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Brood Parasit

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Differential reproductive success of great spotted cuckoos *Clamator glandarius* parasitising magpies *Pica pica* and carrion crows *Corvus corone*: the importance of parasitism costs and host defences

Manuel Soler, Juan J. Soler, Tomás Pérez-Contreras and Juan G. Martínez

We investigated differences in the reproductive success of great spotted cuckoos *Clamator glandarius* and fitness costs of parasitism for their primary host, the magpie *Pica pica* (slightly larger than the cuckoo and showing defensive mechanisms against the parasite), and their secondary host, the carrion crow *Corvus corone* (more than twice the size of the cuckoo, but lacking defensive mechanisms). Because carrion crows started laying before magpies, and the laying season of great spotted cuckoos was longer than either of their hosts', they were able to parasitise both hosts. Hatching success of the parasite was higher in carrion crow than in magpie nests, but fledging success was significantly higher when parasitising magpies than carrion crows. The cost to the hosts of successful parasitism was twice as high in magpie (3.0 fewer magpie nestlings fledged in parasitised compared to unparasitised nests) as in carrion crow nests (1.5 fewer nestlings). Fledging success of great spotted cuckoos was lower in carrion crow nests because nestlings of this host species had a superior competitive ability compared to cuckoo chicks due to their larger size. This also explained why the cost of parasitism was lower for carrion crows than magpie hosts. The larger carrion crow host provided the cuckoo chick with more food than it can eat, and there is thus always enough food for late-hatched host chick(s) that soon become larger and, hence, out-compete the cuckoo chick. The low cost of parasitism for carrion crows explains why this host species has not developed defensive mechanisms.

Key words: brood parasite, host defence, great spotted cuckoo, reproductive success.

Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada; E–18071 Granada, Spain; e-mail: msoler@goliat.ugr.es

Avian brood parasites should not parasitise unsuitable hosts. Most species of brood parasite appear to avoid hosts that are likely to reject their eggs, that are too small or too large, or that feed their nestlings with food inappropriate for parasitic nestlings (Rothstein 1990). Host preferences must be related to differences in fitness obtained by parasitism on different hosts, and certain host characteristics may be responsible for such differential parasite fitness. If brood parasite fitness increases when using hosts of a particular phenotype, natural selection will favour individual parasites selecting hosts with this phenotype (Price 1980). However, generalist brood parasites of the genus *Molothrus* (cowbirds) sometimes parasitise some host species despite the fact that they never or only rarely fledge parasites (Scott 1977, Fraga 1985, Friedmann & Kiff 1985, Kozlovic et al. 1996).

Recently, in a comparative study of host selection in the European cuckoo *Cuculus canorus*, Soler et al. (1999a) provided evidence suggesting that host availability in time (duration of the breeding season) and space (relative population size), as well as the duration of the nestling period of potential hosts relative to their body size, explained host selection by this parasitic cuckoo. The European cuckoo has been reported to parasitise more than 50 host species in Britain, but three of these species accounted for 77 % of all cases of parasitism (Glue & Morgan 1972). Although it is clear that the European cuckoo selects particular species as hosts (Glue & Morgan 1972), no study has yet analysed in this or any other parasitic cuckoo-host system the differential breeding success of the cuckoo when parasitising different host species (but see Soler 1990 for a preliminary analysis).

The parasitic cuckoo chick most commonly evicts the host eggs or chicks from the nest, thus reducing the reproductive output of the host to zero. However, in some species the cuckoo chick does not evict host offspring, leaving the hosts a chance to rear some of their own nestlings, as it is the case in cuckoos of the genus *Clamator.*

The great spotted cuckoo *Clamator glandarius* is a specialist that only occasionally parasitises more than one host species. In the Palearctic, its primary host is the magpie *Pica pica* and its secondary host is the carrion crow *Corvus corone* (Cramp 1985, Soler 1990). In Egypt great spotted cuckoos also use the carrion crow as their primary host but use magpies in northwest Africa (Cramp 1985, Fry et al. 1988). In sub-Saharan Africa the most frequently recorded host is the pied crow *C. albus* but the black crow *C. capensis*, African pied starling *Spreo bicolor*, red-winged starling *Onychognathus morio* and pale-winged starling *O. nabouroup* are also used (Rowan 1983, Fry et al. 1988).

