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Micro-evolutionary change in host response to a brood parasite

Abstract The relationship between brood parasites and their hosts is usually assumed to result in coevolution, and documentation of changes in extant populations should thus be possible. Here we describe how the ejection rate of eggs of an obligate brood parasite, the great spotted cuckoo *Clamator glandarius*, by its host, the magpie *Pica pica*, has recently increased in an area in southern Spain. The ejection rate of great spotted cuckoo eggs in naturally parasitized nests of the magpie increased at a rate of 0.5% year^{-1} during the period 1982–1992. This result was verified in a number of field experiments using nonmimetic and mimetic model eggs. The rate of increase in ejection rate was 4.7% year^{-1} for mimetic eggs and 2.3% year^{-1} for nonmimetic eggs. There were clear differences in parasitism by the great spotted cuckoo between study plots and years, which makes comparisons of rates of parasitism between areas difficult without considering temporal variation. The recent increase in the ejection response of magpies to great spotted cuckoo eggs was not due to magpies using the abundance of cuckoos as a cue to the intensity of parasitism.

Key words Anti-parasite behaviour
Brood parasitism · *Clamator glandarius* · Coevolution
Pica pica

Introduction

Avian brood parasitism has been considered a model system for the study of coevolution (Rothstein 1990). A brood parasite exploits hosts by laying eggs in their

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nests, and all parental care for the parasitic offspring is subsequently provided by the host. The fitness cost of parasitism to hosts is often high because (i) the parasitic young may eject all host offspring or outcompete them during the nestling period, and (ii) the host often provides extensive parental care for considerably longer than when hosts provide care for conspecific young (Payne 1977; Rothstein 1990). Thus, there is strong selection on hosts to evolve discriminatory abilities which reduce or prevent parasitism. The scene is subsequently set for an evolutionary "arms race" between the brood parasite and its host(s)(Dawkins and Krebs 1979; Harvey and Partridge 1988), and this is presumed to result in rapid coevolution.

The assumption that brood parasitism should result in coevolution between parasites and hosts has been supported by three pieces of information: (i) the laying procedure of parasitic cuckoos matches host defences (e.g., rapid laying and laying in the afternoon) (Davies and Brooke 1988); (ii) egg mimicry of cuckoos parallels the discriminatory ability of the host species (Brooke and Davies 1988); and (iii) host species have a stronger anti-parasite response than species unsuitable as hosts (Davies and Brooke 1988). If host responses to parasitic eggs depend on previous exposure to selection pressure by brood parasites, this should result in different responses of hosts to parasitic eggs depending on sympatry. This prediction was fulfilled since individual hosts from allopatric populations actually tolerate nonmimetic parasitic eggs more often than individuals from sympatric populations (Cruz and Wiley 1989; Davies and Brooke 1989; Brown et al. 1990; Soler and Møller 1990; Briskie et al. 1992).

Theoretical investigations of the speed at which host and parasite adaptations evolve have suggested that the phase of rapid increase should last from a few decades to several thousand years, depending on the assumptions of the model (Kelly 1987; Takasu et al. 1993). If the rate of evolution of host-parasite interactions is as rapid as suggested by Takasu et al. (1993), it should be possible to document micro-evolutionary changes in host and

parasite behaviour. To our knowledge, only one study has demonstrated a rapid change in the response of a host to a brood parasite, although the genetic basis of this response remains unknown. The Siberian meadow bunting *Emberiza cioides*, which was the major host of the European cuckoo *Cuculus canorus* 60 years ago in central Japan, is now rarely parasitized because of the evolution of egg discrimination (Nakamura 1990). An alternative host, the azure-winged magpie *Cyanopica cyanea*, has recently become parasitized by the European cuckoo, first leading to a dramatic increase in the frequency of parasitism, and subsequently to an increase in ejection by the host (Nakamura 1990; H. Nakamura, personal communication).

