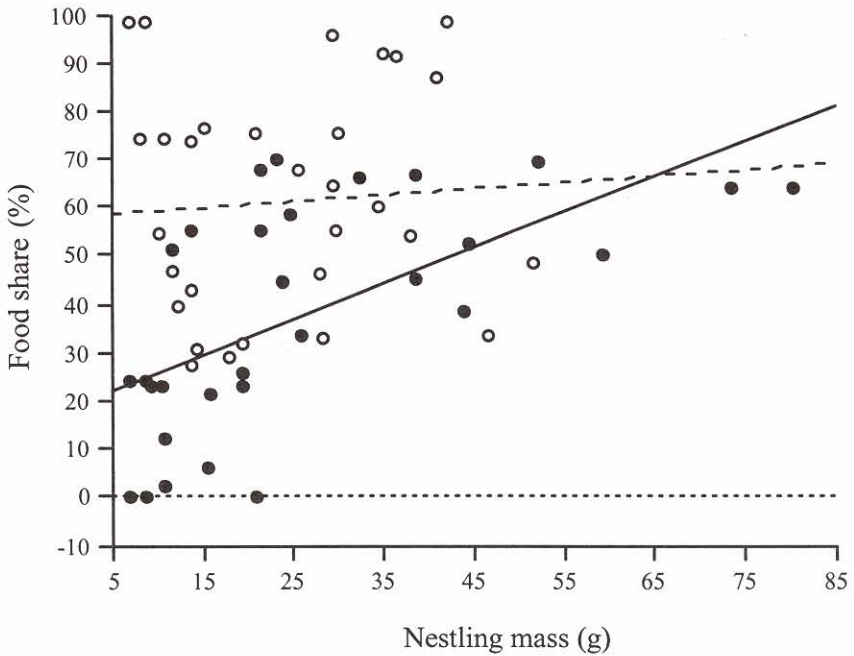


Figure 5. Food share obtained by a cuckoo nestling (open dots, dotted linear regression line) paired with a magpie nestling (black dots, continuous linear regression line) as a function of body mass.

It is interesting to note that, as one might expect from a size-dependent effect upon feeding success, magpie nestlings obtained a larger food share with increasing size. However, cuckoos were usually able to secure a similar (and often larger) share of food, independent of their size. Magpie nestlings did not differ in this respect, whether they shared the nest with a cuckoo or with a conspecific. This means that small cuckoo nestlings received about the same food share as larger ones, because cuckoos were able to compensate for any size differences. In summary, cuckoos received more food and a larger food share as compared to magpie nestlings of a similar absolute or relative size. Magpie nestlings paired with a cuckoo nestling obtained a smaller food share and RFI than magpie nestlings of similar absolute or relative size paired with another magpie nestling. Larger nestlings were fed more, but size effects were much less pronounced for cuckoos, which were fed independent of size.

Some of these results lend support to the conclusion that the higher feeding success of cuckoos was not the result of physical competitive interference between nestlings (i.e. larger nestlings preventing their smaller broodmates from begging at favoured nest locations and/or getting access to food). Instead, cuckoo begging success can be interpreted as the result of parental preferences. Assuming that the total amount of food provisioned by parents remained more or less constant across tests for a given brood mass, competitive interference should have manifested itself as negative covariance between mass gain values of both nestlings. This is because more competitive nestlings would have increased their food intake at the expense of their smaller broodmate, rather than as a result of preferential parental allocation. Total food mass delivered correlated positively with brood mass in both control (linear regression: $r^2 = 0.34$, $F_{1,15} = 8$, $P < 0.010$) and cuckoo-magpie tests ($r^2 = 0.66$, $F_{1,28} = 54.1$, $P < 0.001$). In control tests, no significant correlation was found between mass gains ($r = -0.15$, $df = 15$, $P > 0.5$), but in cuckoo-magpie tests the values of mass gain correlated positively ($r = 0.38$, $df = 28$, $P < 0.050$). Therefore, no nestling category gained mass exclusively at the expense of its broodmate. When parents delivered more food to mixed broods, both cuckoo and magpie nestlings received more food. Parents chose to feed cuckoo nestlings more, as evidenced by the increase in total food delivered to parasitized nests. Although cuckoo parasitism results in reduced fitness of host nestlings, the mechanism appears to be parental preference for cuckoo nestlings, not cuckoo aggression against host nestlings. In support of this, we never observed cuckoos adopting interfering postures during the age range covered by the experiment, as they usually do at older ages.