In Spain, the great spotted cuckoo parasitises magpies (Alvarez & Arias de Reyna 1974, Arias et al. 1982, Soler 1990), carrion crows (Valverde 1953, Soler 1990) and, sporadically, choughs *Pyrrhocorax pyrrhocorax* (4.9 %) and jackdaws *C. monedula* (2.1 %) (Soler 1990). Magpies, which are about half the size of the carrion crow (Cramp & Perrins 1994), are used preferentially as hosts: in one study 30 out of 69 (43.5 %) magpie nests, and only 4 out of 47 (8.5 %) carrion crow nests were parasitised (Soler 1990).

Brood parasitism by the great spotted cuckoo strongly affects the breeding success of its magpie host. On average only 0.6 magpie chicks fledge per parasitised nest, whereas 3.5 magpie chicks fledge from unparasitised nests (Soler et al. 1996). The reproductive failure of the magpie is mainly caused by egg destruction by adult cuckoos, but also by nestling cuckoos out-competing magpie chicks, especially when the cuckoo nestling hatches several days before magpie nestlings (Soler et al. 1996). However, when the cuckoo egg is laid after clutch completion, the cuckoo hatches at the same time or after the host nestlings, reducing the breeding success of the cuckoo and the cost of parasitism for magpies considerably (Soler 1990, Soler et al. 1996, Soler et al. 1997).

Magpies respond aggressively towards adult great spotted cuckoos and they reject cuckoo eggs laid in their nests (Alvarez et al. 1976, Arias et al. 1982, Soler 1990, Soler & Møller 1990, M. Soler et al. 1999). Carrion crows do not attack great spotted cuckoos (Soler et al. personal observation) and do not reject even strongly non-mimetic eggs (Yom-Tov 1976, Soler 1990). In a previous study we found that more great spotted cuckoos fledged from magpie nests than from carrion crow nests, but only four parasitised crow nests were examined (Soler 1990).

In this paper we compare the reproductive success of great spotted cuckoos parasitising magpies and carrion crows, and calculate the fitness costs of parasitism on these host species. We ask two questions: first, why is the breeding success of great spotted cuckoos higher when parasitising magpies, the host species with antiparasite defences, than when parasitising carrion crows, which lacks defences and feeds young large amounts of food? Second, why has the carrion crow never developed defences against the parasite despite long being used as a host by the great spotted cuckoo?

Materials and Methods

Field work was carried out mainly between 1993 and 1997 in Hoya de Guadix, southern Spain (37° 18' N, 3° 11' W), a plateau at an altitude of 1000 m a.s.l. with cultivated cereals (especially barley), and many groves of almond trees *Prunus dulcis* and some groves of holm oaks *Quercus rotundifolia*. Magpies nested preferentially in the almond groves and carrion crows in the holm oak habitat.

We found 144 carrion crow nests, 41 (28.5 %) of which were parasitised by great spotted cuckoos. We have performed several field experiments in magpie nests during other studies but, in this study, we included data only from non-experimental nests. Of 357 magpie nests, 199 (55.7 %) were parasitised. More detailed information on the frequency of parasitism in magpies by year and study plot is given in Soler et al. (1998). To avoid the effect of nest predation when analysing the breeding success of great spotted cuckoos and hosts (magpies and carrion crows), only successful nests (those in which at least one chick fledged) were used in the analyses. Furthermore, to avoid the effect of habitat and year in the analyses of reproductive parameters, we considered only successful nests of both species studied during 1993–1997 in the almond tree habitat. Thus, in these analyses we have used a total of 239 magpie nests (142 parasitised, 59.4 %) and 54 carrion crow nests (33 parasitised, 61.1 %). However, a potential habitat effect will be considered in relation to parasitism rate.