Here we describe evidence for a rapid change in the frequency of egg ejection by the host of a common brood parasite, the great spotted cuckoo *Clamator glandarius*, an obligate brood parasite which in Europe mainly parasitizes magpies *Pica pica* (Cramp 1985). As a rule the great spotted cuckoo's egg hatches several days before those of the magpie host. The parasitic chick never ejects host eggs or nestlings (Cramp 1985). The reproductive success of the host is markedly reduced by intense competition for food between the large, fast-growing cuckoo young and the smaller magpie nestlings (Cramp 1985; Soler 1990; Soler and Soler 1991).

A previous study of the great spotted cuckoo revealed that the response of the magpie host to experimental parasitism differed between areas when experiments were performed in the same year (Soler and Møller 1990). A larger proportion of model eggs were accepted in an area of allopatry between the parasite and its host (Uppsala, Sweden), and in an area of presumed recent sympatry (Guadix, Spain), than in an area of presumed ancient sympatry (Santa Fe, Spain; Soler and Møller 1990). These findings were suggested to support the hypothesis of a coevolutionary arms race between host and brood parasite. The recency of sympatry in the Guadix area was supported by the first great spotted cuckoo being shot there in 1962 (Soler 1990). It was shown to a number of hunters, but nobody recognized the species (Soler 1990). Several of these hunters have an intimate knowledge of the fauna of the Guadix plains since the 1940s. They never saw great spotted cuckoos before 1962, but did so in the following years with increasing frequency. The great spotted cuckoo is a conspicuous bird with a very loud and characteristic call (Cramp 1985) which cannot easily be missed; thus it seems unlikely that it occurred unnoticed at Guadix prior to the early 1960s. Zuñiga and Redondo (1992) cite a record of great spotted cuckoos at Iznalloz (42 km from Guadix) in 1885 as evidence of an early occurrence in the Guadix area. However, Iznalloz is only 30 km from Santa Fe and is separated from Hoya de Guadix by Sierra Harana (altitude 1943 m), and great spotted cuckoos rarely breed in mountains (Soler 1990).

The range expansion of cuckoos onto the Guadix plain first documented in 1962 is consistent with two additional pieces of evidence: (i) The ejection rate of real, mimetic cuckoo eggs in the Guadix area was zero while in Santa Fe it was 33%, similar to what has been reported from other areas of long-lasting sympatry (review in Soler 1990); and (ii) the ejection rate of mimetic model cuckoo eggs by magpies was intermediate between that in an area of allopatry and that in one where parasitism has a long history (Soler 1990). A subsequent study by Zuñiga and Redondo (1992) presented evidence which was presumed to cast doubt on these conclusions. Observations of parasitism from Guadix and Santa Fe were used to suggest that many of the trends in parasitism and ejection were opposite to those reported by Soler and Møller (1990).

The objectives of this study were as follows (i) We describe the recent change in the responses of magpies to parasitism by the great spotted cuckoo using both natural and experimental parasitism. (ii) We test the assumption that measures of parasitism are not simultaneously related to both area and year, using data of various measures of parasitism from a number of study plots in different years. In other words, we test whether comparisons of rates of parasitism among areas are confounded by comparisons among years, as used in the study by Zuñiga and Redondo (1992). (iii) Finally, we test whether a change in host response to parasitism is due to a change in the abundance of parasites, hosts simply becoming more wary of potential parasitic eggs as parasites become more abundant. This is a test of the idea of Zuñiga and Redondo (1992) that magpie ejection behaviour is a conditional response.

Methods

Study area

We studied host-parasite interactions during 1982–1993 in a number of study plots on the high-altitude plateau Hoya de Guadix (37°18′N, 3°11′W), Spain, which is approximately 1000 m above sea level (a. s. l.). This area has supposedly been colonized recently by the great spotted cuckoo, as evidenced by a recent dramatic increase in observations of cuckoos (Soler 1990; Soler and Møller 1990). A total of 11 study plots, 0.57–4.15 km² in area, within the Hoya de Guadix, and separated by arable land with few or no potential nest sites for the magpie, were included in this study. The distance between neighbouring study plots was 0.5–8 km, and the two most distant study plots were 35 km apart. The numbers of study plots in different years were: 1982, 3; 1983, 6; 1987, 1; 1988, 2; 1989, 5; 1990, 5; 1991, 5; and 1992, 11, respectively. A detailed description of the study site and the incidence of great spotted cuckoo parasitism of its magpie host are given in Soler (1990).

