

REPORT

Coevolutionary interactions in a host–parasite system

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Abstract

Interactions between parasitic cuckoos and their hosts represent a classic example of coevolution, where adaptations in the parasite to exploit the host select for defences, which in turn select for new parasite adaptations. Current interactions between the two parties may be at an evolutionary equilibrium or, alternatively, a coevolutionary arms race may be taking place. By taking into account the effect of gene flow in 15 European magpie (*Pica pica*) populations, we studied the coevolutionary interactions with its brood parasite, the great spotted cuckoo (*Clamator glandarius*). Our results suggest that, in Europe, magpies and cuckoos are engaged in an ongoing coevolutionary process because, despite controlling for the large amounts of gene flow among different magpie populations, we still found a positive relationship between host defence (i.e. foreign egg recognition and rejection) and parasite selection pressure.

Keywords

Arms race, autocorrelation, *Clamator glandarius*, coevolution, cuckoo, evolutionary equilibrium, magpie, *Pica pica*, spatial scale.

Ecology Letters (2001) 4: 470–476

INTRODUCTION

Parasitic cuckoos lay their eggs in the nests of one or more host species, which incubate and rear the parasitic offspring, and hosts thereby suffer severe reductions in reproductive success. These costs select for host defences against the brood parasite, which, in turn, select for the ability of parasites to overcome host defences (Rothstein 1990; Davies & de Brooke 1998), giving rise to a coevolutionary arms race between hosts and parasites. This hypothesis has been supported by comparisons of host species with unsuitable, potential hosts, and the fact that allopatric host populations tolerate experimental parasitism more readily than do sympatric populations (Davies & de Brooke 1989; Soler & Møller 1990; Briskie *et al.* 1992; Soler *et al.* 1999a). Similarly, egg mimicry by cuckoos has evolved in response to host rejection of dissimilar eggs from their nests (de Brooke & Davies 1988; Marchetti *et al.* 1998), or through removal of dissimilar eggs by competing cuckoo females (Davies & de Brooke 1988; Brooker & Brooker 1989). However, an evolutionary equilibrium can be reached between host and parasite if the cost of parasitism is compensated for by an adjustment of the host's life history pattern (Brooker & Brooker 1996; but see Soler 1999) or, in general, if, for some individual hosts, the costs of defences

exceed their benefits (Lotem *et al.* 1992, 1995). From this point of view, a prediction of the evolutionary equilibrium hypothesis is the coexistence of adaptive and non-adaptive phenotypes in a host population (Lotem *et al.* 1992, 1995; Winfree 1999), or the complete absence of adaptive phenotypes. However, geographical structure and migration between populations may affect the expected frequency of phenotypes within a host population, and apparently maladaptive phenotypes of hosts in areas suffering from parasitism can be explained by gene flow (Nuismer *et al.* 1999). Gene flow from a host population with a high level of antiparasite defence to host populations allopatric with the parasite, and vice versa, can explain the occurrence of defence in allopatric host populations and the absence of defence in host populations sympatric with the parasite. Moreover, differences in levels of local defence could simply arise from differential gene flow of defensive and non-defensive host phenotypes from sympatric and allopatric populations (Dybdahl & Lively 1996). Thus, because frequencies of defensive and non-defensive phenotypes depend on geographical population structure, the coexistence of these phenotypes within a host population should no longer be considered as a prediction of the evolutionary equilibrium hypothesis, but an immediate consequence of the fact that populations with high parasite selection

pressure are connected by gene flow to others with low or nil parasite selection pressure. Thus, comparisons of antiparasite defence between sympatric and allopatric host populations should take gene flow among these populations into account (Dybdahl & Lively 1996; Thompson 1998, 1999).

In a previous paper, we demonstrated that gene flow (i.e. genetic and geographical distances) among the 15 European magpie (*Pica pica*) populations investigated in the present study explained a significant proportion of variance in the frequency of a defensive (i.e. rejection ability of foreign eggs) phenotype (Soler *et al.* 1999a). However, a large amount of variance in this frequency is still to be explained. If the prevalence of parasitism explained the levels of host defence after controlling for the effect of gene flow among host populations (estimated as genetic distances), this would provide evidence of current interaction between great spotted cuckoos and magpies.