We inspected nests at least once or twice per week, and daily during laying and hatching. Multiple parasitism by one or more adult great spotted cuckoo females was determined on the basis of differences in the appearance of cuckoo eggs and laying dates, a method that has been demonstrated to be quite accurate (Martínez et al. 1998). Breeding parameters such as laying date, clutch size, number of eggs hatched, and number of fledglings were not recorded in all nests. Thus sample size is not the same for all variables. Clutch size was considered as the maximum number of magpies or carrion crow eggs observed in the nest, although some host eggs could have been damaged by cuckoos and removed by hosts before the next nest inspection (Soler et al. 1997, M. Soler et al. 1999). The number of eggs hatched was estimated as clutch size minus unhatched eggs (eggs destroyed by the parasite were considered as unhatched eggs). Hatching success was the mean percentage of eggs hatched, fledging success was the mean percentage of fledglings and breeding success was the mean percentage of eggs that produced fledglings.

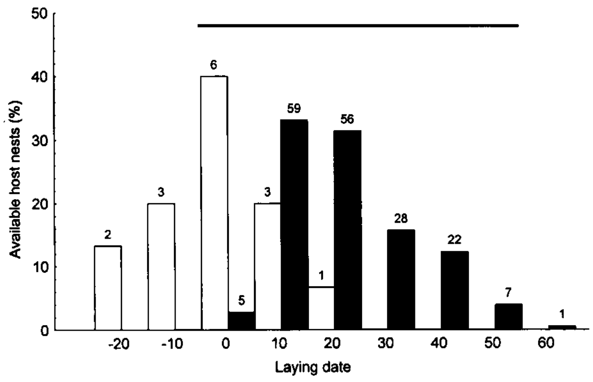

Figure 1. Percentage of available host nests of magpies (black bars, n = 178) and carrion crows (white bars, n = 20) in 10-day periods (1 = 1 April). Numbers above bars are available host nests. The line above the histogram represents great spotted cuckoo laying season.

Analyses of hatching, fledging, and breeding success treated each nest as an independent data point. We have used non-parametric statistics because variables did not fit conditions for parametric tests (Siegel & Castellan 1988). Values are means ± s.e.

Results

Parasitism frequency and laying season of magpies and carrion crows

In the holm oak groves, the habitat preferentially used by carrion crows, we found 81 carrion crow nests of which 6 (7.4 %) were parasitised by the great spotted cuckoo. In this habitat, during the same period, only 32 magpie nests were found but 17 (53.1 %) were parasitised. Parasitism frequency was significantly lower for crows than for magpies (χ^2 = 29.57, df = 1, P < 0.00001). In the almond habitat, during 1993–1997 we found 63 carrion crow nests, of which 35 (55.6 %) were parasitised by great spotted cuckoos. During the same period, we found 325 magpie nests, 182 (56 %) of which were parasitised. Parasitism frequency was similar in the two host species in this habitat, the one preferentially used by the magpie (χ^2 = 0, df = 1, P = 0.95). Considering parasitism rate independently of the habitat, parasitism on magpies (55.7 %) was higher than on carrion crows (28.5 %) (χ^2 = 31.18, df = 1, P < 0.00001). Furthermore, we consider the magpie to be the primary host because in the almond habitat between 1993 and 1997 great spotted cuckoos laid a total of 384 eggs in magpie nests and 54 in carrion crow nests.

Carrion crows began to breed about three weeks earlier than magpies in the same habitat (Fig. 1). The laying season of great spotted cuckoos coincided with that of magpies, so that magpies were parasitised throughout their laying period, whereas carrion crows were parasitised only during the second half of their laying period.

Table 1. Breeding success of great spotted cuckoos in magpie and carrion crow nests. Mann-Whitney U-test, probability levels: * P < 0.025, ** P < 0.005.