The study site at Santa Fe (37°11′N, 3°43′W) is 14 km north of Granada, at 700–800 m a. s. l. It is a cereal-producing rolling plain with a small tamarisk *Tamarix gallica* forest and some holm oak *Quercus rotundifolia* trees.

General field procedures

We examined the incidence of natural parasitism by great spotted cuckoos in magpie nests. Parasitized magpie nests were located during regular, usually weekly, visits to all magpie nests in our study plots from the start of the breeding season. Magpie nests, which are placed in trees, are easily located in the sparse vegetation of Hoya de Guadix. A magpie nest was considered to be

parasitised if it contained one or more eggs of the great spotted cuckoo. A number of different measures of great spotted cuckoo parasitism were recorded: (i) the percentage of magpie nests parasitized in a particular area or year; (ii) the percentage of all magpie nests containing more than one cuckoo egg; (iii) the percentage of parasitized magpie nests with more than one cuckoo egg; (iv) the percentage of parasitized magpie nests with cuckoo eggs laid by more than one female. Multiple parasitism by more than a single female great spotted cuckoo was determined on the basis of differences in the appearance of cuckoo eggs (colour and shape) and laying dates. If two eggs appeared over 2 days, they were assumed to be laid by two cuckoos since on average only two to three eggs are produced weekly (Payne 1973); (v) the number of cuckoo eggs per magpie nest; and (vi) the number of fledgling cuckoos per magpie nest which was estimated as the number of cuckoo nestlings present on the last visit to a parasitized magpie nest on day 14 before the presumed date of fledging (day 15–19 in different nests). The response of magpies to parasitism was classified as either (i) acceptance (the cuckoo egg remained in the nest), or (ii) ejection (the cuckoo egg disappeared between two nest visits).

We estimated the abundance of great spotted cuckoos during our regular visits to the study plots by recording the number of cuckoos seen per hour in line transects. Since we walked at a fixed speed, the results from line transects should give a relative estimate of abundance (Järvinen and Väisänen 1975).

Experimental procedures

Magpie nests found during the egg-laying stage in 1982–1993 were used for an experimental test of ejection behaviour. Nests were randomly assigned to two groups; (i) magpie nests to which a mimetic model egg resembling those of the great spotted cuckoo was added; and (ii) magpie nests to which a nonmimetic model egg was added. Mimetic model great spotted cuckoo eggs were made of plaster of Paris mixed with glue and painted with acrylic paints to mimic real great spotted cuckoos eggs, which have a light blue-green ground colour with small, abundant spots. These eggs were of a similar size and mass to real cuckoo eggs (Soler and Møller 1990). Nonmimetic eggs were quail *Coturnix coturnix* eggs painted red, thereby changing the ground colour but not obscuring the markings of the eggs. Painted quail eggs differed markedly in appearance from mimetic models and real magpie eggs, both with respect to ground colour and markings, and were therefore highly nonmimetic (Soler and Møller 1990: Fig. 1). The magpie nests involved in the experiment were matched with respect to laying date and study plot because of random assignment to treatments.

All magpie nests in the experiment were revisited after 5 days, at which time magpies were classified as (i) ejectors if the model egg was missing, or (ii) acceptors if it was present. The estimate of ejection rate in each sample (plot or year) was simply the percentage of magpies that ejected the model egg.

Statistical procedures

Differences in ejection rate between different plots or years were tested by Fisher exact probability tests or log-likelihood ratio tests depending on the size of the expected values (Siegel and Castellan 1988; Bishop et al. 1975). The temporal change in ejection rate was tested in a model I linear regression with the annual estimates of ejection as the dependent variable and year as the independent variable. The number of magpie nests per plot was 13.6 (SE = 2.1, range = 1–55; $n = 38$ plot years) for the analysis of ejection of natural great spotted cuckoo eggs. The estimates of ejection rate were square-root arcsine-transformed in order to fulfill the requirement of a normal frequency distribution of the dependent variable in a model I linear regression.

