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Micro-evolutionary change and population dynamics of a brood parasite and its primary host: the intermittent arms race hypothesis

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Abstract A long-term study of the interactions between a brood parasite, the great spotted cuckoo *Clamator glandarius*, and its primary host the magpie *Pica pica*, demonstrated local changes in the distribution of both magpies and cuckoos and a rapid increase of rejection of both mimetic and non-mimetic model eggs by the host. In rich areas, magpies improved three of their defensive mechanisms: nest density and breeding synchrony increased dramatically and rejection rate of cuckoo eggs increased more slowly. A stepwise multiple regression analysis showed that parasitism rate decreased as host density increased and cuckoo density decreased. A logistic regression analysis indicated that the probability of changes in magpie nest density in the study plots was significantly affected by the density of magpie nests during the previous year (positively) and the rejection rate of mimetic model eggs (negatively). These results are consistent with a hypothesis (the intermittent arms race hypothesis) of spatially structured cyclic changes in parasitism. During periods of parasitism, host defences continuously improve, and as a consequence, the fitness gains for parasites decrease. When host defences against parasites reach a high level, dispersing parasites have a selective advantage if they are able to emigrate to areas of low resistance. Once parasites have left an area hosts will lose their defensive adaptations due to their cost in the absence of parasitism. The scene is then set for re-colonization by great spotted cuckoos.

Key words Brood parasitism · *Clamator glandarius* · Coevolution · Parasite counter-defences · *Pica pica*

Introduction

Avian brood parasites exploit hosts by laying eggs in their nests, and parental care for parasitic offspring is subsequently provided by the host. Parasitism has a strongly adverse effect on the fitness of hosts, given that the young parasite ejects all host offspring or outcompetes them during the nestling period (Payne 1977; Rothstein 1990). Thus, there is strong selection acting on hosts to evolve defensive mechanisms against a brood parasite which, in turn, will develop adaptive counter-defences. The scenario is thus set for an evolutionary arms race between the brood parasite and its host(s) which is presumed to result in rapid coevolution (Payne 1977; Dawkins and Krebs 1979; Mason and Rothstein 1986; Davies and Brooke 1988, 1989; Moksnes and Røskaft 1989; Rothstein 1990). This assumption has recently received strong experimental support (Brooke and Davies 1988; Davies and Brooke 1988, 1989; Moksnes and Røskaft 1989; Soler and Møller 1990; Briskie et al. 1992; Soler et al. 1994b). However, arms races have usually been considered to be continuous (Payne 1977; Dawkins and Krebs 1979; Davies and Brooke 1988; Rothstein 1990). The puzzling absence of adaptations, such as the lack of chick discrimination, or the lack of egg rejection in some hosts, has been explained in two exclusive ways: a stable outcome of the continuous brood parasite-host arms race (an evolutionary equilibrium explanation) (Rohwer and Spaw 1988; Brooker and Brooker 1990, 1996; Lotem et al. 1992, 1995), or as evolutionary lag in the host's response during a continuing evolutionary arms race (Dawkins and Krebs 1979; Rothstein 1990; Davies and Brooke 1988, 1989; Moksnes et al. 1990).

Davies and Brooke (1989), when describing a number of stages in a continuous coevolutionary arms race between the common cuckoo (*Cuculus canorus*) and its

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hosts, assumed that if the host species is free from parasitism, then, as a consequence of the costs associated with rejection behaviour, defences would disappear from the host population. Furthermore, it has been suggested that the loss of discrimination behaviour in the absence of parasitism could enable subsequent re-exploitation by the parasite (Brooker and Brooker 1990; Marchetti 1992). In order to account for observations and experiments we here propose the intermittent arms race hypothesis, which suggests that periods of frequent parasitism will alternate with periods of no or rare parasitism. During periods of intense parasitism, host defences are continuously improving and, as a consequence, the reproductive benefits for parasites are decreasing. Once host defences have reached a high level, brood parasites will benefit from emigration from the area. After a period of parasites being absent, hosts will lose their defensive adaptations against parasites, and it will then be advantageous for the brood parasite to re-colonize the area. We investigate this hypothesis by analysing data on the history of parasitism by the great spotted cuckoo (*Clamator glandarius*) and its magpie (*Pica pica*) host in a number of study plots in southern Spain over a period of 14 years. The intermittent arms race hypothesis predicts that parasitism rate should continuously increase for a number of years, and after having reached a maximum, decrease, giving rise to a cycle. The evolutionary equilibrium hypothesis predicts a constant parasitism rate, while the continuous arms race hypothesis predicts a continuous increase (or decrease) in parasitism rate, but never a cycle.

Methods

Species and study area

The great spotted cuckoo (38–40 cm) is an obligate brood parasite which in Europe mainly parasitizes the magpie, although other species of the corvid family are known to be used occasionally (Soler 1990). Palaearctic populations of the great spotted cuckoo are migratory and those breeding in Europe are believed to winter in Africa, south of the Sahara (Cramp 1985). They arrive in our study area in late February or early March (Soler 1990). Adults leave the study area in mid-June, disappearing over a few days, while fledglings usually leave during July or the beginning of Au-

gust (Soler et al. 1994a). An average of 2.4 ($n = 411$) cuckoo eggs are laid per magpie nest (Soler et al. in press). As a rule, the egg of the great spotted cuckoo hatches several days before the eggs of the magpie host. After hatching, the cuckoo chick does not eject magpie eggs; however, magpie nestlings usually starve because they lose in intense competition for food with the large, fast-growing cuckoo young (Cramp 1985; Soler 1990; Soler and Soler 1991). Magpies do not recognize the parasitic chick, and thus do not respond by not providing food to a parasite (Rothstein 1990; Soler et al. 1995).