	Magpie			Carrion crow		
	Mean	s.e.	n	Mean	s.e.	n
Number of parasitic eggs per nest	2.1	0.1	140	1.8	0.1	29
Number of parasitic females laying per nest	1.3	0.06	122	1.3	0.1	23
Number of eggs hatched	1.7	0.1	137	1.8	0.1	33
Number of unhatched eggs	0.4	0.06	135	0.07	0.06	29*
Number of chicks fledged	1.5	0.08	141	1.3	0.1	33
Number of dead chicks	0.2	0.04	137	0.5	0.1	33**

Differential reproductive success of great spotted cuckoos

Most variables related to the reproductive success of great spotted cuckoos were very similar when parasitising both magpies and carrion crows (Table 1). However, the hatching success of great spotted cuckoos was significantly higher in carrion crow than in magpie nests (Fig. 2, Mann-Whitney U-test, $z = -2.12$, $P = 0.03$). The opposite result was found for fledging success: the percentage of cuckoo chicks that fledged was significantly higher when parasitising magpies than when parasitising carrion crows (Fig. 2, Mann-Whitney U-test, $z = -2.96$, $P = 0.003$). Overall, breeding success was higher in magpie than in carrion crow nests, although the difference was not statistically significant (Fig. 2, Mann-Whitney U-test, $z = -1.3$, $P = 0.19$).

Different fitness costs of parasitism for magpies and carrion crows

Parasitism by great spotted cuckoos drastically affected the reproductive output of magpies (Table 2). Hatching, fledging and breeding success of magpies were all considerably higher in non-parasitised than in parasitised nests (Fig. 3; Mann-Whitney U-test, $P < 0.00001$ in the three cases). Likewise, in carrion crows the number of eggs hatched and the number of chicks fledged were significantly higher in non-parasitised than in parasitised nests (Table 3). Hatching and breeding success were also significantly higher in non-parasitised than in parasitised nests (Fig. 3, Mann-Whitney U-test, $z = -3.83$, $P = 0.0001$; and $z = -3.42$, $P = 0.0006$, respectively), but the percentage of carrion crow chicks that survived to fledging in parasitised and unparasitised nests was not significantly different (Fig. 3, Mann-Whitney U-test, $z = -0.9$, $P = 0.39$).

Table 2. Breeding success of magpies in parasitised and unparasitised nests. Mann-Whitney U-test, probability levels: * P < 0.00001.

	Parasitised nests			Unparasitised nests		
	Mean	s.e.	n	Mean	s.e.	n
Number of eggs per nest	5.6	0.1	142	6.9	0.1	97*
Number of eggs hatched	1.7	0.2	123	5.5	0.2	89*
Number of unhatched eggs	3.8	0.06	123	1.4	0.03	89*
Number of chicks fledged	0.7	0.1	140	3.6	0.1	94*
Number of dead chicks	1.1	0.04	122	1.9	0.1	86*

All parameters related to loss due to parasitism were significantly higher in parasitised magpie nests than in parasitised carrion crow nests (Tables 2 and 3; Mann-Whitney U-test; number of eggs unhatched, $z = -3.9$, $P = 0.00009$; number of chicks dead, $z = -2.2$, $P = 0.02$). Overall, the number of chicks fledged was significantly lower in magpie than in carrion crow nests (Mann-Whitney U-test, $z = -5.4$, $P < 0.00001$), even though clutch and brood size of magpies are larger than those of carrion crows. The average cost of successful parasitism was therefore almost twice as high in magpie nests (3.0 fewer nestlings fledged in parasitised compared to unparasitised nests) as in carrion crow nests (1.5 fewer nestlings).

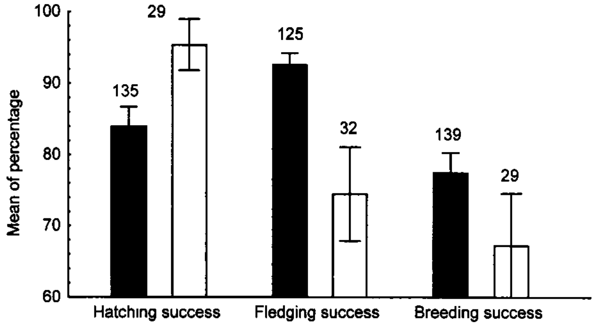

Figure 2. Hatching, fledging, and breeding success of great spotted cuckoos in the nests of magpies (black bars) and carrion crows (white bars). Values are means ± s.e. Numbers above bars are sample sizes.