If ongoing coevolution affects the cuckoo–magpie system, we predict that current levels of parasitism should explain current levels of host defence after controlling for the effects of gene flow at the European population level. We have previously shown that population differences in rejection rates of non-mimetic model eggs have a strong genetic component, while geographical rather than genetic distance explains differences in rejection rates of mimetic model eggs (Soler *et al.* 1999a). Moreover, host populations in areas of sympatry with the cuckoo are not geographically structured (Martínez *et al.* 1999), and genetic and geographical distances are thus not related in sympatric host populations, with only geographical distances explaining differences in rejection rates of mimetic and non-mimetic model eggs (Soler *et al.* 1999a). In this scenario, predictions from the hypothesis of an ongoing coevolutionary process should refer only to differences in the rejection rate of non-mimetic model eggs because of the strong genetic component. Because differences in the rejection rates of mimetic model eggs mainly depend on geographical distance, but not on genetic distance between populations, this parasitism rate should not explain the additional variance of differences in rejection rates of mimetic model eggs because of its smaller genetic component. We tested these predictions on parasitism prevalence and magpie rejection of mimetic and non-mimetic model eggs in 15 host populations, including those both sympatric and allopatric with the brood parasite.

MATERIALS AND METHODS

Study species

The great spotted cuckoo is a specialist brood parasite that mainly uses magpies as hosts in Europe. This host–parasite system is characterized by a number of apparent adaptations and counter-adaptations. For example, magpies living in

sympatry with the great spotted cuckoo reject model cuckoo eggs more frequently than do magpies living in allopatry (Soler & Møller 1990; Soler *et al.* 1999a). Cuckoos are able to force magpies to accept parasitism by depredating nests of rejecter magpies (Soler *et al.* 1995), making it adaptive for rejecter magpies to accept parasitism in replacement clutches (Soler *et al.* 1999b). Great spotted cuckoos break some host eggs when laying, thereby increasing the probability of successful hatching of parasitic eggs and reducing future competition for food with host nestlings (Soler *et al.* 1997; see Soler & Soler 2000 for a review of the great spotted cuckoo–magpie coevolutionary system).

Magpies have a Holarctic distribution with the main range in temperate Eurasia (Birkhead 1991). Great spotted cuckoos are distributed only in southern Europe, the Middle East and Africa, and increased their geographical range considerably during the 20th century (Cramp 1985). Thus, cuckoos have probably come into contact with many magpie populations only relatively recently. This interpretation is supported by findings from the fossil record with the great spotted cuckoo being restricted to the Mediterranean basin during the Pleistocene and Holocene, whereas the European cuckoo *Cuculus canorus* (which may serve as an appropriate control species) occurred throughout Europe in the past and present (Tyrberg 1998). Thus, the occurrence of egg rejection in currently allopatric magpie populations is unlikely to be related to a more extensive distribution of the parasite in the recent past, as is probably the case for the European cuckoo–reed warbler system in England (Lindholm 1999).

Study areas

The study was conducted during 1993–95 in 15 magpie populations throughout the species' range in Europe from Spain to Finland and Bulgaria (see Martínez *et al.* 1999 for the location of these populations). Nine populations were within the distributional range of the brood parasitic great spotted cuckoo (seven in Spain, one in France and one in Bulgaria), while six were outside this range. Although, for some sympatric areas, we did not find parasitized nests in the a priori established field area, when checking other magpie nests close to Badajoz and Les Carmargues we did (one and two parasitized nests, respectively; Martínez *et al.* 1999). However, the results did not vary when taking these parasitized nests into account.