Differences in measures of parasitism between plots and years were tested using three-way log-likelihood ratio tests or two-way ANOVAs, depending on the variables (Bishop et al. 1975; Sokal and Rohlf 1981).

The difference in the abundance of great spotted cuckoos between Guadix and Santa Fe was tested in a Mann-Whitney U-test because of the deviation of the frequency distribution from normality (Siegel and Castellan 1988). The relationship between ejection rate by magpies and cuckoo abundance was tested in a model I regression with the plot estimates of ejection as the dependent variable and the abundance estimate of great spotted cuckoos as the independent variable. The estimate of ejection rate was not square-root arcsine-transformed because it already had a normal frequency distribution. All statistical tests are two-tailed. Values reported are means (SE).

Results

Temporal changes in anti-parasite behaviour

The first prediction tested was that the rate of ejection of parasitic eggs should increase as duration of exposure to the brood parasite increases. The rate of ejection of real great spotted cuckoo eggs by magpies changed in the Guadix area during 1982–1992. Overall, it increased from 0% in 1982, 1983, 1987, 1988, 1989, and 1990, to 6% in 1991, and 10% in 1992 ($n = 9, 36, 5, 9, 41, 75, 115$, and 168 magpie nests found, respectively). None of the pairwise comparisons between years of ejection rates by magpies was statistically significant (Fisher exact probability tests, log-likelihood ratio tests, all NS), although the difference between 1990 and 1991 approached significance ($P = 0.056$). The ejection rate of natural eggs (using study plots as statistically independent observations) has increased significantly (Fig. 1; $F = 6.07$, $df = 1,31$, $r^2 = 0.16$, $P = 0.02$). The mean rate of increase during this short period is 0.5% year^{-1}. Since we increased the number of plots in our study area during the study period, we were only partly able to make comparisons of the same plots in different years. The ejection rate of real cuckoo eggs increased from 1990 to 1991 and from 1991 to 1992 (1990:0% ejection rate (0), 1991:8.6% ejection rate (2.3), $n = 3$ study plots, paired t-test, $t = 3.77$, $df = 2$, $P = 0.06$; 1991:5.9% ejection rate (2.5), 1992:17.6% ejection rate (5.4), $n = 4$ study
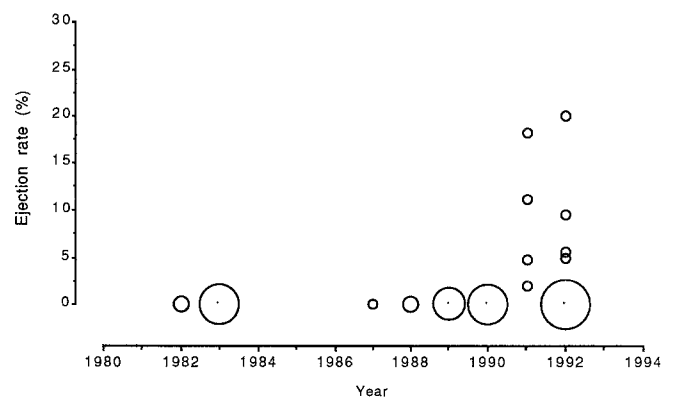

Fig. 1 Ejection rate of natural great spotted cuckoo eggs during 1982–1992. *Data points* are ejection rates per study plot. *Circles of increasing size* represent 1, 2, 4, 5, and 7 study plots, respectively

plots, paired t-test, $t = 3.06$, $df = 3$, $P = 0.06$; Fisher's combined probability test: $\chi^2 = 11.30$, $df = 2$, $P < 0.005$).