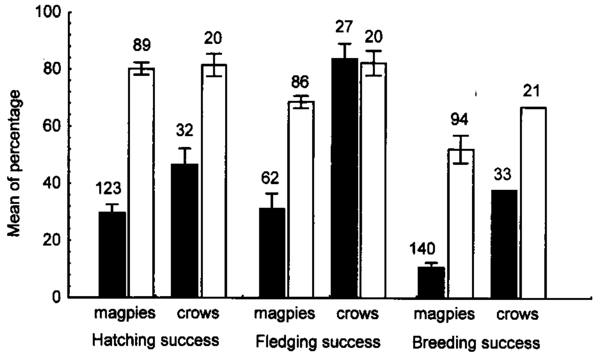

Figure 3. Hatching, fledging, and breeding success of magpies and carrion crows in parasitised (black bars) and unparasitised nests (white bars). Values are means ± s.e. Numbers above bars are sample sizes.

Discussion

Host selection

Some cuckoo females in our study area may use carrion crows as well as magpies as hosts. In a previous study using genetic markers we found that one great spotted cuckoo female laid four eggs in the nests of carrion crows and six eggs in magpie nests (Martínez et al. 1998). The results of the present study show, however, that the cuckoo laying season is synchronised with that of the magpie, and that carrion crows, which begin breeding earlier, are parasitised only as secondary hosts at the beginning of the cuckoo breeding season when few magpie nests are available.

It has been suggested that cuckoos may be habitat specific with regard to their laying area (Teuschl et al. 1998). If so, the different parasitism rates in our two habitats could be explained by habitat specificity alone: 'oak cuckoos' may just be rarer than 'almond cuckoos'. However, this is unlikely because: (1) parasitism rate of magpies in the oak habitat is as high as in the almond

Table 3. Breeding success of carrion crows in parasitised and unparasitised nests. Mann-Whitney U-test, probability levels: * $P < 0.005$, ** $P < 0.00005$.

	Parasitised nests			Unparasitised nests		
	Mean	s.e.	n	Mean	s.e.	n
Number of eggs per nest	4.2	0.2	33	4.6	0.2	21
Number of eggs hatched	1.9	0.2	32	3.7	0.2	20**
Number of unhatched eggs	3.4	0.3	32	0.9	0.2	20*
Number of chicks fledged	1.6	0.2	33	3.1	0.3	21**
Number of dead chicks	0.3	0.1	32	0.6	0.1	20

habitat (see above), and (2) great spotted cuckoo females provided with radio-transmitters visited both habitats (Soler et al. unpubl.).

Why is the breeding success of the great spotted cuckoo higher when using a magpie host?

Great spotted cuckoos parasitising carrion crows gain the advantage of nearly all their eggs hatching successfully, but that is not the case when parasitising magpies (Fig. 2). The difference arises from the different incubation periods of magpies (17.1 days, Arias et al. 1982); and carrion crows (20.7 days, Arias de Reyna 1998). With an incubation period in great spotted cuckoos of c. 13–14 days (Alvarez & Arias de Reyna 1974), a higher synchronisation of cuckoo and host laying dates is necessary when parasitising magpies than carrion crows. A failure to synchronise can give rise to late laying of a cuckoo egg, which is the main factor explaining hatching failure of great spotted cuckoos parasitising magpies, because female magpies stop incubating 4–7 days after the first chick has hatched (M. Soler et al., pers. obs.).

When parasitising magpies, great spotted cuckoo nestlings are of equal size and develop more quickly than magpie nestlings (Soler & Soler 1991). This is essential for nestling cuckoos to be fed preferentially by the magpie foster parents (Soler et al. 1995). When parasitising carrion crows, however, the much larger size of this host provides two clear advantages to the carrion crow nestlings in competition with cuckoo chicks. First, the adult crows provide the cuckoo chick with more food than it can eat, so there is always enough food for late-hatched host chicks. Second, the carrion crow chicks soon become larger than the cuckoo chick, which then loses its greatest advantage.