Experimental procedure

We tested for host responses to parasitism by performing egg rejection experiments. Briefly, the experimental mimetic eggs were made from plaster of Paris and resembled those of the great spotted cuckoo in weight and colour. As a non-mimetic model egg, we used artificial eggs painted red, with

magpies responding similarly to red quail *Coturnix coturnix* eggs (non-mimetic eggs used in this and other studies) and red eggs of plaster of Paris (Soler *et al.* 1999a). During the laying period of the host, we randomly introduced an experimental egg (mimetic or non-mimetic), and responses were recorded 4–5 days later. Magpies were classified as acceptors when the model egg was incubated in the nest, and rejecters when the egg was absent or the nest abandoned. Sample sizes of performed egg recognition tests varied from nine to 44 for mimetic eggs and from four to 39 for non-mimetic model eggs (Table 2, see later).

Genetic distance estimations

We estimated genetic distances between host populations using microsatellite loci as markers and genotyping 173 magpie nestlings (6–22 from each population). Three loci, namely Ppi 1, Ppi 2 and Ppi 3, were isolated from magpies and the primer sequences designed (Martínez *et al.* 1999). These loci have 11, 16 and 14 alleles, respectively, and a mean observed heterozygosity per population of 0.80, 0.85 and 0.72. All loci were in Hardy–Weinberg (H–W) equilibrium, showing non-significant deviations from H–W equilibrium, as a global exact test (Fisher's test; Rousset & Raymond 1995) for all populations and loci was non-significant ($\chi \leq 86.8$, d.f. = 82, $P = 0.34$). We found no evidence of linkage for all combinations of loci (Fisher's test; Raymond & Rousset 1995; $P > 0.05$). We found significant structure for magpie populations, with F_{ST} values being significantly different from zero for the three loci and over all loci ($F_{ST} = 0.088$ for Ppi 1, $F_{ST} = 0.056$ for Ppi 2, $F_{ST} = 0.076$ for Ppi 3 and $F_{ST} = 0.075$ for all loci). We also detected isolation by distance, with genetic differentiation

between populations (paired $F_{ST}/(1 - F_{ST})$ values) being significantly positively correlated with distance ($r_s = 0.58$, $n = 105$, $P < 0.001$, Mantel test). More detailed information on magpie population structure can be found in Martínez *et al.* (1999). Calculations of allele frequencies and tests were carried out using the computer programs GENEPOP (version 3.1; Raymond & Rousset 1995) and FSTAT (version 1.2; Goudet 1995). We estimated the genetic distances between pairs of populations using the chord distance (Cavalli-Sforza & Edwards 1967), calculated with the computer program GENDIST (PHYLIP package; Felsenstein 1993). Data on the genetic and geographical distances between magpie populations and a discussion of the adopted methodology can be found in Soler *et al.* (1999a).

Statistical procedures

We tested the significance of the relationships between variables by performing autocorrelation analyses using the computer program "Le progiciel R" (Legendre & Vaudor 1991). We chose the methodology of Smouse *et al.* (1986), which is the only technique allowing the calculation of partial correlation coefficients while taking spatial patterns into account (Smouse *et al.* 1986). This calculation was performed by making a matrix of residuals (A') of the relationship between the dependent matrix (A) and one of the independents (C), and another matrix of the residuals (B') of both independent variables (B and C). Later, the program ran a Mantel test between these two residual matrices (A' and B'), with the resulting r being the partial correlation coefficient between A and B controlling for the effect of matrix C . The probabilities of the correlation coefficients were calculated using 1000 permutations.

Table 1 Matrix of differences in parasitism prevalence between magpie populations. Number of nests per study is also shown

