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Nest defence by Magpies *(Pica pica)* and the brood parasitic Great Spotted Cuckoos *(Clamator glandarius)* in parasitized and unparasitized nests

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Summary

Nest defence is a frequent and widespread parental behaviour which enhances brood survival. We have found that in a Spanish Magpie population which is heavily parasitized by the brood parasitic Great Spotted Cuckoo, Magpies defend (1) unparasitized more frequently than parasitized nests, and (2) at the end of the nestling period more frequently than in other stages of the breeding cycle. Great Spotted Cuckoos are brood parasites, which means that their eggs are incubated and their nestlings are raised by members of a host species. Brood parasites are not thought to take care of their own offspring. However, we have found that Great Spotted Cuckoos sometimes scolded us on our regular visits to parasitized magpie nests (but never on those to unparasitized nests). Frequency of nest defence by cuckoos differed significantly among years, being significantly higher at the beginning of the study. Although sporadic observations of adult brood parasites feeding juveniles have been recorded, nest defence has not previously been suggested for any brood parasite.

Key words: brood parasitism, parental care, predation risk

Zusammenfassung

Nestverteidigung von durch den Häherkuckuck *(Clamator glandarius)* parasitierten und unparasitierten Nestern bei Elstern *(Pica pica)*

Nestverteidigung ist ein häufiges und weit verbreitetes elterliches Verhalten zur Erhöhung des Bruterfolges. In einer spanischen Elsterpopulation, die sehr intensiv vom Häherkuckuck parasitiert ist, wurden unparasitierte Nester häufiger verteidigt als parasitierte, und zum Ende der Nestlingsperiode wurden Nestern häufiger verteidigt als zu früheren Phasen des Brutzyklus. Häherkuckucke sind Brutparasiten, deren Eier von den Wirtseltern bebrütet und die Nestlinge von ihnen aufgezogen werden. Solche Brutparasiten kümmern sich im allgemeinen nicht selbst um ihre Nachkommen. Manchmal jedoch haßten Häherkuckuck auf uns, wenn wir parasitierte Nester der Elster kontrollierten, während an unparasitierten Nestern ein solches Hassen niemals erfolgte. Die Häufigkeit dieser Nestverteidigung der Kuckucke variierte zwischen Jahren und war signifikant häufiger zu Beginn unserer Untersuchung. Zwar wurde gelegentlich schon Füttern der Jungvögel durch elterliche Brutparasiten beobachtet, die hier festgestellte Nestverteidung ist bisher aber von keinem Brutparasiten beschrieben.

Introduction

Parasitic cuckoos are birds which do not build a nest, but lay their eggs in the nests of other bird species, the hosts, which incubate the parasitic eggs and subsequently rear the young (Payne 1977, Rothstein 1990). This definition implies the absence of parental care in brood parasitic cuckoos, that is, parasitic cuckoos are assumed to exploit to the maximum the parental care provided to their progeny by their hosts (Payne 1977, Rothstein 1990).

The Great Spotted Cuckoo (*Clamator glandarius*) is an obligate brood parasite which in Europe mainly parasitizes the Magpie (*Pica pica*) although other species of the corvid family are known to be selected occasionally (Soler 1990). Palearctic populations of the Great Spotted Cuckoo are migratory, adults arrive in our study area in late February or early March (Soler 1990) and leave it in mid-June, while fledglings usually leave during July or at the beginning of August (Soler et al. 1994a). Soon after leaving the nest, fledgling cuckoos form groups which are fed communally by a group of Magpies, which is frequently larger than the group involved in cuckoo chick rearing (Soler et al. 1995a).

The aims of this paper are: first, to provide evidence that the Great Spotted Cuckoo in our study area exhibits parental behaviour, something not previously suggested for any brood parasite (though some sporadic observations of adult parasites feeding juveniles have been recorded; Friedmann 1968, Cramp 1985, Brooker & Brooker 1989); second, to discuss the potential efficiency of this parental behaviour in increasing the survival probabilities of cuckoo fledglings; and third, to analyse nest defence by Magpies during the different stages of the breeding cycle in both parasitized and unparasitized nests.

