

EXPERIMENTAL BROOD PARASITISM OF THE MAGPIE (*PICA PICA*)

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Abstract. Egg and chick features were tested on natural magpie (*Pica pica*) nests. The stimuli best accepted were those of greater size and weight and of a white background and black specks. Stimuli with a shape different from oval and of low weight were the most readily expelled. Relative quantity of eggs in the nests had no strong influence on the expelling response. Chicks of house sparrows, spotless starlings, jackdaws and swallows were readily accepted and reared by the magpies. Amongst some chicks of other species introduced, a 'parasitic' form of behaviour appeared which led them to eliminate competitors in the nests.

Brood parasitism among Old World cuckoos appears as the result of an array of physiological, structural and behavioural adaptations, such as synchronous laying with the host, short incubation period, use of tactics to divert attention enabling the host's nest to be approached, destructive behaviour on the part of the parasitic chicks, and laying of mimetic eggs. One species, the great spotted cuckoo (*Clamator glandarius*), in Europe chiefly parasitizes birds of the corvid family, mainly the magpie (*Pica pica*). Among other devices used in this parasitism, the cuckoo appears to use mimicry in the size and colour of the eggs and perhaps in the general appearance of the young (Lack 1968; Alvarez & Arias de Reyna 1974a).

Although egg mimicry is apparent in this case, to the extent that it took a long time and much effort to reliably distinguish the eggs of the parasite from those of the host, the mimicry in the cuckoo's chicks is not so obvious. In any case, the evolution of mimicry should be the direct effect of the hosts' response to the presence of strange eggs and chicks in their nests. A study of their response appears then to be the first step necessary towards understanding mimicry associated with brood parasitism.

Observation of Cuculinae in their natural state shows that the hosts of *Cuculus canorus* frequently abandon the nest or eject the eggs of the parasite (Jourdain 1925) and the magpie, host of *C. glandarius*, also ejects some of the eggs (Alvarez et al. 1974a). Studies in which the eggs of parasites, or models of the eggs, have been introduced experimentally have shown that there is a tendency by the owners of the nests to abandon or to eject the parasites' eggs (Swynnerton 1916, 1918; Rensch 1924; Smith 1968; Weller 1971; Rothstein 1974, 1975).

In some cases the responses to various characteristics of experimentally introduced

eggs or models have been compared. Although these experiments did not involve birds which are customarily parasitized, the results are interesting and perhaps applicable to the phenomenon of brood parasitism if we think that the responses of the hosts have evolved from a non-parasitic stage. The herring gull (*Larus argentatus*) for instance, discriminates with great accuracy the species-typical colour and pattern of the eggs, and less so the shape, accepting a wide variety of sizes (Baerends 1959). The mourning dove (*Zenaidura macroura*), on the other hand, accepts and incubates eggs of various colours (McClure 1945).

The present study was undertaken to help understand the phenomenon of egg mimicry in connection with brood parasitism and to evaluate the magpie's (*P. pica*) response to various features of model eggs and chicks, and to the usual parasite (*C. glandarius*).

Methods

The experiment was carried out at the Doñana Reserve, in Southwestern Spain, during the breeding seasons of 1973, 1974 and 1975.

A previous study of the breeding conditions of Doñana magpies provided results on nest building and nest location (fringe meadows of marshlands, mainly on brambles), breeding season (from the end of March to the middle of June), clutch size (four to eight eggs, mean: 6.1), laying period (four to nine days, mean: 6.3), incubation period (gradual start, 15 to 21 days, mean: 18.0) and egg features (average: length 3.37 cm, width 2.37 cm, volume 9.2 ml, weight 8.22 g). The typical natural colour of the eggs is a pale bluish green background with abundant dark brown specks (Alvarez & Arias de Reyna 1974b).

To determine the magpie's response to oological and chick characteristics, 428 stimuli

were introduced into 354 nests. Each nest received only one stimulus at a time and no birds were experimented on twice with an egg or egg model or chick. The state of each nest was subsequently recorded every other day, counting the length of stay of the stimulus in the nest until it was ejected or showed peck marks.