DISCUSSION

Do Cuckoos Beg More Because They Are in Greater Need?

Begging intensity can be defined as a complex variable incorporating postural and auditory components of begging co-varying with each other and with deprivation time (see R.M. Kilner this volume). In this sense, magpies begged more intensely with increasing need (see also Redondo & Castro 1992a), but was this the result of differential nutritional requirements between the species? Absolute energetic requirements of nestlings mainly depend upon growth and maintenance (e.g. metabolism and activity; O'Connor 1982). Therefore, because cuckoo and magpie nestlings in Experiment 1 grew at similar rates (ca. 10-12g per day, T. Redondo & J.

Zuñiga unpublished data), the total nutritional requirements must have been greater for the larger magpie nestlings. Recently, Soler et al. (1999) measured daily metabolic rate (from oxygen consumption), and the daily energy budgets of pre-fledging cuckoo and magpie nestlings were found to be surprisingly similar. In the laboratory, nestlings of both species were isolated and mostly inactive except while begging (i.e. at this age preening is not yet developed). The degree of plumage development and thermal insulation must also have been similar for both species, which operated at identical ambient temperatures. Therefore, differences in nestling energy budget between the two species must have been small, and unlikely to compensate for the 40% difference in body mass of magpie nestlings. Nestling assimilation efficiency is remarkably constant (ca. 70%) across species feeding on the same diet (O'Connor 1982). Cuckoo and magpie nestlings are adapted to an identical feeding regime at magpie nests (ca. one feeding per hour; Birkhead 1990), and should thus respond digestively in a similar way to variation in deprivation time. All of this suggests that any differences in need between nestlings were very unlikely to have been biased towards cuckoos. However, compared to magpies, begging by cuckoos was dishonest in the sense of being: (i) exaggerated (i.e. more intense for a similar level of need); and (ii) unreliable (i.e. not varying predictably in relation to deprivation time).

Direct Factors Limiting Escalation: Costs

Factors that limit exaggeration are those affecting the benefit/cost ratio of begging, including direct (energetic and predation) and indirect (inclusive fitness) costs. Unlike cuckoos, magpies refrained from exaggerated begging and consumed almost half the food intake of their cuckoo nestmates. This result demands explanation in terms of the factors limiting begging escalation in magpies, because they refrained from the dishonest begging that appeared effective for cuckoos in providing the reward of extra food.

Direct energetic costs of begging per unit time are unlikely to account for the more intense begging of cuckoo nestlings. Measurements of the energetic costs for both species have shown few differences in metabolic rate and energy utilization during begging, and these appear to contribute relatively little in terms of daily energetic expenditure (Soler et al. 1999; M.A. Chappell & G.C. Bachman this volume).

Direct predation costs are probably important (Haskell 1994; D.G. Haskell this volume), but it seems unlikely that they affect the two species of nestlings differentially. The most powerful predictor of predation risk is

nest vulnerability (e.g. concealment, abundance of nearby predators), which depends on nest location and proximate habitat (Yahner & De Long 1992). There was no evident trend in the population studied for a differential habitat distribution of parasitized versus non-parasitized nests. If predation were a major determinant of begging intensity, we should expect: (1) a lower predation rate for cuckoos, so they could afford to beg more; (2) differences in predation to be more pronounced following enlarged brood sizes and increased age; and (3) differences in brood failure to be caused by predators other than adult cuckoos. The last prediction follows from the fact that female *Clamator* cuckoos routinely revisit nests and destroy the contents during incubation and early nestling periods (Soler et al. 1996).