Methods

This study was carried out in the Hoya de Guadix, (38°18'N, 3°11'W), southern Spain, a high altitude plateau which is approximately 1000 m a. s. l. This is an area believed to have been recently colonized by the Great Spotted Cuckoo (Soler 1990, Soler et al. 1994b). The vegetation is sparse, but there are many groves of almond trees (*Prunus dulcis*) in which Magpies nest at high density.

Nest-defence behaviour was studied during the 1992–1994 breeding seasons in 146 Magpie nests in 1992, 159 in 1993 and 127 in 1994. The parasitism rate was 66.4%, 63.5% and 52.0% for 1992, 1993 and 1994 respectively, (see Soler et al. 1998, for more detailed information on Magpie nest density, cuckoo abundance and dispersion of nests). Nest defence was studied by recording the number of times that the hosts or the parasites scolded us as potential nest predators. In actual fact, in our study area, humans do plunder Magpie nests. Each nest was visited on average 0.85 ± 0.03 times during the laying period, 1.73 ± 0.04 times during the incubation period, 1.35 ± 0.04 times during the first half and 1.32 ± 0.05 times during the second half of the nestling period. During each visit, if there was nest defence behaviour, we recorded the identity of the scolding bird species (the host or the parasite). To avoid pseudoreplication (Hurlbert 1984), we used the percentage of visits in which Magpies or cuckoos defended the nest in every stage of the host breeding cycle. Thus, we are using only one datum per nest in each stage of the host breeding cycle.

The scolding behaviour of the cuckoos was very similar to that of the Magpies: instead of flying away, some cuckoos remained in the vicinity of the nest and scolded us while we climbed the tree and checked the nest. The cuckoo scolding behaviour consisted in perching near the nest calling and staring at the person climbing to the nest. In the case of the Magpies, it has been proven that scolding is a good indicator of a Magpie's willingness to defend its nest, being highly positively correlated with propensity of attack (Röell & Bossema 1982).

All tests are two tailed. We transformed percentages using the arcsin transformation (Sokal & Rohlf 1981) in order to carry out parametric tests. Values given are means ± SD.

Results

Nest defence by Magpies

Frequency of nest defence by Magpies did not differ among years either in parasitized (Anova,

$F_{262,2} = 2,27$, $p > 0.05$) or unparasitized nests (Anova, $F_{165,2} = 2,65$, $p > 0.05$; Table 1). Differences were also not significant when each stage of the breeding cycle was considered separately in parasitized or unparasitized nests in any of the study years (Anovas, ns; see data in Table 1).

The frequency of nest defence by Magpies reached higher values in unparasitized than in parasitized nests (Table 1). This trend was very clear in all stages of the nestling cycle (Table 1); however, differences were not statistically significant in any case (Student-t test, ns), though sometimes differences were marginally significant (i.e. in 1992, when data for the whole period were pooled, $t_{144} = 1.76$, $p = 0.08$).

Magpies tended to defend more frequently at the end of the nestling cycle than in the other stages, though differences were significant only in unparasitized nests during 1994 ($F_{152,3} = 3.38$, $p < 0.02$). In a post-hoc comparison, differences were significant between nest defence during incubation and the second half of the nestling period (Scheffe test, $p < 0.05$) and between the first and second halves of the nestling period (Scheffe test, $p = 0.05$).

Nest defence by Great Spotted Cuckoos

Sometimes, in our regular visits to parasitized Magpie nests, we were scolded by cuckoos perching on the nest tree or a nearby tree, whereas at no time did an adult Great Spotted Cuckoo scold us at an unparasitized Magpie nest (Table 1).