Population	Sample size	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
Doñana (1)	52	—	-74.2	-40.2	-68.5	11.5	11.5	9.2	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5
Santa Fe (2)	21		—	33.9	5.7	85.7	85.7	83.4	85.7	85.7	85.7	85.7	85.7	85.7	85.7	85.7
Guadix (3)	85			—	-28.2	51.8	51.8	49.5	51.8	51.8	51.8	51.8	51.8	51.8	51.8	51.8
Laujar (4)	10				—	80.0	80.0	77.7	80.0	80.0	80.0	80.0	80.0	80.0	80.0	80.0
Badajoz (5)	32					—	0.0	-2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calahorra (6)	33						—	-2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Torres del Segre (7)	43							—	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3
Les Camargues (8)	32								—	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Milano (9)	33									—	0.0	0.0	0.0	0.0	0.0	0.0
Bern (10)	49										—	0.0	0.0	0.0	0.0	0.0
Freneuse (11)	38											—	0.0	0.0	0.0	0.0
Sheffield (12)	28												—	0.0	0.0	0.0
Eljovo (13)	34													—	0.0	0.0
Jyväskylä (14)	24														—	0.0
Trondheim (15)	45															—

RESULTS

Differences in the prevalence of parasitism (Table 1) were significantly positively related to genetic distance (Mantel test, $r = 0.29$, $r_{std} = 0.72$, $P = 0.025$), but not to geographical distance among populations (see matrix in Soler *et al.* 1999a) (Mantel test, $r = 0.10$, $r_{std} = 0.18$, $P = 0.25$). Moreover, when using only sympatric host populations, the results did not change (differences in parasitism prevalence vs. genetic distance: Mantel test, $r = 0.50$, $r_{std} = 0.94$, $P = 0.01$; differences in parasitism prevalence vs. geographical distance: Mantel test, $r = 0.04$, $r_{std} = 0.06$, $P = 0.42$). These results indicate that the predictions of an ongoing interaction between magpies and cuckoos were based on defences with a strong genetic component (i.e. rejection of non-mimetic model eggs), but not on defences with a strong geographical component (i.e. rejection of mimetic model eggs).

In accordance with the hypothesis, population differences in the rejection rate of non-mimetic model eggs (Table 2) were positively related to population differences in the prevalence of parasitism after controlling for genetic distances (Mantel test, partial correlation coefficient, $r = 0.37$; $r_{std} = 0.73$, $P = 0.011$) and geographical distances (Mantel test, partial correlation coefficient, $r = 0.38$; $r_{std} = 0.66$, $P = 0.012$) (Fig. 1). However, population differences in the rejection rate of mimetic model eggs (Table 2) were not significantly related to differences in parasitism prevalence after controlling for geographical distances (Mantel test, partial correlation coefficient, $r = 0.11$; $r_{std} = 0.35$, $P = 0.15$) or genetic distances (Mantel test, partial correlation coefficient, $r = 0.09$; $r_{std} = 0.26$, $P = 0.26$) (Fig. 1). Moreover, when only magpie populations in sympatry with the great spotted cuckoo were used ($n = 9$), differences in parasitism prevalence were still positively related to differences in the rejection rate of non-mimetic model eggs after controlling for the effect of geographical distance (Mantel test, partial correlation coefficient, $r = 0.33$; $r_{std} = 0.50$, $P = 0.05$), but not when controlling for the effects of genetic distance (Mantel test, partial correlation coefficient, $r = -0.19$; $r_{std} = -0.36$, $P = 0.14$), nor when using rejection rates of mimetic model eggs (controlling for genetic distance: Mantel test, partial correlation coefficient, $r = -0.24$; $r_{std} = -0.41$, $P = 0.09$; controlling for geographical distance: Mantel test, partial correlation coefficient, $r = -0.15$; $r_{std} = -0.31$, $P = 0.17$).

DISCUSSION

Genetic but not geographical distances among host populations explain the differences in the prevalence of parasitism of the different populations. Thus, populations suffering from a similar level of parasitism are those more genetically related, but not those more proximate. These

Table 2 Matrix of differences in rejection rate of mimetic and non-mimetic eggs between magpie populations. The values above the diagonal are differences in rejection rate of mimetic model eggs (%) and the values below the diagonal are differences in rejection rate of non-mimetic model eggs (%). Sample sizes of tests performed with mimetic (S.S. (M)) and non-mimetic (S.S. (n-M)) model eggs are also shown