Each nest under observation was visited briefly (not more than approximately three minutes) every 2 days, the parent magpies being very often aware of the observers and frequently flying only a few metres away to call and then return to the nest after we left. On each visit we recorded the number of eggs or chicks in the nest, the presence or absence of the stimulus, whether there were peck marks indicating that the magpies had tried to destroy the foreign object in situ, and whether the eggs and stimulus were or were not warm.

The egg stimuli were introduced at random into a nest, the only condition being that it should contain at least two eggs. Since a record was kept of the dates of laying and incubation for each nest, comparisons could subsequently be made of the responses during these two breeding stages. Of the total number of nests, seventy-four of them were subjected to two kinds of stimuli (one egg or model egg and one chick introduced or transformed), the time interval between presentations depending on breeding development, since eggs or model eggs were introduced into nests containing only eggs and chicks were introduced or transformed in nests containing only chicks.

Apart from the experiments testing the effect of relative quantity of the stimuli, the stimulus egg was always an additional one. In this respect we followed the behaviour of the great spotted cuckoo, who does not substitute eggs.

Oological Characteristics

Shape. In each of fifty-three nests, one wooden model of the same volume, weight, colour and pattern as the natural eggs of the magpie was introduced. Of these, eighteen were the shape of magpie eggs, nineteen were spherical and sixteen cubical.

Colour. In a total of seventy-six nests, one of the eggs of the clutch was painted a uniform light-blue colour (sixteen nests), a uniform white (eighteen nests), a uniform light-brown (fourteen nests), a light-blue background with light-brown specks (thirteen nests) and a white background with black specks (fifteen nests).

Size. In a total of forty-eight nests, models having the following characteristics were introduced: in sixteen of them, large-sized models were introduced, consisting of empty hens' eggs, into which were added lead shot uniformly distributed inside and fastened with glue, until the weight of 10 g was reached. The hole through which the lead was introduced was then covered with glue and the exterior of the egg was painted the typical colour of that of the magpie.

In fourteen nests, a stimulus of normal size made of orange wood was introduced, reproducing the characteristic size and shape of the magpie egg and the weight of 10 g; this model was also painted the colour of the natural magpie eggs.

The third stimulus (small size) had the characteristic colour, shape and weight of the magpie egg, and was made of ebony wood, so that it was approximately half the normal size (introduced into 18 nests).

Weight. In a total of forty-eight nests, the response to the weight characteristics of the eggs was tested. In sixteen of the nests, one of the eggs of the clutch was emptied and the hole was covered with glue. In fifteen of the nests one of the eggs of the clutch was emptied and refilled with wax; lead shot was then uniformly distributed amongst the wax so that the total weight was 18 g. In each of seventeen clutches, two holes were made with a pin through the shell and the shell membranes in one of the eggs, and two abrasions 1 cm in length made in the shell with the same pin, with the result that weight was gradually lost by evaporation.

Movable and immovable interior. In seventeen nests, a hole was made in one of the eggs of the clutch, and lead shot was introduced until the weight was 18 g, the lead shot moving freely inside; the hole was then sealed over. For the purpose of comparisons we used as an immovable stimulus the wax and lead shot filled egg weighing 18 g. This was introduced into fifteen nests and was the same in all respects as the movable stimulus except that the wax inside kept the lead from moving.

Given that previous experiments have demonstrated that not even strong smells affect the incubation of birds (Kirkman 1937; Marples 1931), this characteristic was not tested in the present study.

Artificial Eggs of Great Spotted Cuckoo

A model egg, made of orange wood and having approximately the characteristic size,

shape, colour pattern, and weight (10 g) of the typical egg of the great spotted cuckoo was added to each of forty nests.

The shine of all model eggs was obtained by covering them with a fine layer of egg-white, and before they were placed in the nests they were warmed to a temperature approximately the same as that of the eggs found in the nest.