Table 1. Temporal pattern of nest defence by magpies and great spotted cuckoos in parasitized and unparasitized magpie nests in relation to the hosts' breeding cycle. Only one date from each nest is used (the percentage of visits in which magpies or cuckoos defended the nest in every stage of the host breeding cycle).
Tab. 1. Zeitliches Auftreten der Nestverteidung bei Elster und Häherkuckuck in parasitierten und unparasitierten Nestern der Elster während des Brutverlaufs der Wirts. Je Nest wurde jeweils nur eine Beobachtung verwendet. Die Prozentzahlen beziehen sich auf die Summe aller Nester, die entweder von Elstern oder von Häherkuckucken verteidigt wurden.

Health breeding cycle	Parasitized nests Frequency of defence (%)				Number of nests	Unparasitized nests Frequency of defence (%)				Number of nests
	Cuckoo	Magpie	Both	None		Cuckoo	Magpie	Both	None	
1992										
Laying	6.1 ± 3.1	7.0 ± 3.2	0	86.8 ± 4.2	57	0	15.5 ± 6.7	0	84.5 ± 6.7	28
Incubation	12.5 ± 2.7	20.6 ± 3.3	4.9 ± 1.6	71.7 ± 3.7	89	0	27.0 ± 6.3	0	73.0 ± 6.3	42
Nestling (First half)	7.4 ± 2.4	16.9 ± 3.7	1.8 ± 1.0	77.5 ± 4.1	85	0	20.8 ± 6.3	0	79.2 ± 6.3	34
Nestling (Second half)	10.5 ± 3.2	22.4 ± 4.0	4.7 ± 2.2	71.8 ± 4.4	71	0	28.4 ± 6.8	0	71.6 ± 6.8	37
Total	10.1 ± 1.7	18.1 ± 2.1	3.9 ± 1.0	75.5 ± 2.3	97	0	28.0 ± 4.9	0	72.4 ± 4.9	49
1993										
Laying	3.2 ± 2.5	7.1 ± 4.0	0	89.7 ± 4.6	42	0	20.0 ± 8.2	0	80.0 ± 8.2	25
Incubation	4.8 ± 1.7	17.7 ± 3.7	0	77.4 ± 4.0	90	0	27.9 ± 6.0	0	72.1 ± 6.0	51
Nestling (First half)	2.4 ± 1.7	17.4 ± 4.1	1.2 ± 1.2	81.2 ± 4.2	81	0	18.3 ± 5.7	0	81.7 ± 5.7	42
Nestling (Second half)	0	21.5 ± 4.8	0	78.5 ± 4.8	65	0	33.3 ± 8.4	0	66.7 ± 8.4	30
Total	2.5 ± 0.8	18.2 ± 2.8	0.3 ± 0.3	79.1 ± 3.0	101	0	25.4 ± 4.6	0	74.6 ± 4.6	58
1994										
Laying	0	6.7 ± 4.6	0	93.3 ± 4.6	30	0	14.3 ± 6.7	0	85.7 ± 6.7	28
Incubation	0.9 ± 0.9	11.2 ± 3.9	0	87.9 ± 4.0	55	0	12.5 ± 4.1	0	87.5 ± 4.1	52
Nestling (First half)	0	14.9 ± 5.2	0	85.1 ± 5.2	47	0	12.8 ± 4.9	0	87.2 ± 4.9	47
Nestling (Second half)	0	21.9 ± 6.7	0	80.7 ± 6.4	66	0	15.2 ± 3.5	0	84.8 ± 3.5	61
Total	0.4 ± 0.4	13.0 ± 3.4	0	87.0 ± 3.4	66	0	15.2 ± 3.5	0	84.8 ± 3.5	61

The frequency of nest defence by cuckoos differed significantly among years ($F_{261,2} = 21.3$, $p < 0.0001$) being significantly higher in 1992 than in the other two years (Post-hoc comparison, Scheffe test, 1992–1993, $p < 0.0001$; 1992–1994, $p < 0.0001$; Table 1), and not significantly different between 1993 and 1994 (Post-hoc comparison, Scheffe test, 1993–1994, $p > 0.1$).