The magpie is a medium-size, omnivorous passerine bird (43–50 cm) that occurs in widely differing environments. It builds large domed nests in bushes or trees. The breeding success of magpies is strongly reduced by the brood-parasitic great spotted cuckoo. Most parasitized nests produce no magpie chicks; on average, there are only 0.6 magpie fledglings per parasitized nest while the success of unparasitized nests in comparison is 3.5 magpie fledglings (Soler et al. 1996). The reproductive failure of the magpie is due to both egg destruction by adult cuckoos and nestling cuckoos outcompeting magpie chicks (Soler et al. 1996).

The field work was carried out in Hoya de Guadix, an area of presumably recent sympatry between cuckoos and magpies, a high-altitude plateau at about 1000 m above sea level, with a semi-arid climate. It is covered by sparse vegetation and agricultural crops. Habitat is patchy, treeless areas alternating with holm oak (*Quercus rotundifolia*) patches and almond (*Prunus dulcis*) plantations; the preferred nesting habitat of magpies. A total of ten study plots separated by treeless areas were studied in Hoya de Guadix over more than 3 years. Relevant information about each study plot is given in Table 1. The distance between neighbouring study plots was 0.5–8 km, and the two most distant study plots were 25 km apart. More detailed information about the study area and a map can be found in Soler et al. (in press).

In some analyses we have distinguished between study plots with abundant resources and resource-poor plots. The former are on irrigated land, which considerably increases the abundance of invertebrates [the main food of magpies (Soler and Soler 1988) and their chicks (Martinez et al. 1992)] in this otherwise very dry part of Spain.

General field procedures

We studied host-parasite interactions during 1982–1995, but most data were collected in 1982–1983 and 1990–1995. In Hoya de Guadix, a total of 912 magpie nests were found, 496 of which (54.4%) were parasitized by the great spotted cuckoo. Magpie nests were located during regular visits (usually once per week) to our study plots from the start of the nest-building period. The nests were visited at least once a week. We recorded the percentage of magpie nests parasitized in each plot counting a nest as parasitized if it contained at least one cuckoo egg.

The size of study plots was calculated using aerial photographs taken in 1990 at a scale of 1:8,000. These areas were subsequently used for calculating population density.

Table 1 Characteristics of study plots in Hoya de Guadix

Plot	Quality	Area (km ²)	Duration of study (years)	No. of magpie nests	
				Minimum	Maximum
Ladihonda	Poor	1.80	9	2	10
Hueneja	Poor	4.14	11	5	20
Fuente Alamo	Rich	0.82	8	3	21
Hernan Valle	Rich	0.94	5	5	8
Zaragüil	Poor	0.92	6	0	7
La Fuente	Poor	0.50	6	2	9
La Calahorra	Rich	3.01	6	35	67
Carretera	Poor	3.30	5	19	24
Ferreira	Rich	1.60	4	21	45
Via	Rich	0.90	4	0	3

The abundance of great spotted cuckoos was estimated by recording the number of cuckoos seen per hour while walking through the study sites at a constant speed during our regular visits to the plots. This method is similar to line transects, which are known to give a relative estimate of bird abundance (Järvinen and Väisänen 1975).

Experimental procedure

We tested magpie responses to both mimetic and non-mimetic model eggs. Mimetic models were made of plaster of Paris and painted with acrylic paints to resemble great spotted cuckoo eggs, which have a light blue-green ground colour with abundant spots. As non-mimetic egg models we used quail *Coturnix coturnix* eggs painted red (between 1982 and 1992) or models made of plaster of Paris and painted red (during 1993–1995). In order to determine whether magpies responded differently to these two kinds of non-mimetic models, we conducted an experiment in 1995 in which a non-mimetic model was introduced in 23 magpie nests. Nests were randomly assigned to one of two groups: (1) magpie nests in which a quail non-mimetic model was added; and (2) magpie nests in which a non-mimetic model of plaster of Paris was added. The response of magpies to model eggs was checked after 5–7 days, and a trial was classified as acceptance, if the model egg remained in the nest, or rejection, if the model egg disappeared before nest checking, or if the clutch was abandoned. The result was very similar in both treatments since 90.9% ($n = 11$) of quail non-mimetic models and 91.7% of plaster of Paris models were ejected (Fisher exact test, $P = 1.0$). Thus, we concluded that magpies responded similarly to the two non-mimetic egg models used.

Statistical analyses

All variables used in the analyses were normally distributed after transformation (Kolmogorov-Smirnov tests, all n.s.). Parasitism rate, percentage of mimetic eggs ejected and percentage of non-mimetic eggs ejected were arcsin transformed, while density of magpie nests and number of great spotted cuckoos observed per hour were square-root transformed.

A quadratic regression was used to test whether variables such as parasitism rate, cuckoo density and magpie nest density had a significant quadratic fit; the proportion of variance accounted for (R^2) is given together with sample size and P -level. In order to determine whether the relationship was quadratic, we tested whether both linear and quadratic terms were statistically significant.