The percentage of cuckoo chicks that fledged was significantly lower when parasitising carrion crows than when parasitising magpies (Fig. 2). When great spotted cuckoo nestlings were reared without carrion crow nestlings (n = 6), however, all chicks survived to fledge, even when there was more than one cuckoo chick per nest (n = 4). These results imply that cuckoo chicks are frequently outcompeted by the much bigger carrion crow nestlings. Similarly, parasitic cowbirds of the genus *Molothrus* suffer a reduction in breeding success when using larger hosts, because cowbird chicks usually starve (Fraga 1978, 1985, Gochfeld 1979, Lichtenstein 1998, Lorenzana & Sealy 1999). Great spotted cuckoos therefore gain greater reproductive success by parasitising magpies, but when magpie nests are unavailable, they use secondary carrion crow hosts.

Why has the carrion crow not developed defensive mechanisms against the parasite?

The lack of host defences against brood parasites can be explained by two different hypotheses: the 'evolutionary lag' and the 'evolutionary equilibrium' hypotheses (Rothstein 1990). The 'evolutionary lag' hypothesis (Rothstein 1982, 1990) states that defences would be adaptive and would spread among the population by natural selection as soon as they appeared, but that the necessary genetic variants have not yet arisen. Alternatively, the 'evolutionary equilibrium' hypothesis (Rohwer & Spaw 1988, Lotem et al. 1992, 1995) posits that defence behaviour has costs greater than non-defensive behaviour, and it is therefore less beneficial.

Selection pressures arising from parasitism may result in the evolution of host defences, but this outcome depends on two main factors: (1) the duration of sympatry between host and parasite and (2) the magnitude of costs imposed by brood parasitism. The duration of sympatry between the brood parasite and its hosts determines the development and the efficacy of host defence strategies (Soler & Møller 1990, Briskie et al. 1992, Davies & Brooke 1998, Soler et al. 1999b). Thus, a possible explanation for the lack of defences against the great spotted cuckoo in the carrion crow could be that this species has been used as a host by the cuckoo only recently. This seems unlikely because the carrion crow is the primary host of the great spotted cuckoo in Egypt (Cramp 1985, Fry et al. 1988), though unfortunately there is no information about defensive mechanisms used by carrion crows in Egypt. Moreover, parasitism by this cuckoo on carrion crows was documented in Spain about 50 years ago (Valverde 1953). Considering that magpies were able to increase rejection rate of non-mimetic eggs from about 50 % to nearly 100 % and that of mimetic eggs from 10 % to 50 % in only 12 years (Soler & Soler 2000), we can assume that carrion crows have apparently been exposed to cuckoo parasitism sufficiently long to develop defensive strategies against the brood parasite.

The 'evolutionary equilibrium' hypothesis suggests that in species with no recognition ability, the costs of developing defences should outweigh the benefits (Rohwer & Spaw 1988, Lotem et al. 1992, 1995). The cost of parasitism directly affects the strength of selective pressures favouring the evolution of host defences. The cost of parasitism to carrion crows was about 1.5 fewer young fledged per nest, whereas in magpie nests 3.0 fewer chicks fledged. Perhaps the absence of defensive mechanisms in the carrion crow is attributable to the relatively small costs resulting from great spotted cuckoo parasitism, because parasitised individuals are able to rear most of their own young. Large hosts of the parasitic brown-headed cowbird *Molothrus ater* are also able to raise their own chicks (Ortega & Cruz 1988, 1991, Weatherhead 1989).

Given the low costs of cuckoo parasitism on carrion crows and its relatively infrequent occurrence, parasitism by the great spotted cuckoo may not constitute a sufficiently strong selection pressure for anti-parasitic defences to evolve in the carrion crow, supporting the 'evolutionary equilibrium' hypothesis.

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