Magpies defended parasitized nests more frequently than did Great Spotted Cuckoos in all stages of their breeding cycle. Differences were not significant during the laying period in any of the three years (Student-t test, ns), but differences were significant in all the other stages of the breeding cycle (Student-t test, $p < 0.05$ in all cases).

One Magpie and one Great Spotted Cuckoo scolded us simultaneously in 18 out of 97 parasitized nests (18.6%) in 1992. This simultaneous defence by both species was observed only sporadically in 1993 (only in two nests), and did not occur in 1994.

The frequency of nest predation did not differ significantly according to whether Magpies, cuckoos, both or neither species defended the nest in any of the years (1992, $c^2_3 = 5.2$, ns; 1993, $c^2_3 = 2.9$, ns; during 1994 the frequency of nest defence by cuckoos was very low and does not merit comparison; Fig. 1). Furthermore, the trend observed during the two years was very different: in 1992 the nests more heavily predated were those which were defended by neither Magpies nor cuckoos, but in 1993 the nests defended by Magpies were more frequently predated than those which were not defended by either species (Fig. 1).

Discussion

Parental care is almost universal in birds and mammals (Clutton-Brock 1991), and nest defence is an essential life-history trait in reproductive investment which increases the probability of successful breeding at an increased risk of being injured by the predator (Montgomerie & Weatherhead 1988).

Parasitic cuckoos are assumed to be a major exception: parental effort consists only of the laying of eggs by the female (Payne 1977). This assumption is supported by the large clutch size of parasitic cuckoos, which is larger than in other altricial birds, including non-parasitic cuckoos (Payne 1977). The reason for this is that clutch size is evolutionarily linked to the amount of parental investment (Clutton-Brock 1991). Natural selection is presumed to optimize lifetime parental investment strategies (Clutton-Brock 1991). The way in which natural selection determines the amount of effort allocated to each individual offspring is largely a consequence of the organism's life history. Parental care evolves according to the fitness benefits gained by the offspring, as well as the degree to which care reduces the parent's residual reproductive capacity (Trivers 1972).

Nest defence by Magpies

Magpies are known to be birds which actively defend their nests against potential nest predators (Erpino 1968, Röell & Bossema 1982, Buitron 1983, Redondo & Carranza 1989). Frequency of nest defence by Magpies in this study ranged between 13% (1994 in parasitized nests) and 28% (1992 in unparasitized nests) (Table 1).

Magpies from unparasitized nests defended their nests more frequently than Magpies from parasitized nests (though differences did not reach significance). Considering that in some host species it has been demonstrated that they react to the brood parasite similarly to the way they react to a potential nest predator (Neudorf & Sealy 1992, Bazin & Sealy 1993), this would suggest that nests were parasitized by the Great Spotted Cuckoo because of the high reluctance of those particular Magpies to defend them, while the nesting-cue hypothesis (Robertson & Norman 1976) is not supported. This hypothesis posits that nest defence behaviour by hosts directed towards brood parasites would act as

an indicator to locate nests. It predicts that nest defence should be more frequent and intense in parasitized than in unparasitized nests (Gill et al. 1997) but our results show the opposite trend.

Magpies tend to defend more frequently at the end of the nestling cycle than in the other stages, an observation which is in alignment with previous reports (Montgomerie & Weatherhead 1988, Redondo & Carranza 1989). This increase of nest defence with offspring age has given rise to two different functional hypotheses: "the brood value hypothesis" which suggest that the value of offspring for their parents increases as they approach fledging (Trivers 1972, Andersson et al. 1980), and "the vulnerability hypothesis" holding that young become increasingly more vulnerable as they age because older nests are more conspicuous and more profitable to predators (Skutch 1976, Greig-Smith 1980). Our results do not permit us to assess which of these two explanations is more likely to be correct; however, Redondo & Carranza's (1989) results on Magpies supported "the brood value hypothesis" (but see Onnebrink & Curio 1991).