We computed predation rates for broods of two to six nestlings containing either magpies or cuckoos exclusively during the first 20 days of life, excluding cases of total brood failure caused by humans. Between zero and ten days, predation rates were slightly higher for magpie (8/61, 13.1%) as compared to cuckoo broods (7/82, 8.5%), but this difference was nonsignificant (Fisher's exact probability test, $P = 0.540$). This nonsignificant difference diminished further between 10 and 20 days (7/115, 6.1%, and 9/215, 4.0%, respectively; Fisher's test, $P = 0.540$). Predated broods at both ages were not larger than non-predated broods, indeed predated broods were smaller in magpies when younger than 10 days (Mann-Whitney U test, $P < 0.010$). This brood size and age effect on predation is contrary to that expected from the second prediction, because larger and older broods will be noisier. In a different population of non-parasitized magpie nests but with high abundance and diversity of predators (Doñana National Park), noisier magpie broods have been shown to suffer higher predation and at earlier ages (Redondo & Castro 1992b). Further analyses of unpublished data from the Redondo and Castro (1992b) study reveals that predated broods younger than 20 days were significantly larger at the time of predation than non-predated ones. In the current study population at Santa Fe, most instances (87.5%) of predation in magpie broods younger than 10 days were restricted to broods of three nestlings or less, despite the fact that such broods contributed only a minority of the total (23.0%, Fisher's test, $P = 0.001$). In these broods, hatching success was low (41.1%), compared with 79.4% in non-predated broods. Egg breakage caused by adult cuckoos occurred in 100% of all-magpie broods predated before 10 days, as compared to 24.5% of non-predated ones. This strongly suggests that differential predation upon magpie broods was largely due to adult cuckoos. Summarizing this section, all-cuckoo broods were not predated any more frequently than all-magpie broods. The tendency for higher predation in magpie nests below 10 days of age was probably a

consequence of adult cuckoos destroying nest contents in non-parasitized nests early in the nestling period.

Direct Factors Limiting Escalation: Benefits

Magpie and cuckoo nestlings may not differ greatly in the costs of begging, but they might differ in the benefits gained. Lotem (1998) suggested that exaggerated begging benefits the cuckoo more in species where it remains the sole occupant of the nest, than it does a host nestling which always shares the nest with several siblings. This is because extra food gained via begging is diluted among all broodmates, but the extra costs of begging are not. This comparison may not apply here, because both magpies and cuckoos share their nests and so they would accrue similar benefits (Redondo 1999). The present study also provides ample evidence against Lotem's (1998) suggestion. For example, singleton cuckoos actually begged the least, and larger magpie nestlings in non-parasitized broods begged less but obtained more food. This suggests similar benefits for both species.

Nestlings of both species would also benefit from maximizing body mass at independence. In many species, survival dramatically increases with fledgling mass, due to the combined effects of several factors related to foraging ability and social dominance (Garnett 1981; Richner et al. 1989; Magrath 1991). An adequate food supply at the nest can be the most powerful predictor of survival prior to breeding maturity (Spear & Nylin 1994), which makes levels of food intake almost equivalent to lifetime reproductive value. In this system, there is evidence of size-biased mortality for fledglings of both species (Eden 1985; Soler et al. 1994). For cuckoo fledglings, this is because they have to migrate to Africa, requiring fat reserves. Magpie nestlings suffer from size-biased mortality, both in the nest and before their first breeding season. The heaviest nestlings in successful magpie broods (already distinguishable within a few days of hatching) had a higher probability of fledging than their lighter siblings (0.83 versus 0.41 respectively, $n = 40$). And of the 10% of juveniles surviving to their first spring, more than 80% comprise the heaviest fledgling from their natal brood (T. Redondo unpublished data).