Population	S.S. (M)	S.S. (n-M)	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
Doñana (1)	23	25	—	10.2	-20.1	10.2	-0.3	-19.0	5.4	24.7	18.5	17.2	21.3	22.1	32.4	36.3	26.8
Santa Fe (2)	12	10	-16.0	—	-30.3	0.0	-10.4	-29.2	-4.8	14.6	8.3	7.0	11.1	11.9	22.2	26.2	16.7
Guadix (3)	44	39	-5.7	10.3	—	30.3	19.9	1.1	25.5	44.9	38.6	37.3	41.4	42.2	52.5	56.5	47.0
Laujar (4)	6	3	17.3	33.3	23.0	—	-10.4	-29.2	-4.8	14.6	8.3	7.0	11.1	11.9	22.2	26.2	16.7
Badajoz (5)	16	14	5.4	21.4	11.2	-11.9	—	-18.8	5.7	25.0	18.8	17.4	21.5	22.3	32.6	36.6	27.1
Calahorra (6)	16	13	14.8	30.8	20.5	-2.6	9.3	—	24.4	43.6	37.5	36.2	40.3	41.1	51.4	55.4	45.8
Torres del Segre (7)	21	21	12.6	28.6	18.3	-4.8	7.1	-2.2	—	19.4	13.1	11.8	15.9	16.7	27.0	31.0	21.4
Les Camargues (8)	16	16	21.5	37.5	27.4	4.2	16.1	6.7	8.9	—	6.3	-7.6	-3.5	-2.7	7.6	11.6	2.1
Milano (9)	16	16	27.8	43.8	33.5	10.4	22.3	13.0	15.2	6.3	—	-1.3	2.8	3.6	13.9	17.9	8.3
Bern (10)	19	19	26.1	42.1	31.9	8.8	20.7	11.3	13.5	4.6	-1.6	—	4.1	4.9	15.2	19.2	9.7
Freneuse (11)	18	17	31.1	47.1	36.8	13.7	25.6	16.3	18.5	9.6	3.3	5.0	—	0.8	11.0	15.1	5.6
Sheffield (12)	14	14	26.9	42.9	32.6	9.5	21.4	12.1	14.3	5.4	-0.9	0.8	-4.2	—	10.3	14.3	4.8
Eljovo (13)	9	4	59.0	75.0	64.7	41.7	53.6	44.2	46.4	37.5	31.3	32.9	27.9	32.1	—	4.0	-5.6
Jyväskylä (14)	14	16	-3.5	12.5	2.2	-20.8	-8.9	-18.3	-16.1	-25.0	-31.3	-29.6	-34.6	-30.4	-62.5	—	-9.5
Trondheim (15)	6	6	-16.0	0.0	-10.3	-33.3	-21.4	-30.8	-28.6	-37.5	-43.8	-42.1	-47.1	-42.9	-75.0	-12.5	—