Eggs of Other Magpies

An egg of another magpie was placed in each one of a total of twenty nests. Some of the eggs tested were of the most typical colour, while others had less pigmentation and were therefore of a lighter colouring. All the receiving nests contained eggs of a typical coloration.

Eggs of Other Species of Birds

One egg was placed in each of forty-four nests: The introduced eggs were of the spotless starling, *Sturnus unicolor* (six nests), jackdaw *Corvus monedula* (eight nests), swallow *Hirundo rustica* (seven nests), wood pigeon *Columba palumbus* (three nests), green woodpecker *Picus viridis* (six nests), skylark, *Alauda arvensis* (four nests), kestrel *Falco tinnunculus* (six nests) and the great spotted cuckoo *Clamator glandarius* (four nests).

Relative Quantity of Eggs in the Nest

To determine the effect of the quantity of stimuli presented, a comparison was made of the response to the introduction of one or several stimulus eggs of the same kind. In the latter case all except one egg of the host's clutch were replaced by experimental eggs. In this series of tests, the stimuli used were artificial eggs of *C. glandarius* (in four nests), and natural eggs of *F. tinnunculus*, *S. unicolor*, *H. rustica*, and *C. monedula* (in only one nest for each of the last four species).

Chicks of Other Species

One featherless chick of the following species was introduced into each nest containing only chicks at approximately the same stage of development as the introduced ones: *H. rustica* (eight chicks), *Passer domesticus* (four chicks), *C. monedula* (four chicks) and *S. unicolor* (six chicks).

Host's Chicks Transformed

The crown of the head of one chick of the brood was dyed grey (seventeen nests), red (eleven nests), green (eleven nests), or yellow (thirteen nests).

Results

Response to Shape

The length of time that the stimuli of different shape (oval, spherical or cubical) remained in the nest, compared with that of eggs of other magpies introduced into the control nests, demonstrated that in all cases the magpies recognized the three kinds of artificial stimuli, and these remained in the nests for a significantly shorter time than the controls (oval: $t = 3.08$, $df = 36$, $P < 0.01$; spherical: $t = 4.33$, $df = 37$, $P < 0.01$; cubical: $t = 4.90$, $df = 34$, $P < 0.01$; see Table I). From this, it is deduced that the magpies were capable of distinguishing the artificial stimuli, even those of an actual egg shape. Comparison between the lengths of stay of each shape shows that those of an oval shape remained in the nests longer than the artificial eggs of a cubical or spherical shape ($t = 2.11$, $df = 32$, $P < 0.05$; $t = 2.36$, $df = 35$, $P < 0.05$; respectively). The response to the stimuli of a cubical or spherical shape was approximately the same.

If we compare the length of stay in the nests of all the eggs of the host that were painted with that of the other magpies' eggs introduced into the control nests, it is observed that, as a whole, the owner of the nest recognized and rejected the painted eggs first ($t = 3.38$, $df = 94$, $P < 0.01$). This significance level of difference held when each colour was considered separately, except for 'uniform white' and 'white with black specks' which were not ejected so quickly and did not differ significantly from the controls (see Table II). The differences between the lengths of stay of the different colour stimuli were not statistically significant.

Response to Size

As Table III shows, of the three sizes of egg models tested, the largest of all stayed in the nests the same amount of time as the natural control eggs. The differences between the responses to the three kinds of artificial stimuli were not statistically significant.