Indirect Inclusive Fitness Costs

We are led to the conclusion that the more intensive begging of cuckoos was a consequence of their lower (indeed zero) inclusive fitness costs. Small

magpie nestlings obviously have an evolutionary interest in the survival prospects of their larger siblings, and may gain little from completely outcompeting them. In species where parents readjust feeding rates after brood reduction, the benefits to remaining nestlings of sibling starvation are small (Graves et al. 1984; Mock & Lamey 1991; Martins & Wright 1993), and this is likely to be the case here. Parent magpies not only feed young in relation to brood size (Redondo & Castro 1992b), but also according to brood mass. Nestlings may therefore benefit from the presence of nestmates, both directly (e.g. thermal insulation, post-fledging social support) and indirectly (kin selection), and this may select for tolerance towards smaller, lower quality siblings (Forbes & Ydenberg 1992; B. Glassey & S. Forbes this volume).

Field experiments show that magpie nestlings suffered from a lower food intake when sharing the brood with a cuckoo as compared to a magpie nestmate of a similar relative size. Any mutant magpie begging dishonestly would have had the same effect. On average, a magpie hatchling had a 0.81 probability of fledging in a successful brood if reared with other magpies ($n = 73$). However, this figure falls to 0.24 if one cuckoo was present in a brood of a similar size ($n = 66$). When two or more cuckoos were present, the probability of magpie nestling survival drops to 0.02 ($n = 102$). We computed survival probabilities attributed to nestling starvation before 10 days of age from synchronously hatched broods containing one cuckoo nestling. This would represent a reasonable estimate of the indirect cost of dishonest begging incurred by a hypothetical mutant magpie begging like a cuckoo (T. Redondo & J. Zuñiga unpublished data). Following parasitism by one cuckoo, a normal magpie nestling had a 0.47 probability of fledging, and a 0.45 probability of being accompanied by a sibling, as compared with figures of 0.85 and 0.83, respectively, in similar all-magpie broods. Among those magpie broods where at least two magpie siblings hatched, the probability that a nestling other than a focal survivor would fledge successfully (i.e. the probability of a sibling also leaving the nest) was 0.77, but the presence of a cuckoo lowered it to 0.36. Therefore, the presence of a single dishonest nestling of a similar age and size represents roughly a 0.50 reduction factor in nestling survival, without considering additional size-related post-fledging effects of insufficient food intake (Soler & Soler 1991).

Another experimental simulation of a mutation endowed with a more vigorous begging behaviour, not necessarily associated with brood parasitism or stronger physical competition, was performed by Alvarez et al. (1976), who placed jackdaw (*Corvus monedula*) nestlings in magpie broods (see also M. Soler this volume). Jackdaws beg more vigorously than magpie

nestlings (louder and for longer, but less than cuckoos) and have an effect similar to that of cuckoos.

Three pieces of evidence lend additional support to the conclusion that begging honesty was mainly the consequence of indirect costs:

(1) Magpies begged more when in greater need, but the amount of food that they were willing to eat (i.e. hunger) depended upon deprivation time to a much lesser extent. Irrespective of need, magpie begging bouts were inhibited by feeding, and magpies 'prudently' stop begging after receiving a few meals. In contrast, cuckoos begged independently of need but consumed food in proportion to need, and failed to terminate begging in response to food.

(2) As in most birds, begging by magpies was expressed in discrete, well-defined units. This gives siblings the opportunity to be fed as nestlings cease to gape and vocalize between feedings. In contrast, cuckoos beg continuously, which is the rule among brood parasites (Redondo 1993; Davies et al. 1998).