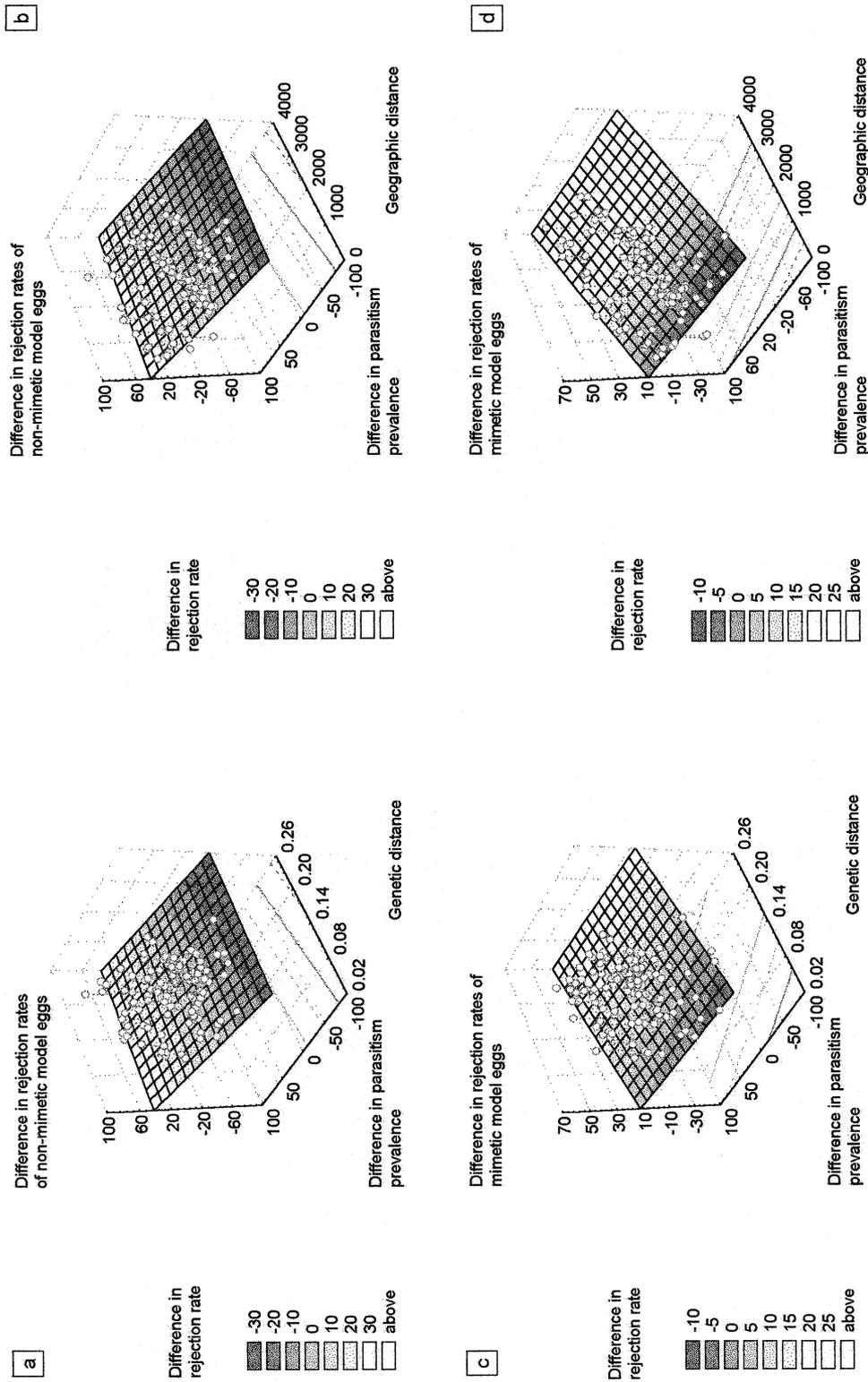


Figure 1 Differences in rejection rates of non-mimetic (a and b) and mimetic (c and d) model cuckoo eggs by black-billed magpies in different populations in relation to parasitism prevalence of the great spotted cuckoo and genetic (a and c) and geographical (b and d) distances among populations. Data points are pairs of magpie populations and the surface is the regression plane.

results, in accordance with the mosaic theory of coevolution (Thompson 1994), imply that there are hotspots, occurring relatively independently of geographical location, from which phenotypes (i.e. rejecters, acceptors) are exchanged with other host populations. Moreover, this finding explains the absence of a geographically structured differentiation among populations in sympatry, found previously (Martínez *et al.* 1999).

We have previously demonstrated that genetic distance explains a significant proportion of variance in magpie rejection behaviour of non-mimetic model eggs across populations (Soler *et al.* 1999a). Here, we have shown that the prevalence of parasitism also explains a significant proportion of the variance in rejection rate of non-mimetic model eggs. However, as parasitism prevalence and genetic distances are significantly related (see “Results” section), it is difficult to distinguish between the effects of gene flow and current selection. One estimate of the relative importance of current selection can be inferred from the partial correlation between differences in the rejection rate of non-mimetic model eggs and differences in parasitism prevalence, while controlling for genetic distance between populations.