Response to Weight

The distribution of length of stay of the heavy eggs belonged to the same population as that of the control eggs (the average of the first ones was even a little longer). The empty eggs were immediately ejected while the perforated eggs that gradually lost weight stayed a little longer in the nests (the difference between both and the controls were statistically significant, $t = 4.36$,

Table I. Number of Two-day Blocks for Which the Shape Stimuli Remained in the Nests

	Egg models			Controls (natural eggs of other magpies)
	Oval	Spherical	Cubical	
\bar{x}	3.2	1.4	1.3	7.3
N	18	19	16	20
<i>Comparisons with control</i>				
t	3.08	4.33	4.90	
P	< 0.01	< 0.01	< 0.01	

Table II. Number of Two-day Blocks for Which the Colour Stimuli Remained in the Nests

	Painted eggs					Controls (natural eggs of other magpies)
	Uniform blue	Uniform white	Uniform brown	Blue background and brown specks	White background and black specks	
\bar{x}	3.6	4.4	2.4	3.2	5.9	7.3
N	16	18	13	13	15	20
<i>Comparisons with control</i>						
t	2.54	1.77	3.42	2.86	0.82	
P	< 0.05	NS	< 0.01	< 0.01	NS	

Table III. Number of Two-day Blocks for Which the Size Stimuli Remained in the Nests

	Egg models			Controls (natural eggs of other magpies)
	Maximum	Normal	Minimum	
\bar{x}	8.1	3.2	5.1	7.3
N	16	14	18	20
<i>Comparisons with control</i>				
t	0.96	3.08	1.36	
P	NS	< 0.01	NS	

$df = 34, P < 0.01; t = 3.28, df = 35, P < 0.01;$ respectively, see Table IV).

The differences between the lengths of stay of the heavy stimulus and the other two, of medium and minimum weight, were also statistically significant ($t = 2.46, df = 30, P < 0.05;$ $t = 3.27, df = 29, P < 0.01;$ respectively).

Response to Movable Interior

The eggs of movable interior were ejected from the nests before those of immovable interior, although, perhaps due to their heavier

weight as compared to the controls, the former still remained in the nests an average of 8 days. The difference between the lengths of stay of the eggs with movable and immovable interior was not significant (see Table V).

The graphical representation of the response to the diverse egg characteristics appears in Fig. 1.

Response to Artificial Eggs of Great Spotted Cuckoo

These models remained in the nests on average only 2 days less than the control eggs, and a

Table IV. Number of Two-day Blocks for which the Weight Stimuli Remained in the Nests

	Eggs transformed			Controls (natural eggs of other magpies)
	Maximum weight (18 g)	Holes in shell	Empty eggs	
\bar{x}	7.4	3.0	1.9	7.3
<i>N</i>	15	17	16	20
<i>Comparisons with control</i>				
<i>t</i>	0.05	3.28	4.36	
<i>P</i>	NS	< 0.01	< 0.01	

comparison of the lengths of stay for models and controls showed that both distributions belonged to the same population (see Table VI).

Response to Eggs of Other Magpies

Amongst the magpie eggs coming from other nests which were introduced into the control nests, some were very similar to those of the clutch into which they were introduced and typical in coloration, and others distinctly different in colouring, showing less specks than the typical ones and being therefore of a generally lighter appearance. The receptor nests all contained clutches typical in coloration. Although the eggs which were similar to those of the receptors and typical in coloration stayed a little longer in the nests than the light-coloured eggs, the difference in length of stay was not statistically significant.

Response to Eggs of Other Birds

Although eggs of seven other species of birds were introduced into the magpies' nests, in the

Table V. Number of Two-day Blocks for which the Stimuli of Movable and Immovable Interior (18 g) Remained in the Nest

	Eggs transformed		Controls (natural eggs of other magpies)
	Movable interior	Immovable interior*	
\bar{x}	3.9	7.4	7.3
<i>N</i>	17	15	20
<i>Comparisons with control</i>			
<i>t</i>	2.38	0.05	
<i>P</i>	<0.05	NS	

*This stimulus appears also in Table IV as 'Maximum weight'.

interests of conservation only three to eight eggs of each of these species were used. As can be seen in Table VII, all the single eggs introduced were eliminated much earlier than the controls ($t = 5.55, df = 62, P < 0.01$). Nevertheless, the eggs of another species which were best accepted were those of the jackdaw, the nearest in egg pattern, colouring and size to those of the magpie.