The relationship between parasitism rate and independent variables of presumed importance was determined using a stepwise multiple regression analysis. Year had to be entered as an independent variable in order to obtain a time-independent estimate of parasitism rate. Standardized year data were estimated subtracting 1989 from the year in which the data were collected. Number of great spotted cuckoos observed per hour, density of magpie nests (number of magpie nests km^{-2}), and percentage of mimetic and non-mimetic eggs ejected were entered in the regression model to test whether they explained any additional residual variation in parasitism rate.

Logistic regression was used to study the relationship between change in magpie breeding density (decrease or increase between years t and $t + 1$; dependent variable) and year, parasitism rate, density of great spotted cuckoos (number observed per hour), density of magpie nests (number of magpie nests km^{-2} in year t), and percentage of mimetic and non-mimetic eggs ejected (independent variables). Initially, a logistic model was fitted to the pooled data which considered the effects of all presumably important variables using the maximum-likelihood method of Cox (1970). The deviance ($2 \times \log$ -likelihood) associated with this model was also calculated, and the effect of omitting each variable in turn was examined by fitting the model with that variable excluded. The significance of the effect of each variable was assessed by considering the difference in deviance between models including

and excluding the variable being tested as a chi-square statistic with one degree of freedom. The final model was considered to have been identified when omission of any of the remaining variables caused a significant decrease in deviance ($P < 0.05$). That is, in the logistic regressions, a saturated model was run first, then the non-significant factors were removed to find the most parsimonious model to fit the data.

Results

Parasitism rate

Considering all plots, parasitism rate in Hoya de Guadix increased continuously from 1983 to 1992, but started to decrease in 1993 (Fig. 1). The same trend of a rapid increase followed by a continuous decrease during the last three years was observed in most plots (Table 2). Parasitism rate during the study period was described by a quadratic equation (Fig. 2a; $R^2 = 0.23$, $n = 51$, $P = 0.0003$) with the quadratic term being highly significant ($b_1 = -0.039$ (SE = 0.011), $t = -3.54$, $df = 48$, $P = 0.0009$).

Cuckoo density

The density of great spotted cuckoos showed a similar trend to parasitism rate, increasing until 1992, but decreasing between 1993 and 1995, both for the Guadix area as a whole and in most of the plots (Table 3). Cuckoo abundance during the study period was also significantly described by a quadratic equation (Fig. 2b; $R^2 = 0.25$, $n = 49$, $P = 0.0002$), with a significant quadratic term ($b_1 = -0.02$ (SE = 0.008), $t = -2.94$, $df = 46$, $P = 0.005$).

Magpie nest density

The number of magpie nests km^{-2} was lowest during the second (1990) and the last (1994 and 1995) years of the study in the Guadix area as a whole (Table 4). However,

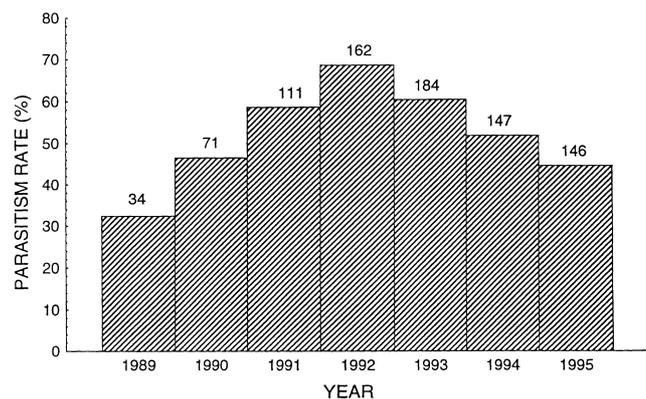


Fig. 1 Temporal change in parasitism rate of magpie nests during 1989–1995, when large samples of both nests and plots were available