Evaluation of temporal changes in host responses to parasites based on observational data may be suspect since (i) cases of parasitism may go unnoticed because of egg ejection by hosts before the contents of host nests have been checked, (ii) differences in the abundance of parasites may affect the rate of parasitism, and (iii) phenotypic differences between hosts may affect the frequency of parasitism and the intensity of anti-parasite behaviour. It is therefore imperative to check host responses using an experimental approach. The ejection rate of mimetic model eggs increased from 14% ($n = 14$ nests) in 1989 to 27% ($n = 11$ nests) in 1992 to 33% ($n = 21$ nests) in 1993. This increase is marginally significant ($F = 139.45$, $df = 1,1$, $r^2 = 0.99$, $P = 0.054$; the rate of increase in ejection rate was 4.72% (S-E $= 0.40$) year^{-1}). The ejection rate of nonmimetic model eggs, which was 61% ($n = 31$ nests) in 1983 and 1984, increased to 71% ($n = 14$ nests) in 1989, 73% ($n = 11$ nests) in 1992, and 89% ($n = 18$ nests) in 1993. This increase was statistically significant ($F = 12.78$, $df = 1,3$, $r^2 = 0.81$, $P = 0.037$; the rate of increase in ejection rate was 2.27% (SE $= 0.63$) year^{-1}). These results suggest that the ejection rate is currently increasing in the Guadix area.

Differences in ejection behaviour between plots and years

To be valid, comparisons of rates of parasitism among areas must not be confounded by comparisons among years. We restricted the analysis of variation in parasitism among study plots to the years 1990–1992, when we checked all nests in five large study plots. There was a high frequency of parasitism however this was measured (Table 1). More than 60% of all host nests contained great spotted cuckoo eggs. Analyses of parasitism ($n = 228$ nests) revealed that there were statistically significant differences among study plots and an interaction between study plots and years in magpie nests parasitized, magpie nests containing more than one cuckoo egg, and parasitized magpie nests with more than one cuckoo egg (Table 2). There was a statistically significant interaction between study plots and years in the number of parasitized magpie nests with cuckoo eggs laid by more than one female, while there were significant effects of study plots, years and their interaction on the number of cuckoo eggs per magpie nest (Table 2). Finally, there was a statistically significant interaction between study plots and years in the number of fledgling cuckoos per magpie nest (Table 2). These differences were due to a successive increase from 1990 to 1992 in the percentage of parasitized magpie nests and in the percentage of nests containing more than one cuckoo egg, although these measures of parasitism varied between study plots. The frequency of parasitism

Table 1 Estimates of great spotted cuckoo parasitism of magpie nests in the Guadix study area 1990–1992

Parasitism variable	Estimate	N
Magpie nests parasitized (%)	61.0	228
Magpie nests containing more than one cuckoo egg (%)	36.2	228
Parasitized nests with more than one cuckoo egg (%)	60.6	132
Parasitized nests with cuckoo eggs laid by more than one female (%)	44.2	132
Cuckoo eggs per nest (mean (SE))	2.44(0.18)	132
Fledgling cuckoos per nest (mean (SE))	0.69(0.14)	132

Table 2 Differences in great spotted cuckoo parasitism and magpie anti-parasite behaviour between study plot and years

Parasitism variable	Test statistic	df	P
Magpie nests parasitized [a]			
Years	1.56	2	0.46
Study plots	18.37	4	0.0001
Interaction	31.82	8	<0.0001
Magpie nests containing more than one cuckoo egg [a]			
Years	2.95	2	0.19
Study plots	22.92	4	<0.0001
Interaction	31.83	8	<0.001
Parasitized nests with more than one cuckoo egg [a]			
Years	2.56	2	0.28
Study plots	7.24	4	0.03
Interaction	17.25	8	0.03
Parasitized nests with cuckoo eggs laid by more than one female [a]			
Years	8.15	2	0.017
Study plots	5.62	4	0.06
Interaction	17.60	8	0.024
Cuckoo eggs per nest [b]			
Years	4.22	2,123	0.017
Study plots	8.30	2,123	0.00042
Interaction	7.27	4,123	<0.001
Fledgling cuckoos per nest [b]			
Years	0.35	2,65	0.71
Study plots	1.88	2,65	0.16
Interaction	3.31	4,65	0.016

[a] G^2, three-way log-linear model
[b] F, two-way ANOVA

in different areas therefore cannot be compared without considering temporal effects.