Response to Relative Abundance of Eggs in the Nest

In this series of experiments, model eggs of the great spotted cuckoo or natural ones of

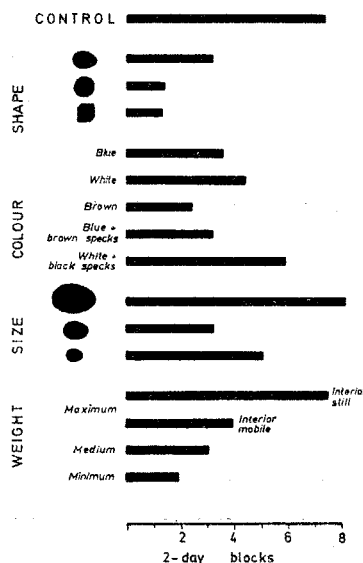


Fig. 1. Mean length of stay of the stimuli showing the various egg characteristics.

spotless starling, kestrel, swallow, and jackdaw were also substituted in each nest for all but one of the eggs of the clutch.

The response to model eggs of the great spotted cuckoo was similar if they were introduced into the nests individually or if all the eggs of the clutch but one were substituted (averages of 11 and 12 days, respectively).

To test the effect of relative quantity using the natural eggs of other species, the experiment was performed with only one nest for each one of the three species indicated above. The results demonstrate that a certain connection exists between the quantity of eggs and their acceptance by the magpies. Thus, if only one egg of *F. tinnunculus* was introduced into the nest, it did not remain there for more than 6 days, but when four of the five magpie eggs of the clutch in one nest were substituted with kestrel eggs, they hatched and the chicks were fed normally, fledging afterwards. Very much the same happened with the eggs of spotless starlings: The magpies went from the situation of not tolerating the eggs more than 2 days in the nest when introduced individually, to hatching several properly and rearing the chicks normally until they flew.

Table VI. Number of Two-day Blocks for which the Models Imitating the Eggs of the Great Spotted Cuckoo Remained in the Nests

	Egg models	Controls (natural eggs of other magpies)
\bar{x}	5.9	7.3
<i>N</i>	40	20
Comparisons with control		
<i>t</i>	1.04	
<i>P</i>	NS	

However, when eggs of the swallow and jackdaw were introduced (substituting all but one of the eggs of the clutch) the response of the magpies did not differ from when only one egg was introduced.

Response to Chicks of Various Species

In general, the response to the introduction of chicks was very different from that shown towards the eggs, the former being accepted much more readily ($t = 2.34$, $df = 64$, $P < 0.05$)

Thus, of the four sparrows (*P. domesticus*) which were introduced individually into the nests, two of them disappeared from the nests after 8 days and before they were able to fly but the other two were normally fed and flew at the proper time. Of the six chicks of spotless starling which were introduced individually into the nests, two were ejected (they remained there for 6 and 8 days) but the remaining four reached the point of flying. The four jackdaws which were introduced were fed normally and reached the point of flying. Finally, of the eight swallows which were introduced into the nests, three were ejected immediately and the other five were fed normally and reached the point of flying.

In the comparisons of the length of stay of the chicks, the jackdaw appears to be accepted more readily than any other bird: statistically significant differences resulted from the comparison of the lengths of stay of jackdaw chicks with those of the swallows ($t = 2.88$, $df = 10$, $P < 0.05$), of sparrows ($t = 24.68$, $df = 6$, $P < 0.01$) and of spotless starlings ($t = 5.00$, $df = 8$, $P < 0.01$).