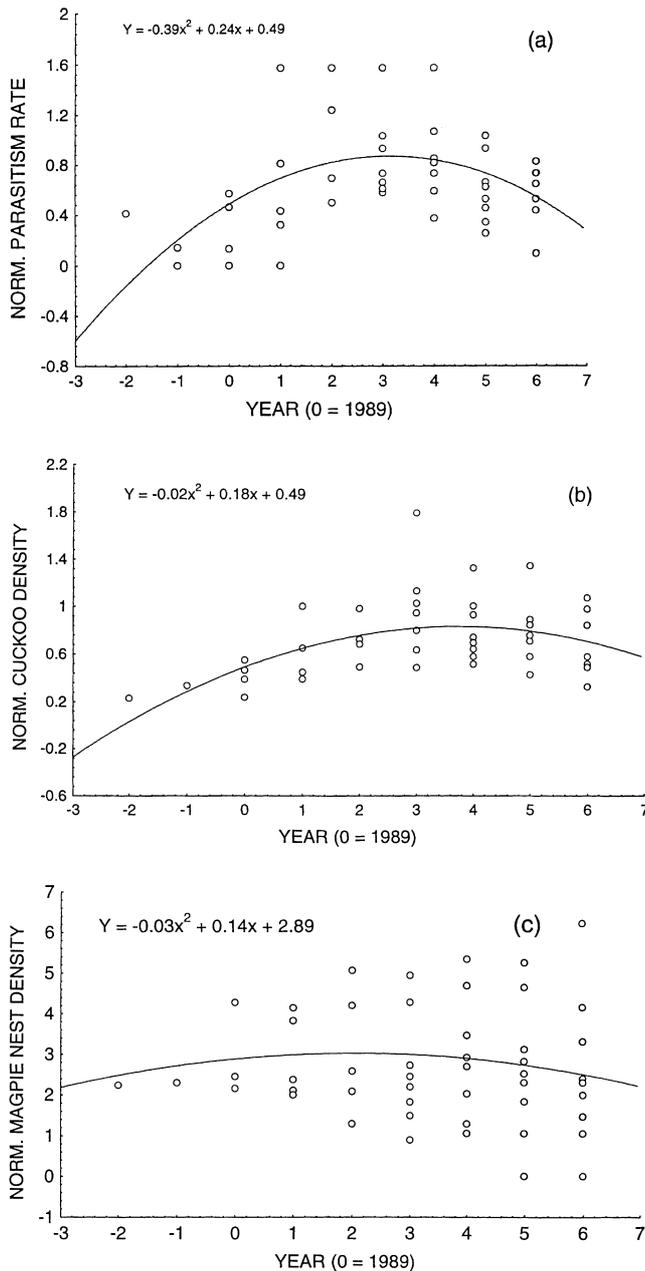


Fig. 2 Temporal change in **a** normalized parasitism rate, **b** normalized cuckoo density and **c** normalized magpie density. The quadratic equations that fit the data are shown. Three data points for 1982–1983 have not been considered in order to avoid the discontinuity between 1983 and 1989

the quadratic relationship is not as clear as for parasitism rate and cuckoo density. The trend in the different plots was highly variable (Table 4), and the data are not significantly fitted by a quadratic equation (Fig. 2c; $R^2 = 0.02$, $n = 53$, $P = 0.36$), since the quadratic term is non-significant ($b_1 = -0.03$, $SE = 0.04$, $t = -0.78$, $df = 50$, $P = 0.44$). This result is probably a consequence of the quality of the plots strongly affecting magpie density. There was no statistically significant relationship between magpie nest density and year in

rich plots ($r = 0.05$, $n = 27$, $P = 0.80$), while population density continuously decreased in poor plots (Fig. 3; $r = -0.51$, $n = 32$, $P = 0.003$). In two out of five poor plots magpies disappeared completely the last years.

Magpie egg recognition

We experimentally parasitized 106 magpie nests with a mimetic and 108 with a non-mimetic model egg. Ejection rates of mimetic and non-mimetic models according to plot and year are shown in Tables 5 and 6, respectively. More experimental tests (mainly using non-mimetic models) were made before 1989, but without recording the plot. Changes during a long-term study in magpie response to parasitic eggs have been analysed in previous papers (Soler et al. 1994b; M. Soler, J.J. Soler and A.P. Møller, unpublished work). Between 1982 and 1993, the rate of increase in ejection rate was 4.7% year⁻¹ for mimetic, and 2.3% year⁻¹ for non-mimetic model eggs (Soler et al. 1994b). Between 1982 and 1996, with more data, a logistic growth model showed a statistically significant increase in ejection rate of mimetic models, and that 50% of the recorded increase in ejection rate had occurred after 4.14 years (M. Soler, J.J. Soler and A.P. Møller, unpublished work). The increase in ejection rate of non-mimetic models, according to the logistic growth model, was also significant, and 50% of the recorded increase had occurred after 6.21 years (M. Soler, J.J. Soler and A.P. Møller, unpublished work). In conclusion, ejection rate of both mimetic and non-mimetic models increased very rapidly in Hoya de Guadix.

Determinants of brood parasitism

In a stepwise multiple regression analysis (F to enter = 2.5) three variables explained parasitism rate, namely cuckoo density, density of magpie nests and rejection rate of mimetic model eggs ($F = 17.50$, $df = 3,9$, $R^2 = 0.85$, $P = 0.0004$), although only the first two were statistically significant. The relationship between parasitism rate and cuckoo density was significantly positive (b (SE) = 0.99 (0.147), $P = 0.00009$), while the relationship between parasitism rate and density of magpie nests was significantly negative (b (SE) = -0.75 (0.152), $P = 0.0008$). We forced the year variable into the model in order to control for any effects of annual variation, but the effects of cuckoo density and magpie nest density were still significant (partial correlations: year = -0.21, $P = 0.53$; cuckoo density = 0.9, $P = 0.00005$; density of magpie nests = 0.87, $P = 0.0003$; ejection rate of mimetic model eggs = 0.48, $P = 0.13$).

A logistic regression analysis indicated that the change in magpie breeding density (increase or decrease) in the different plots was significantly and positively

Table 2 Parasitism rate (%) of magpie nests in different plots and years (*plots where magpies disappeared)

Plot	Year										
	1982	1983	1987	1988	1989	1990	1991	1992	1993	1994	1995
Ladihonda	66.7	20.0	–	0.0	0.0	100	–	–	66.7	50.0	50.0
Hueneja	83.3	30.0	40.0	14.3	53.8	72.2	94.4	80.0	87.5	85.7	66.7
Fuente Alamo	–	33.3	–	–	13.3	41.7	47.6	61.1	55.6	61.1	66.7
Hernan Valle	–	83.3	–	–	–	–	–	57.1	75.0	80.0	60.0
Zaragüil	–	100	–	–	–	–	100	100	*	*	*
La Fuente	–	–	–	–	44.4	0.0	–	66.7	100	25.0	50.0
La Calahorra	–	–	–	–	–	31.4	45.3	54.5	36.4	43.7	9.6
Carretera	–	–	–	–	–	–	63.6	65.0	66.7	33.3	42.1
Ferreira	–	–	–	–	–	–	–	85.7	72.7	58.1	73.3
Via	–	–	–	–	–	–	–	100	100	*	*