Differences in parasite density between areas

Differences in host response between areas may be due to a conditional response of the host as a result of differences in population densities of cuckoos between areas. Our estimate of the abundance of great spotted cuckoos was based on line transects in the study plots. The frequency of cuckoo parasitism in different plots could reliably be predicted from our estimate of cuckoo abun-
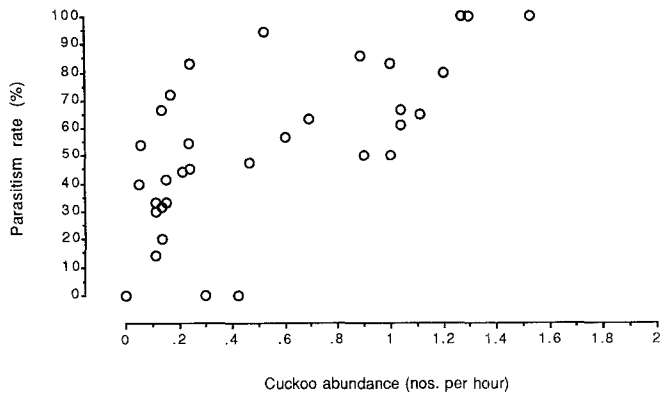
Fig 2 The relationship between parasitism rate of magpie nests by great spotted cuckoos (%) and the abundance of great spotted cuckoos. *Data points* are parasitism rates per study plot
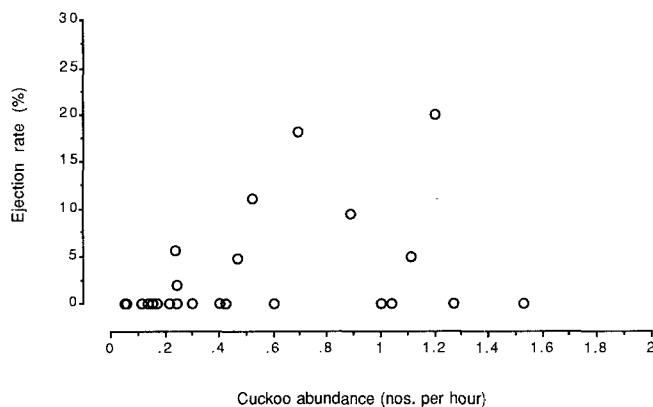

Fig 3 The relationship between ejection rate of great spotted cuckoo eggs (%) and the abundance of great spotted cuckoos. *Data points* are ejection rates per study plot

dance since these two variables were strongly positively related [Fig. 2; $F = 18.16$, $df = 1,31$, $r^2 = 0.37$, $P = 0.0002$; parasitism rate (%) = 33.44 + 37.74 (SE = 8.86) cuckoo abundance (Cuckoos h^{-1})]. This suggests that the abundance estimate is a reliable predictor of the frequency of cuckoo parasitism.

The difference in rate of ejection of cuckoo eggs between the two study areas cannot be due to conditional host responses. Our estimates of cuckoo population density in the two study areas (Santa Fe and Guadix) indicate that parasites were more abundant in Guadix, where the ejection rate was low, than in Santa Fe where the ejection rate was high [Guadix: 1.01 (0.14) cuckoos h^{-1}), $n = 6$ plots; Santa Fe: 0.22 (0.02) cuckoos h^{-1}, $n = 3$; Mann-Whitney U-test, $U = 0$, $P = 0.02$].

We also tested whether differences in ejection rate of cuckoo eggs among study plots in the Guadix area were positively related to differences in the abundance of great spotted cuckoos. Again, the relationship between ejection rate of parasitic eggs and cuckoo abundance was not significantly positive, as predicted by the hypothesis (Fig. 3; $F = 3.66$, $df = 1,28$, $r^2 = 0.12$, $P = 0.07$). The hypothesis assumes that rejection de-

pends on a genetic tendency toward rejection and on detection of cuckoos. If 'ejector alleles' are absent from a site, there will be no rejection of cuckoo eggs regardless of local cuckoo abundance. If the analysis is repeated after exclusion of plots with no rejection, the previous conclusion is maintained ($F = 3.66$, $df = 1,6$, $r^2 = 0.12$, $P = 0.15$). A similar result was obtained if years were considered as independent data points.