(3) Unlike magpies, cuckoos stored food in their guts for at least 12 hours after eating, as evidenced by tracking barium-labelled food with Computerized Axial Tomography (Redondo 1993). This storing of food is obviously advantageous for individual cuckoos when prospective requirements (e.g. growth and thermoregulation) are great and a sustained, sufficient food supply is uncertain (e.g. due to variation in foraging conditions), and especially when energetic reserves are low, as in most altricial nestlings. This feature also suggests that food intake by cuckoos was determined by the available digestive capacity, whilst that of magpies was strictly under motivational control.

Therefore, in the absence of indirect costs, it is hard to explain why magpie nestlings refrain from escalating begging until their storage capacity is filled. Experimental evidence has shown that even minute supplemental increases in food intake early in the nestling period have enormous consequences for subsequent nestling survival (Graves et al. 1984), an effect that is also observed in magpies (Högestedt 1981; Hochachka & Boag 1987). The pattern of cuckoo and host nestling behaviour seen here is exactly what we might expect if costs do not depend upon how much a nestling begs *per se*, but instead upon the distribution of parental feedings. This is because the direct begging costs experienced by cuckoos should vary continuously in proportion to begging effort, whilst the honest begging of their hosts is also shaped by indirect fitness costs. Indeed, McCarty (1996) has suggested that honest begging itself could be maintained by such indirect inclusive fitness costs.

Do Cuckoos Beg More to Counteract Parental Neglect?

Experiments showed that magpies neglected the smallest nestling of two when its larger broodmate was roughly three times larger (equivalent to an index of asymmetry of one, Figure 1). There is a 0.70 probability ($n = 326$ parasitized broods) that cuckoo nestlings hatch out within an older, already parasitized brood. This indicates an adaptive value to exaggerated begging as a mechanism to prevent neglect by magpie parents if, as we suggest, exaggerated begging can compensate for the disadvantage of small relative size. Small magpie nestlings also begged more, but such begging was within the range of begging intensities for this species, and it was obviously not sufficient to prevent neglect (Figure 1). Manipulations of nestling begging and relative size showed that the more intense begging of small magpie nestlings was often insufficient to counteract parental favouritism towards larger nestlings, and progressively less so with increasing size differences (Redondo 1993). However, despite their extra begging, cuckoo nestlings still had a 0.11 probability of starving when hatching into broods containing older cuckoos ($n = 716$ nestlings in 199 successful broods).

Host Manipulation

Exaggerated begging by cuckoos elicited preferential feeding by magpie parents. We can be reasonably sure of this conclusion because we failed to find evidence for cuckoo feeding success being the consequence of direct physical competition with host nestmates, at the ages considered in the experiment. This explanation agrees with honest signalling models, in that preferential feeding of larger nestlings is a direct outcome of parental preferences rather than of the superior competitive ability of larger nestlings (Parker 1985; Mock & Parker 1997). Variation in feeding rates were, in part at least, tuned to differences in begging, even if other factors also contributed to the greater feeding success of cuckoos (e.g. a more conspicuous gape; Soler et al. 1995b).

Great spotted cuckoo nestlings exploited a set of magpie nestling-feeding rules that favoured nestlings of a large size and those begging intensively. A preference for larger nestlings is adaptive in fulfilling their higher absolute requirements due to a heavier mass and faster growth (during the earliest half period of exponential growth), but it may become amplified by directional selection in species where larger nestlings are more valuable, for instance those with size-biased survival, such as magpies (Haig 1990). It may also help in facilitating facultative brood reduction (selectively starving

smaller nestlings), a trait that has been demonstrated to be adaptive in magpies (Husby 1986). Signalling theory accounts for the occurrence of dishonesty as part of an otherwise honest, stable signalling system, whenever a minority of signallers differ in advertising costs and thus can afford to emit higher-intensity signals when of a similar quality. Dishonest signals are consistently misinterpreted by receivers due to their inability to assess the difference in signaller category, thereby allowing the existence of stable manipulation (Johnstone & Grafen 1993). Begging by cuckoos and magpies fits well with this scenario.