Table 3 Great spotted cuckoo density in different plots and years. Values are number of cuckoos seen per hour of field work (*plots where magpies disappeared)

Plot	Year										
	1982	1983	1987	1988	1989	1990	1991	1992	1993	1994	1995
Ladihonda	0.14	0.13	–	–	0.30	1.00	–	0.40	0.33	0.50	0.50
Hueneja	0.24	0.11	0.53	0.11	0.56	0.20	0.52	3.20	0.41	0.57	0.27
Fuente Alamo	–	0.11	–	–	0.15	0.15	0.47	0.41	0.55	0.79	0.71
Hernan Valle	–	–	–	–	–	–	–	0.60	1.00	1.80	1.14
Zaragüil	–	–	–	–	–	–	–	–	*	*	*
La Fuente	–	–	–	–	0.21	0.42	–	1.04	0.86	0.33	0.67
La Calahorra	–	–	–	–	–	0.19	0.24	0.24	0.48	0.34	0.11
Carretera	–	–	–	–	–	–	0.96	0.63	0.26	0.18	0.24
Ferreira	–	–	–	–	–	–	–	0.89	1.04	0.71	0.96
Via	–	–	–	–	–	–	–	1.27	1.75	*	*

Table 4 Magpie density (pairs km⁻²) in different plots and years (*plots where magpies disappeared)

Plot	Year										
	1982	1983	1987	1988	1989	1990	1991	1992	1993	1994	1995
Ladihonda	5.26	6.25	–	–	4.65	4.44	–	–	1.67	1.11	1.11
Hueneja	6.12	9.90	5.00	5.26	6.02	5.64	4.34	4.82	4.10	3.38	2.17
Fuente Alamo	–	13.04	–	–	18.29	14.63	25.61	24.39	21.95	9.76	10.98
Hernan Valle	–	6.38	–	–	–	–	–	7.45	8.51	5.32	5.32
Zaragüil	–	7.78	–	–	–	–	1.67	0.80	*	*	*
La Fuente	–	–	–	–	18.0	4.00	–	6.00	12.00	8.00	4.00
La Calahorra	–	–	–	–	–	17.16	17.61	18.27	22.26	21.59	17.28
Carretera	–	–	–	–	–	–	6.67	6.06	7.27	6.36	5.76
Ferreira	–	–	–	–	–	–	–	24.42	28.45	27.59	38.79
Via	–	–	–	–	–	–	–	3.33	1.11	*	*

affected only by density of magpie nests in the previous year ($-2 \times \log\text{-likelihood} = 54.36$, $\chi^2 = 8.20$, $df = 1$, $P = 0.004$). The only variable that improved significantly the previous model was rejection rate of mimetic model eggs (difference in deviance between the models = 54.12, $P < 0.0001$) which affected negatively the change in magpie nest density. The addition of any other variable did not improve the previous model (difference in deviance between the models ≤ 0.23 , $P \geq 0.6$). Breeding density of magpies increased in high density plots, while nest density decreased in plots with low nest density and a high rejection rate of mimetic model eggs. This conclusion is supported by the fact that a dis-

criminant analysis using these two variables (magpie nest density and ejection rate of mimetic model eggs) correctly classified 100% of the cases in which magpie nest density either increased or decreased (Wilks' Lambda = 0.47, $F = 6.24$, $df = 2, 11$, $P < 0.01$), being significant for each variable separately (magpie nest density: Wilks' Lambda = 0.87, $F = 9.41$, $df = 1, 11$, $P = 0.01$; ejection rate of mimetic model eggs: Wilks' Lambda = 0.79, $F = 7.67$, $df = 1, 11$, $P = 0.02$).

These results support the idea that magpies, as a response to brood parasitism by great spotted cuckoos, tend to nest at a high density. However, this response is only possible in resource-rich habitats with abundant

food availability. In poor habitats magpie density is limited by habitat quality, and movements to rich habitats, as well as low reproductive success due to parasitism, will decrease magpie density over time. This explanation was supported by a natural experiment. At the end of 1991, part of one of our poor plots (Hueneja) became irrigated. While all magpie nests were evenly distributed in this plot in 1991 ($n = 18$) in an area of 4.14 km², they were aggregated in the irrigated land or its surroundings in 1992 (20 nests on 0.9 km²).

The change in abundance of great spotted cuckoos (number of cuckoos observed per hour) was significantly affected by all six independent variables (logistic regression model, $-2 \times \log\text{-likelihood} = 2.72$, $\chi^2 = 15.22$, $df = 6$, $P = 0.020$). However, the only variable that could be excluded while maintaining the level of significance of the model was rejection rate of non-mimetic model eggs ($-2 \times \log\text{-likelihood} = 4.64$, $\chi^2 = 14.48$, $df = 5$, $P = 0.012$; difference in deviance = 1.92, $P = 0.16$).