Discussion

Temporal changes in anti-parasite behaviour by hosts

Coevolution between hosts and parasites implies evolutionary change in one species in direct response to a trait in another species that has been modified in response to selection arising from the first species (Futuyma and Slatkin 1983). Long-term studies of the relationship between hosts and parasites should be able to document micro-evolutionary changes in host and parasite behaviour, particularly if current theoretical considerations of the speed of evolution in brood parasite-host interactions are reliable (Takasu et al. 1993). Monitoring the frequency of ejection of cuckoo eggs by magpies indeed revealed a significant increase in ejection rate during 1982–1992 (Fig. 1). The rate of ejection of cuckoo eggs by magpies increased by an average of 0.5% year^{-1}, with a particularly dramatic increase during the years 1990–1992.

First we would like to consider the possiblity that the recent change in rejection behaviour by magpies may have been caused by a response of magpie hosts to our research activities. We do not find this explanation likely because we have visited our study plots at a similar frequency during the period 1989–1992, although the number of study plots has increased. A constant research effort should not have resulted in an increase in the rejection frequency of great spotted cuckoo eggs, as demonstrated in our study (Fig. 1).

Although the analysis of the temporal change in rejection frequency of great spotted cuckoo eggs suggests that there has indeed been an increase in ejection behaviour by magpies, this interpretation may be confounded by the fact that the result is based on natural cases of parasitism. Observations of host responses to parasitism may not be particularly informative because observed rates of parasitism depend on (i) parasite abundance, (ii) anti-parasite responses by the host, and (iii) differences in the phenotypic quality of hosts. Natural parasitism may go unnoticed if hosts eject cuckoo eggs before they have been recorded, and such an effect will obviously differ between areas with different rates of ejection. It is virtually impossible to deduce differences in host responses to parasitism using only observational evidence, and estimates of ejection rates based on experimental parasitism will therefore be less biased than those based on natural parasitism. This difference also has important implications for the conclusions from the

studies by Soler and Møller (1990) and Zuñiga and Redondo (1992); while the former is experimental, the latter is entirely observational. Observations of parasitism and host responses to parasitism are uninformative, since cases of parasitism may go undetected because hosts eject cuckoo eggs before they are recorded (Rothstein 1977), and this effect will obviously differ between areas with different ejection rates. Estimates of the rate of parasitism used to infer population differences by Zuñiga and Redondo (1992) will only prove informative when the ejection rate of cuckoo eggs is low, and this was not the case in Santa Fe (the presumed area of ancient sympatry) (Soler and Møller 1990). Our experiments on egg ejection by magpies demonstrated that there was indeed an increase in the ejection rate during the period 1982–1992. This result implies that there has been an increase in the tendency to discriminate against alien eggs, even when the potentially confounding effects of other variables were controlled experimentally.

Few potential cases of recent changes in the response of hosts to brood parasitism have been documented. Nakamura (1990) describes how the azure-winged magpie recently has become parasitized to an increasing extent by the European cuckoo, and azure-winged magpie hosts now eject parasitic eggs more frequently than a few decades ago. However, this change in host response to parasites has not been verified experimentally. A second example, provided by Cruz and Wiley (1989), suggests that discrimination against parasitic eggs has disappeared in an introduced weaver in the absence of its previous brood parasite. This conclusion rests on the assumption that the ancestral, introduced host population indeed displayed ejection of parasitic eggs. An alternative explanation is that the introduction of the weaver resulted in a bottleneck which gave rise to secondary loss of the "egg ejector gene" due to genetic drift.