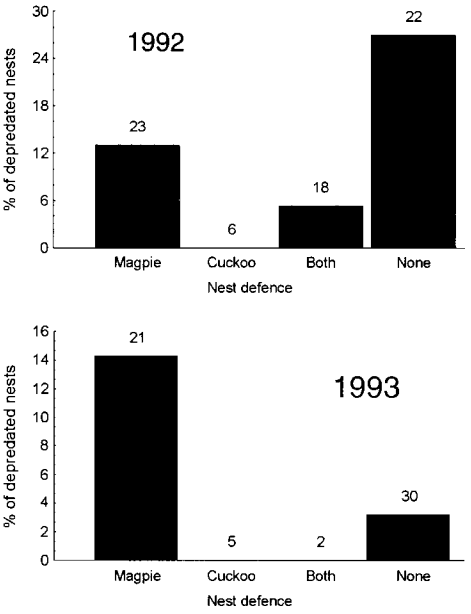

Fig. 1. Percentage of nests which were predated according to the species which defended the nest (only the magpies, only the cuckoos, both, or neither of them). Numbers at the top of the histogram are number of nests (sample sizes).
Abb. 1. Anteil ausgeraubter Nester in Abhängigkeit davon, welche Art das Nest verteidigte (Magpie: Elster allein; Cuckoo: Häherkuckuck allein; Both: beide Arten; None = keine Verteidigung). Die Zahlen über den Säulen geben die Stichprobengröße an.

Nest Defence by Great Spotted Cuckoos

The main finding of the present study is that adult Great Spotted Cuckoos sometimes defend parasitized Magpie nests. In the case of this cuckoo species, as in other brood parasites, the expenditure of time and energy on reproduction is enormous, both in obtaining the food necessary to produce the 23 eggs which a female typically lays in one season (Payne 1974) and in locating appropriate host nests in which to lay the eggs. Therefore, for the Great Spotted Cuckoo there may be a trade-off between parental expenditure in defence and activities necessary for finding food and nests. This may explain the conspicuous differences observed in Great Spotted Cuckoo parental behaviour between years (see above). Differences among years are even more conspicuous when account is taken of the fact that in 1991, during the laying period and the first ten days of incubation, cuckoos scolded us on 25% of 56 visits to 30 parasitized Magpie nests, while Magpies scolded us on only 5% of our visits (Soler et al. 1995b).

The important question is why Great Spotted Cuckoos defended parasitized Magpie nests. Assuming that cuckoos which defend are the biological parents of the egg or eggs present in the Magpie nest, the question is whether parental behaviour increases in any way the survival probability of the parasite's offspring. We have found that the species defending the nest did not affect significantly the frequency of nest predation and, furthermore, the trend observed during each of the two years was very different (Figure 1). Thus, the idea that nest defence by

cuckoos increases the fitness of their offspring is not supported by our observations.

However, there is an alternative explanation: sometimes it is better to accept a parasitic egg than to eject it because only then will hosts avoid "punishment" by the mafia cuckoo (Zahavi 1979). In a previous study (Soler et al. 1995b), we showed that Magpies that respond to parasitism by Great Spotted Cuckoos by ejection or abandonment do not have higher reproductive success than acceptors of the parasite egg, because ejection frequently results in further nest predation by the brood parasite. In this scenario, nest defence behaviour could be advantageous to adult cuckoos if, by defending parasitized Magpie nests, the Great Spotted Cuckoos may further reduce the cost for the host of accepting parasite eggs.

In conclusion, we have reported nest defence behaviour by Great Spotted Cuckoos of parasitized Magpie nests, but conspicuous differences existed between years, this behaviour being frequent at the beginning of the season and almost nonexistent during the second year. This decrease could be the consequence of a trade-off between time spent in nest defence and time spent in finding food and nests.

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