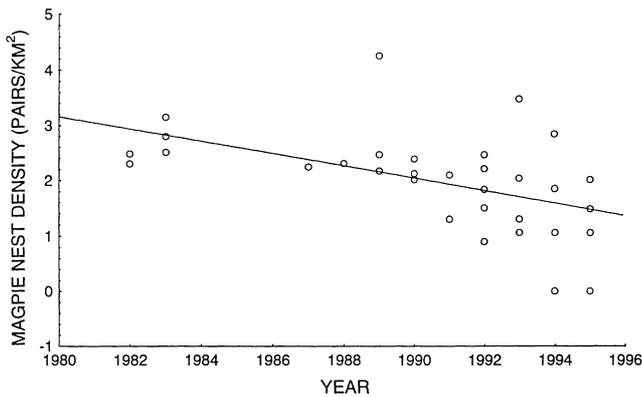


Fig. 3 Temporal change in population density of magpie nests in poor-quality plots

Table 5 Ejection rate (%) of mimetic model eggs from magpie nests. Numbers in parentheses are sample sizes

Plot	Year			
	1992	1993	1994	1995
Hueneja	–	37.5 (8)	75.0 (4)	33.3 (3)
Fuente Alamo	100.0 (3)	–	–	–
La Calahorra	–	40.0 (10)	64.3 (14)	46.7 (15)
Carretera	–	0.0 (5)	33.3 (9)	0.0 (3)
Ferreira	–	20.0 (5)	72.7 (11)	66.7 (6)

Table 6 Ejection rate (%) of non-mimetic model eggs from magpie nests. Numbers in parentheses are sample sizes

Plot	Year				
	1989	1992	1993	1994	1995
Hueneja	55.6 (9)	80.0 (5)	66.7 (3)	60.0 (5)	–
Fuente Alamo	100 (4)	66.7 (3)	–	–	–
La Calahorra	–	66.7 (3)	72.7 (11)	91.7 (12)	100 (4)
Carretera	–	–	100 (7)	80.0 (5)	100 (3)
Ferreira	–	–	57.1 (7)	100 (13)	85.7 (14)

Discussion

Avian brood parasitism has been considered a model system for the study of coevolution, and systems where only a few species interact (pairwise coevolution, as is the case of the great spotted cuckoo) provide one of the clearest examples of coevolution (Rothstein 1990). The lack of egg (or chick) ejection behaviour in some host populations, and the fact that ejector and acceptor individuals usually coexist within a host population, is generally explained as the consequence of an evolutionary lag in the response of the host during the continuing evolutionary arms race between brood parasites and their hosts (Dawkins and Krebs 1979; Brooke and Davies 1988; Davies and Brooke 1989; Rothstein 1982, 1990; Moksnes et al. 1990). Alternatively, parasitic birds and their hosts have reached an evolutionary equilibrium based on the costs and benefits of rejection (Zahavi 1979; Rohwer and Spaw 1988; Brooker and Brooker 1990; Rothstein 1990; Petit 1991; Lotem et al. 1992, 1995).

The possibility of an evolutionary mechanism intermediate between evolutionary equilibrium and the continuing arms race has never been considered, although Davies et al. (1996) recently suggested that variation in rejection behaviour may be the consequence of a mixture of systems that are evolving and others that are at equilibrium.

Our intermittent arms race hypothesis suggests that in host-brood parasite systems, periods of parasitism alternate with periods of no or very little parasitism. During a period of parasitism, host defences are continuously increasing and, as a consequence, parasite advantages are decreasing. Once host defences reach a high level, brood parasites will start to emigrate. After a period without parasitism hosts lose their defensive adaptations, because of the fitness costs of anti-parasite defences (Davies and Brooke 1988; Rohwer et al. 1989; Røskaft et al. 1990; Moksnes et al. 1991; Marchetti 1992). It might subsequently become advantageous for the brood parasite to re-colonize the area. This process implies an evolutionary arms race which begins with clear advantages for cuckoos and finishes with the hosts as temporary winners, but after a period during which the hosts have lost most of their defensive mechanisms the arms race may start again. This process is an intermittent arms race which in an evolutionary sense can be considered to be in evolutionary equilibrium. Therefore, studies of interactions between brood parasites and their

hosts at a particular time will detect an apparent arms race, while the system will be considered to be in evolutionary equilibrium if studied over an extended period.

We have shown that parasitism rate continuously increased from 1982 to 1992, when it reached a maximum (68.5% of 162 magpie nests found that year; Fig. 1), and then decreased. In a stepwise multiple regression analysis we found that parasitism rate increased with increasing cuckoo density and decreased with increasing magpie density. These results suggest that increasing magpie density is an efficient defensive mechanism against cuckoos. Increased proximity to other magpie nests and especially synchronous laying both reduced the probability of magpies being parasitized (Martínez et al. 1996) due to more active nests being available than parasite eggs ("swamping effect", Clark and Robertson 1979). Actually, breeding synchrony in our study area is higher than in the Rivelin Valley (UK) where the great spotted cuckoo does not occur (Parrot 1995). The high magpie nest density as a defensive mechanism against great spotted cuckoos is suggested by magpies disappearing from poor plots (those without irrigated land) where nest density cannot be high because of food shortage. The same phenomenon can be observed in very small, isolated rich plots like Fuente Alamo, Hernan Valle and Via, in which there are few neighbouring nests, thus weakening the swamping effect. Magpies may have increased their nest density early during the recent colonization by cuckoos since (1) the size of breeding territories tended to be smaller in Guadix than in the Rivelin Valley, (2) territory boundaries were less well delineated in Guadix than in the Rivelin Valley, and (3) territory overlap was significantly greater in Guadix than in the Rivelin Valley (Parrot 1995).