It is interesting at this point to outline the parasitic role which appeared in various cases where chicks were introduced experimentally. Thus each of the four jackdaws which were introduced was soon alone in the nest, all the accompanying magpies dying, probably due to the fact that when jackdaw chicks beg for food

Table VII. Number of Two-day Blocks for Which the Stimuli of Natural Eggs of Various Species of Birds Remained in the Nests*

	<i>Alauda arvensis</i>	<i>Clamator glandarius</i>	<i>Columba palumbus</i>	<i>Corvus monedula</i>	<i>Falco tinnunculus</i>	<i>Hirundo rustica</i>	<i>Picus viridis</i>	<i>Sturnus unicolor</i>	Control <i>Pica pica</i>
\bar{x}	2.0	1.0	1.0	4.0	1.5	1.0	1.0	1.0	7.3
<i>N</i>	4	4	3	8	6	7	6	6	20

*Comparison of all introduced eggs with the controls: $t = 5.55$, $df = 62$, $P < 0.01$.

they keep their mouths open for much longer than the magpies, thereby receiving more nourishment, very much like the parasitic strategy used by the great spotted cuckoo chick.

Another example of experimental parasitism was shown by three of the introduced chicks of the spotless starling, which, although the same age and size as the chicks of the magpie in the receiving nests, were much more active, crushing and killing the small magpies, again very much like the great spotted cuckoo chick does. Another example of parasitic convergence which is even more noteworthy was shown by one of the swallow chicks. This case was not reported above since it was the only chick introduced into a magpie nest with eggs instead of chicks. This nest was slightly shallower than

normal and contained three magpie eggs. After the introduction of the swallow chick we noted over a period of 3 days that one of the eggs had fallen onto the ground below the nest. Since the egg was not damaged we replaced it in the nest. On our next visit we were able to observe that the swallow chick repeatedly loaded an egg onto its back whilst climbing onto the edge of the nest, dropping the egg on the ground below the nest twice in front of our eyes (see Fig. 2).

Response to the Experimental Change of Colour of Own Chicks

To test the response of the magpies to the colour of chicks different from their own, the crown of the head (skin or feathers) of one of the

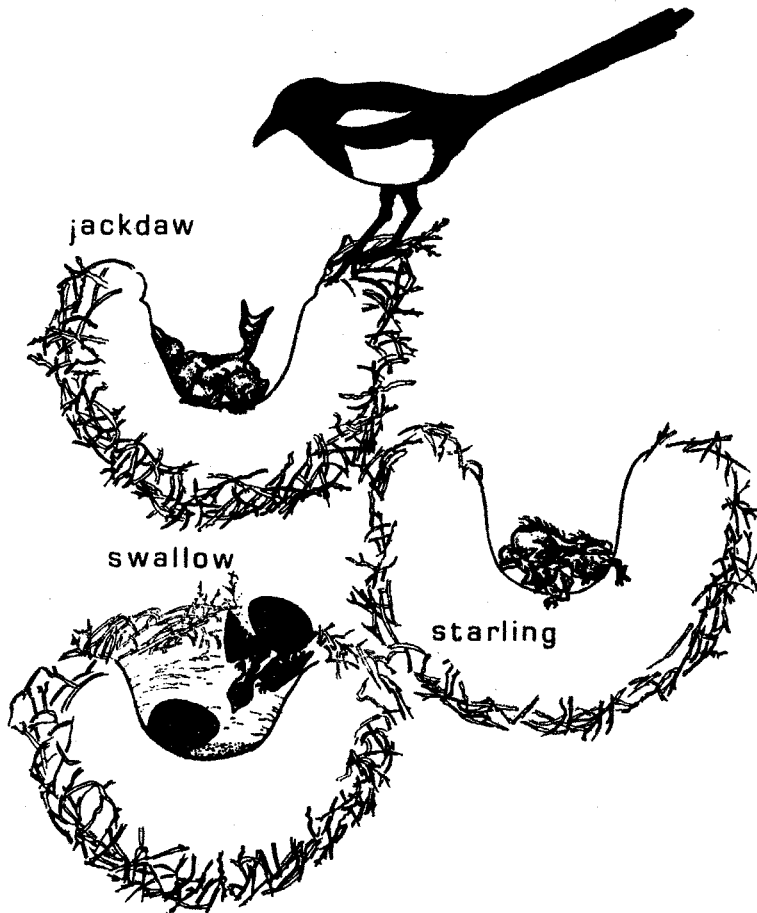


Fig. 2. Jackdaw, spotless starling and swallow chicks showing 'parasitic' behaviour, resulting in the death or elimination of accompanying magpie chicks or eggs.