Differences in parasitism between areas and years

Magpies respond differently to experimental parasitism in relation to the presumed duration of sympatry with the great spotted cuckoo. While magpies from an allopatric population readily accepted model cuckoo eggs, this was less often the case in a population of apparent recent sympatry (Guadix), and magpies from a population of presumed ancient sympatry (Santa Fe) frequently ejected model eggs (Soler and Møller 1990). This conclusion was subsequently challenged by Zuñiga and Redondo (1992) who showed that differences in the rate of parasitism between Guadix and Chimeneas [not Santa Fe as stated by Zuñiga and Redondo (1992)] appeared to be contrary to those previously reported by Soler and Møller (1990). This conclusion may be unwarranted because Zuñiga and Redondo did not study magpies in Santa Fe as stated in their paper, but in Chimeneas (T. Redondo, pers. comm.) which is approximately 16 km from our Santa Fe study site. The habitat in Chimeneas (*Prunus dulcis* and *Olea europaea*) differs from that in

our study site in Santa Fe (*Tamarix gallica* and *Quercus rotundifolia*), and this may affect both the ability of cuckoos to parasitize magpies and the ability of magpies to defend their nests against parasites. While Soler and Møller (1990) compared experimental data from three areas during the same year, Zuñiga and Redondo (1992) compared observational data from Guadix during 1982–1984 with observational data from Chimeneas during 1985 and 1989–1991. Any difference between these two samples could be due to differences between areas, between years, or both. Our analyses of patterns of parasitism in different plots and years clearly demonstrate that plot as well as year independently affected the frequency of parasitism (Table 1). It is therefore of paramount importance that rates of parasitism are compared between areas in the same year.

In conclusion, the comparison of rates of cuckoo parasitism of magpies by Zuñiga and Redondo (1992) confuses variation between years with variation between areas, and this renders their conclusion about differences in rates of parasitism between study areas invalid.

Cuckoo abundance and host responses to parasitism

The rapid increase in ejection rate of great spotted cuckoo eggs by magpies at the Guadix study site could either be genetic or entirely environmental. The difference in host behaviour to wards parasitic eggs between Guadix and Santa Fe could be due to a conditional ejection response by the host to the presence of potential parasites near the nest (Zuñiga and Redondo 1992). A higher population density of parasites might result in an increase in the ejection rate of parasitic eggs, if hosts use the presence of potential parasites as a cue to intensity of parasitism. To infer that relationships between brood parasites and their hosts represent coevolution, one must assume that parasite and host adaptations are genetically determined (Payne 1977; Rothstein 1990). Although this assumption of genetic determinance seems reasonable, there have been no direct tests of it. A high rate of rejection of parasitic eggs in areas of allopatry, as found by Briskie et al. (1992), clearly suggests that there is a genetic tendency to reject parasitic eggs. Experiments have also shown that the tendency for potential hosts to reject dissimilar eggs from their nests clearly appears to be innate, while the type of egg that a bird considers its own is a learned response (Rothstein 1974, 1978). This does not preclude the possibility that the tendency to reject eggs can be modified by experience, and recent studies of brood parasites and their hosts have provided evidence for such modified host responses (Davies and Brooke 1988; Moksnes and Røskaft 1989; Lotem et al. 1992). We determined whether differences in magpie response to parasitism were affected by the abundance of great spotted cuckoos in two different ways. First, cuckoos were much more abundant in Guadix than in Santa Fe, while the ejection rate of model cuckoo eggs was higher in Santa Fe. This suggests

that the difference in rejection rate between the two study areas is not only due to differences in the abundance of great spotted cuckoos. Second, we related the rate of ejection of cuckoo eggs laid by great spotted cuckoos to the local abundance of cuckoos in different study plots in the Guadix study area. The relationship was not significantly positive as would be predicted by the hypothesis.

In conclusion, analyses of the relationship between ejection of parasitic eggs and cuckoo abundance both in different study areas and in different study plots suggest that anti-parasite behaviour by magpies is not a simple response to exposure to parasitic cuckoos. However, the rapid increase in host response to cuckoo eggs could either be due to an evolutionary change or to a conditional response.

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