Finally, the probability of change of magpie nest density in different plots was significantly affected by the rejection rate of mimetic model eggs. Rejection behaviour is another important magpie defence against great spotted cuckoos, and the rejection rate of both mimetic and non-mimetic models has been increasing rapidly in the Hoya de Guadix study area (Soler et al. 1994b; M. Soler, J.J. Soler and A.P. Møller, unpublished work).

Phases of the brood parasitism cycle

The intermittent arms race hypothesis implies the existence of three phases in the process for the great spotted cuckoo and two for the magpie. A simple graphical model shows these phases (Fig. 4).

Phases of the cycle of the great spotted cuckoo

The first phase is the period during which parasitism is increasing. When great spotted cuckoos start to parasitize a new area, as happened in Hoya de Guadix in the 1960s (Soler 1990; Soler and Møller 1990; Soler et al. 1994b; see also Lotem and Rothstein 1995), magpie

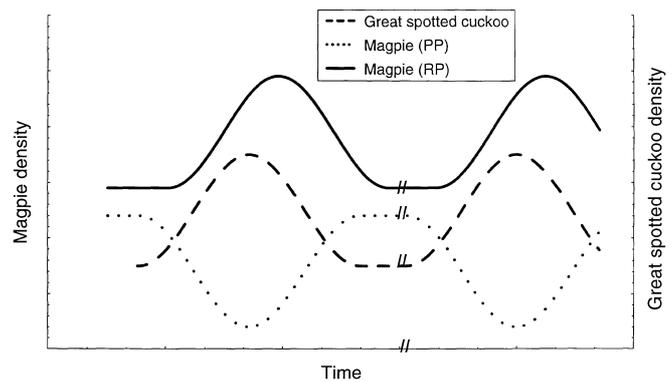


Fig. 4 Hypothetical changes in great spotted cuckoo and magpie densities according to phases of their temporal interactions described in the text (*PP* resource-poor plots, *RP* resource-rich plots, // indicates that this phase may last a very long time)

defences are not well developed, cuckoos enjoy high fitness advantages and cuckoo density increases (Fig. 4). Parasitism rate continuously increased between 1989 and 1992 when it reached a maximum (Fig. 1). Since the first great spotted cuckoo was shot in the Guadix area in 1962 (Soler 1990), we assume that our Hoya de Guadix area was colonized by great spotted cuckoos in the 1960s. If that is the case, the first phase lasted approximately 30 years.

The second phase lasts from the moment when the parasitism rate by great spotted cuckoos stops increasing until they emigrate from the area. Once magpie defences reach a high level of efficiency, parasitism rate and cuckoo density start to decrease. This tendency started in our study area in 1993 and the process seems to be very quick. In one of our plots, La Calahorra, parasitism rate decreased from 43.7% in 1994 to 9.6% in 1995 (Table 2), and during 1996 none of 85 magpie nests was parasitized. In La Calahorra, this second phase lasted only 3 years. Thus, it looks as if this second phase can be very short in resource-rich areas with a high density of hosts, as is the case in La Calahorra (Table 4), although it may last longer in areas with a low density of magpie nests.

The third phase occurs when cuckoos stop parasitizing magpies in an area. When parasitism is not advantageous for cuckoos due to anti-parasite defences, they may emigrate, and magpie nests will only sporadically become parasitized in such an "abandoned" area. Perhaps this is the case in many areas of ancient sympatry. We know of three such cases

1. Doñana National Park, S. Spain. According to information in the collections of the British Museum of Natural History, 21 of 44 (48%) magpie nests were parasitized in 1915. However, in 1992 we found only 1 of 34 (4.2%), and in 1994, 6 of 52 (11.5%) nests parasitized (J.J. Soler, J.G. Martínez and M. Soler, unpublished work).
2. Sierra Morena, S. Spain. Parasitism rate in this area was 22% in 1978 and 19% in 1979 (Arias et al. 1982), but in the following years a drastic decrease occurred,

and since 1985 cuckoos do not exist in this area (L. Arias de Reyna, personal communication).

3. Badajoz, W. Spain. Until 1985 parasitism by great spotted cuckoos was very common and the species was very frequent in the area. However, since 1985 great spotted cuckoos have been uncommon (F. de Lope, personal communication). In 1992 we studied host-parasite interactions in the Badajoz area and found only 1 parasitized nest out of 33 (3.0%). These three examples, and the detailed data from our study area in Guadix, demonstrate that dramatic changes in the abundance of cuckoos are not uncommon.

Phases of the cycle of the magpie

The first phase for the magpie is the period with cuckoos present in an area, thus including the first and second phases of cuckoo parasitism (Fig. 4). When cuckoos start parasitizing a magpie population, overlap in breeding territories of hosts increases as does breeding density and breeding synchrony. However, this will only be possible in resource-rich areas, while magpies in poor areas will slowly disappear (perhaps by emigration to rich areas). Aggregation of magpies in areas with abundant resources may be considered a response against great spotted cuckoos because magpies in areas without cuckoos are highly sedentary (Buitron 1988; Birkhead 1991). The ability of magpies to discriminate between own and alien eggs will increase and rejection rate therefore also increase.