chicks of the brood was dyed grey, red, green and yellow, in a total of fifty-two nests. In general, the magpies did not respond to this change of colouring, but continued to feed forty-nine of the fifty-two chicks in the same manner as before. The three other chicks had been dyed immediately after birth, and were ejected on the same day as the change of colour was made. The chicks ejected were: one whose head was painted grey (two newly born chicks were painted grey, one in each nest); another was painted red (here also, two newly born chicks were painted red) and another was painted yellow (three newly born chicks were painted yellow).

Relationship of the Responses with the Stage of Nidification

To test the effect of the stage of nidification on the response of the magpies to the stimuli, two stages were considered, namely laying (the period during which the female deposits the eggs in the nest), and the incubation stage (the period from the beginning of incubation of the eggs to when they hatch). Considering these two phases of the experiment and the response of the magpies to each kind of stimulus, no great differences were found to exist between them. The only three modalities in which the comparison of the response between the two phases resulted in statistically significant differences were colour brown ($t = 2.49$, $df = 12$, $P < 0.05$) white background and black specks ($t = 2.82$, $df = 13$, $P < 0.05$) and large size ($t = 6.20$, $df = 14$, $P < 0.01$). These three differences found should, however, be treated with caution, since considering the large number of comparisons made, some of them may yield statistically significant differences purely by chance.

Discussion

The stronger response of the magpies in ejecting eggs of other birds from their nests while keeping chicks of other species in them is to be interpreted as an effective mechanism against parasitism, since it is eggs and not chicks which the parasitic cuckoos deposit in their nests. If we now try to analyse the characteristics of the defence in the recognition and ejection of eggs, it is interesting that the artificial eggs of the great spotted cuckoo were accepted much more readily than the natural eggs introduced, except those of other magpies, which objectively confirms the mimetic function of the eggs of the parasite. Of the natural eggs which were offered, those which were best accepted were those of

other magpies, followed by those of the jackdaw, the most similar in size and colour to the natural magpie eggs.

The characteristic to which the magpies most readily responded by ejection was a shape different from oval (cubical and spherical models were immediately ejected), followed in duration of stay by low weight (empty eggs were also immediately ejected) and by non-light colouring (models painted a uniform brown followed the previous ones in duration of stay).

On the other hand, the characteristics of stimulus eggs which the magpies kept for the longest time in their nests were very large size (hens' eggs with a weight, colour, etc. of those of the magpie were kept for even longer than the controls), very weighty eggs (weight double the normal was retained for longer than the controls) and also eggs of a white background with black specks (length of stay slightly inferior to the controls).

The rapid elimination of empty eggs evidently functions to save energy and space used in the incubation of eggs inviable due to cracks in the shell and loss of the contents. However, the rapid response in eliminating the stimuli which were different in shape and colour from the normal might be interpreted as a defence against parasitism, these results contrasting with those obtained with herring gulls where egg shape was not very important, although oval models were preferred to any other (Baerends 1959).

The great acceptance on the part of the magpies of eggs of a large weight and size (even more so than the eggs of their own species) agrees with the results for herring gulls (Baerends 1959) and with the similar tendency shown by other birds, e.g. the black-headed gull (Beer 1961) and the oyster-catcher (Tinbergen 1951). If greater weight and size represent an advantage with regard to reserves for the embryo, this probably explains why the mimetic eggs of the parasitic cuckoos tend to be slightly larger in size than those of the most frequently parasitized hosts (Cott 1940). The case of the great spotted cuckoo is of special interest, as it lays eggs which are relatively larger than those laid by any other Cuculinae (Payne 1974), seemingly in order to parasitize corvids which lay large eggs.