FUTURE DIRECTIONS

Some of the evidence provided by this study is not conclusive and awaits further observations and experiments. This study has also generated many new hypotheses that require testing in the future. Here we enumerate the major points that should be addressed, at least in the short term.

Our conclusions regarding parental preferences and potential manipulation require observations at natural nests, to exclude the possibility of physical interference between nestlings as the causal factor explaining patterns of food allocation. Experiment 2 should perhaps have included video recordings of experimental broods in order to observe how parents and nestlings interacted.

More experimental data are required to quantify and compare the energetic cost of begging in cuckoos and magpies. In recent work (Rodríguez-Gironés et al. 2001) we assigned magpie nestlings to two treatments: group A was fed immediately after begging while group B was fed a similar amount of food but only after begging a lot. We detected significant differences in growth rates during the experimental period (three days): nestlings in group B grew at a lower rate after controlling for the effects of body mass and food intake. This is direct evidence for a negative effect of begging effort upon fitness (heavier nestlings surviving better to the next breeding season), which has gone undetected in studies measuring the oxygen consumption of begging as an estimate of its energetic cost (see M.A. Chappell & G.C. Bachman this volume). We failed to repeat the same experiment with cuckoo nestlings because they begged so much and independently of treatment. However, a new experimental protocol creating two treatment groups for cuckoos and magpies will test the hypothesis that cuckoos beg more because it is less costly than for magpies. Our results concerning differential predation costs for cuckoos and magpies should be interpreted with caution because the Santa Fe population studied is biased in

two undesirable ways. First, it contains many cuckoos which destroy nest contents, but are not predators in a strict sense. Second, it lacks a sufficient number and diversity of predators because it is highly disturbed, agricultural land. Ideally, a study should be conducted on a non-parasitised population containing a high abundance and diversity of predators (e.g. Doñana National Park population, Redondo & Castro 1992a,b) in order to demonstrate that sound-guided predators are attracted to nests. Calls from magpie and cuckoo broods could be broadcast from natural rates and intensities from artificial nests to remove parental effects, such as differential nest guarding or defence. It would also be interesting to study how begging calls of both species propagate in the environment, to understand how they attenuate and degrade at varying distances from the source. Perhaps cuckoos beg at similar intensities to magpies but their calls degrade more easily and are less detectable (see D.G. Haskell this volume).

Studies on the digestive physiology of both species would be very desirable in order to understand the proximate causal factors underlying begging and satiation (see A.B. Clarke this volume; W.H. Karasov & J. Wright this volume). This information is crucial for the interpretation of the results of Experiment 1. There are several possible mechanisms (e.g. food mass or volume, number of meals eaten, caloric or nutrient content of food) that may cause hunger and satiation to vary between species. We would predict that cuckoos have a 'selfish' physiology; for example they can store food in their guts for several hours while magpies do not (Redondo 1993). We are currently addressing these questions.

Thus far, we have ignored the precise mechanisms determining which particular nestling is fed (e.g. position in the nest, relative height or proximity to a parent's beak) and the behavioural rules followed by parents in making a feeding decision. This requires video recordings of parent-offspring interactions under natural conditions, but would answer many issues arising from this study. For example, singleton cuckoos begged less than nestlings coming from multiple broods, and last-hatched nestlings begged more in multiply-parasitized broods. Is this evidence of cuckoos being honest concerning their nutritional need, or of their responsiveness to variation in the level of within-brood competition? Another example concerns the proximate causal factors underlying neglect of very small magpie nestlings. How do cuckoo nestlings under similar conditions manage to obtain a relative food intake similar to that ingested by their larger magpie nestmate?

Unfortunately, all our attempts to place video cameras, and even minute microphones (less than one cm in diameter), close to magpie nests have failed. The problem is that magpies are extremely wary of any strange

device placed near their nests, and refrain from staying at the nest for as long as the device is present. We would like to conclude by taking this opportunity to ask readers for suggestions which could help us to solve this logistical obstacle.

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