The second phase occurs when cuckoos abandon an area, and magpies lose their defensive adaptations due to the costs involved in absence of parasitism. Magpie nest density will then decrease (Fig. 4), each pair increasing the size of its territory due to the costs of cuckoldry (Birkhead and Møller 1992), and increased competition for food. Rejection rate will also decrease because rejection behaviour entails costs such as rejection or damage of own eggs during attempts to reject parasitic eggs (Davies and Brooke 1988; Rohwer et al. 1989; Røskaft et al. 1990; Moksnes et al. 1991; Marchetti 1992). The loss of ejection behaviour has been demonstrated in the village weaver (*Ploceus cucullatus*), which is parasitized by cuckoos in Africa where it rejects dissimilar eggs. Populations introduced to Hispaniola in the 17th century have, in the absence of parasitism, almost completely lost rejection behaviour (Cruz and Wiley 1989). The scenario is then set for parasites to start parasitism again.

We assumed that fluctuations in magpie populations and cuckoo parasitism are directly related. However, alternative explanations should be considered. First, although rainfall in Mediterranean areas occurs irregularly, variation in climatic conditions cannot account for changes in parasitism rate and cuckoo density, since these occurred in 1992 in the middle of a severe drought which affected southern Spain until 1995. Second, habitat modification cannot account for fluctuations

in magpie and cuckoo populations because habitat conditions changed only in one of our ten plots (Hueneja). Third, fluctuations in food availability for the cuckoo cannot account for the temporal patterns because pine processionary larvae (*Thaumetopoea pityocampa*), the main food of the cuckoo, are very abundant in pine forests in the surrounding mountains, and there is no reason to believe that food availability for the magpie has changed since habitats have remained unaltered.

Importance of the intermittent arms race hypothesis

Cycles similar to those described here for great spotted cuckoos and their magpie hosts could also occur in other parasites such as the European cuckoo (*Cuculus canorus*). However, a practical problem may arise because the duration of one cycle will depend on the strength of selection caused by brood parasitism. Parasitism by the European cuckoo definitely has a strongly adverse effect on parasitized hosts, but the parasitism rate is much lower [usually below 5% (Brooke and Davies 1987)] than that of the great spotted cuckoo [more than 50% (Soler 1990; Zuñiga and Redondo 1992; Soler et al. 1994b, this study)]. Thus, a cycle in the European cuckoo and its hosts could easily last very long time, making it very difficult to detect. Cycles could also occur for Cuculinae species in general, because it has been pointed out that cuckoos are frequently common in parts of their range while they may be absent in adjacent areas with a similar habitat (Rowan 1983).

Cycles may also occur in the brown-headed cowbird (*Molothrus ater*) and its hosts. Certain host species or even assemblages of host species are heavily parasitized in some regions, but scarcely if ever parasitized elsewhere (Rothstein and Robinson 1994). Another piece of evidence supporting the existence of cycles in this parasite is the fact that parasitism rate and rejection rate of cowbird eggs by hosts can be highly variable among areas. In a population of northern orioles (*Icterus galbula*) in California that was not parasitized by brown-headed cowbirds (parasitism rate = 0%), a rejection rate of 100% was recorded (Rothstein 1977) while another population of the same host in Washington State that was strongly parasitized (parasitism rate = 90%), a rejection rate of 60% was recorded (E. Røskaft and S. Rohwer, unpublished work).

The intermittent arms race hypothesis could explain two of the most important evolutionary enigmas in co-evolutionary theory, namely, (1) the coexistence of acceptors and rejectors in the same host population, and (2) the fact that hosts usually do not recognize highly dissimilar chicks (Rothstein 1990). In order to obtain 100% rejectors in a host population, a continuous strong selection pressure from the brood parasite would be necessary (continuous arms race). However, when half (or more) of the population have become rejectors,

parasites may benefit by abandoning that host population and starting to exploit naïve host populations. Thus, host populations will never reach a rejection rate of 100%.

A second problem is the lack of cuckoo chick recognition by hosts. In hosts like those of the European cuckoo, where only the parasitic nestling remains in the nest, it has been shown that learning to recognize nestlings is not adaptive because the cost of misimprinting (learning to recognize the parasite nestlings as the parents' own) may exceed the benefit of correct learning (an evolutionary-equilibrium explanation, Lotem 1993). However, in the great spotted cuckoo-magpie system and other brood parasite-host systems, where both cuckoo and host young are reared together, a capacity for chick recognition should evolve (Davies and Brooke 1988; Lotem 1993). In fact, some ability to discriminate chicks has been demonstrated in the magpie (Soler et al. 1995). Why has parasite-chick rejection never been found under natural conditions in these brood parasite-host systems? It is easier to discriminate among eggs than nestlings (Davies and Brooke 1988), and chick recognition would therefore take longer to evolve than egg recognition. Thus, before chick discrimination can reach a high level or spread in a population, other defensive mechanisms like egg recognition may increase and render the host population inappropriate for exploitation by the parasite.

We suggest that the intermittent arms race hypothesis will be able to explain most of these relationships between brood parasites and their hosts. This hypothesis contributes to unification of the evolutionary equilibrium and the continuous arms race hypotheses. It would still be possible for a particular brood parasite-host system, in a particular population, to be in either an evolutionary equilibrium or a continuous arms race (depending on parasitism rate, host and parasite density and costs and benefits involved in rejection of parasitic eggs), but on a larger scale of spatial and temporal interaction, an intermittent arms race should be detected.

In conclusion, our results suggest that a brood parasite-host interaction that in a short-term study may seem to be an arms race, in a long-term study appears to be described as an evolutionary equilibrium due to cycles in the abundance of cuckoos and parasites. Hence, the process is an intermittent arms race.

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