The fact that the variation in the rejection rate of non-mimetic model eggs is significantly explained by the variation in parasitism rate, after controlling for the effect of both genetic and geographical distances, can be interpreted as evidence of genetic variation in rejection not due to gene flow, but to current selection pressures from cuckoo parasitism. These observations provide evidence of current coevolutionary interactions in the European magpie population. By correcting for genetic distances (i.e. gene flow) and geographical distances among populations, we are rendering the possible effect of selection pressures by parasitism in the geographically structured host population independent of gene flow.

Coevolution between hosts and parasites implies changes in the phenotype of two or more interacting species caused by exploitation by one species, the evolution of counter-defences by the other species and the evolution of novel ways of exploitation by the first species. Hence, differences in host and parasite behaviour among populations arise from the accumulation of microevolutionary changes in such responses on a short time scale. Consistent with this idea, we have found, in a long-term study of the magpie–great spotted cuckoo system in Guadix, that temporal changes in the rate of parasitism within plots are followed by parallel changes in host rejection of cuckoo eggs (Soler *et al.* 1998; Soler & Soler 2000), but there is, as yet, no evidence of microevolutionary change in cuckoo egg types.

Genetics, geography and ecology could be confounded in the analyses of genetic and geographical distances in relation to differences in parasitism and rejection rates. Distant populations are likely to include sympatric and allopatric

comparisons, and they are also expected to be genetically most distant and most different in rejection ability and parasitism prevalence. However, gene flow was significantly greater in sympatric than in allopatric host populations (Martínez *et al.* 1999), and genetic and geographical distances were not significantly related in these sympatric populations (Soler *et al.* 1999a). Even in sympatric host populations in which genetic differentiation was greatly reduced, we found a positive relationship between parasitism pressure and rejection rate of non-mimetic model eggs, while controlling for geographical distances, but not while controlling for genetic distances (Fig. 1). Therefore, current interactions between cuckoo and magpie seem to be important when using a meta-population approach. If we assume that the recognition of non-mimetic model eggs is genetically determined, as indicated by a strong relationship between rejection and genetic distance (Soler *et al.* 1999a), and that the costs of this ability are very low, because recognition errors are uncommon (J. J. Soler *et al.* unpublished data), such phenotypes will be preserved in allopatric magpie populations if no negative pleiotropic effects occur. Magpie populations sympatric with the cuckoo would act as source populations of rejecter phenotypes migrating to allopatric sink populations, while allopatric populations would act as sources of acceptor phenotypes for sympatric sink populations. In sympatric populations with a high prevalence of parasitism, rejecter phenotypes are selectively favoured, and selection in these coevolutionary hotspots will create ongoing coevolutionary interactions between the cuckoo and the magpie meta-population, because the frequency of rejecter phenotypes is increasing due to this ongoing interaction.

ACKNOWLEDGEMENTS

We are indebted to F. Cezilly, J. Clobert, P. Fitze, A. Jacot, J. Kilpimaa, J.P. Lena, F. de Lope, B. Milchev, J. Minguela, D.R. Opdahl, D. Parrot, H. Richner, N. Saino, A. Sanchez and C. Zamora for their help in data collection. D. Dawson helped with cloning the magpie microsatellite loci. T. Burke allowed J.G.M. to stay and work in his laboratory. J. Blondel advised us on palaeontology. M. Hochberg, J. Shykoff, G. Sorci and J.N. Thompson kindly provided critical comments. J.J.S. and J.G.M. were supported by EC postdoctoral fellowships (HCM programme), and M.S. and A.P.M. by the Human Capital and Mobility Programme of the European Community.

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BIOSKETCH

Juan José Soler and his research group have studied coevolutionary interactions between brood parasites and their hosts for many years. He is interested in the evolutionary ecology of parasite–host systems, in particular how environmental conditions affect the evolution of defences and counter-defences, and how parasitism influences life history and sexually selected traits of hosts.

Editor, J. Burdon

Manuscript received 22 February 2001

First decision made 4 April 2001

Manuscript accepted 28 May 2001