The preference of the magpies for eggs of a light, and above all, white background colour seems evident, although the presence of specks is also important, as is shown in the response to painted eggs of the bird's own clutch and to

models imitating eggs of the great spotted cuckoo. The high level of acceptance of eggs of a white background and black specks seems to indicate a preference more for the contrast than for any definite colours of the eggs. In any case, the preference of the magpies for eggs of a generally light colouring, similar to their own, and with a speckled background, may be the determining factor for the colour mimicry in the eggs of the great spotted cuckoo.

The acceptance by the magpies of chicks of different species in their nests, and the general lack of response to painting the head of their own chicks, could indicate an absence of discrimination between chicks. Considering that the only three chicks with the head painted which were ejected were those recently born, everything seems to indicate that some process of habituation takes place as the chicks develop, or that discrimination against newborn chicks is especially intense. For the moment, the possible mimicry of head colouring between the chicks of the great spotted cuckoo and the magpie (Lack 1968) needs reconsideration.

At this point and considering the response of the birds to the various egg characteristics we can think of the interpretation of the phenomenon as 'own egg recognition' as misleading, since not all the stimuli accepted in the nests for a long time (sometimes longer than the controls) are present in the natural magpie egg, the animals apparently not responding to the exact combination of stimuli present in them, but to different stimulus intensities. The likely intrusion of a learning process in the response (Rothstein 1974, 1975), the animals taking their own eggs in this process as baseline for ulterior comparisons, would mean that while it is accomplished not all the stimuli present in the eggs are handled in the same way.

The artificial parasitism observed by us, derived from the experimental conditions and resulting in the death of the magpie chicks when jackdaw and starling chicks had been introduced in their nests, and the ejection of magpie eggs by a swallow chick, indicate some widespread mechanisms by which brood parasitism must have become established. For example, the effectiveness in food begging by the introduced jackdaws, which apparently made them the only survivors in the nests, and the intense activity of the spotless starlings, which led them in several cases to crush and to kill the newly born magpies are found in a combined form in

the parasitic behaviour of cuckoos such as *Clamator jacobinus* and *C. glandarius* (Jensen & Jensen 1969; Alvarez et al. 1974a). The repeated ejection of magpie eggs observed by a swallow chick is also a well known characteristic of the parasitic behaviour of *Cuculus* and *Chrysococcyz*.

It seems then, that some parts of the typical behaviour of the parasitic cuckoo chicks, which contribute so much to the success of reproduction, are already present in a generalized form in a great variety of birds, and it is on this pre-parasitic behaviour that some of the adaptations of the cuckoos have been based.

Furthermore, when comparing the magpies' nestling success in unmolested nests in the area of study (69.1 per cent over forty-three nests, Alvarez et al. 1974b) with the lower nestling success in the nests of the present study where chicks of other species were introduced (48.2 per cent over twenty-two nests) and the still lower success in those nests known to be parasitized by *C. glandarius* (10.9 per cent over fifteen nests, Valverde 1971; Alvarez et al. 1974a) it appears as evident that some kind of equilibrium exists in the behaviour of untouched magpie chicks in the same nest toward each other and toward the parents, resulting in a great proportion of them reaching the point of flying. We can visualize this equilibrium as a tendency by all the young in one nest not to overplay their 'psychological tactics' (Trivers 1974) to gain advantage over their brothers and sisters, this altruistic behaviour being of survival value since the recipients are close genetic relatives of the actor.

When a chick of another species is introduced into a nest or when a parasitic cuckoo emerges in it we should not expect an equilibrium in the behaviour of the chicks to exist. The genetic make-up of the former is presumably adapted to another parental and fraternal environment. The absence of equilibrium appears to be exploited to their advantage by the parasitic cuckoos: now that the chick is unrelated to the fosterers and to their present and future young, there is no need for any check on the overplay of 'psychological tactics' of the chick toward the fosterers, or for the continuation of parental investment in its care.

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