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GENETIC AND GEOGRAPHIC VARIATION IN REJECTION BEHAVIOR OF CUCKOO EGGS BY EUROPEAN MAGPIE POPULATIONS: AN EXPERIMENTAL TEST OF REJECTER-GENE FLOW

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Abstract.—Host responses toward brood parasitism have been shown to differ among populations depending on the duration of sympatry between host and parasite, although populations not currently parasitized show rejection behavior against parasitic eggs. The persistence of rejection behavior in unparasitized host populations and rapid increases of rejection rate in parasitized ones have sometimes been explained as the result of gene flow of rejecter genes from sympatry to allopatry (rejecter-gene flow hypothesis). We present data on the rejection behavior of magpies (*Pica pica*), the main European host of the great spotted cuckoo (*Clamator glandarius*), in 15 populations (nine sympatric, six allopatric) across their distribution range in Europe. Rejection rates of mimetic and nonmimetic model eggs were significantly higher in sympatric than in allopatric magpie populations, although differences in rejection rate of both mimetic and nonmimetic model eggs between magpie populations were significantly correlated even after controlling for phylogenetic effects, with differences between sympatric and allopatric magpie populations being larger for mimetic than for nonmimetic model eggs. Differences in rejection of mimetic model eggs were related to both genetic and geographic distances between populations, but differences in rejection rate of nonmimetic model eggs were unrelated to these distances. However, when comparing only sympatric populations, differences in rejection rate of both mimetic and nonmimetic model eggs were related to geographic distances. A multiple autocorrelation analysis revealed that differences among populations in rejection rates of mimetic model eggs had a strong geographic component, whereas the main component of rejection rate of nonmimetic model eggs was genetic rather than geographic. These results support the rejecter-gene flow hypothesis. We discuss differences in rejection rates of mimetic and nonmimetic model eggs that suggest the egg-recognition ability of the host is genetically based, but is affected by a learning process for fine tuning of recognition.

Key words.—Brood parasitism, *Clamator glandarius*, coevolution, gene flow, host defense, *Pica pica*.

The extent of gene flow among populations is considered an important factor for explaining evolutionary processes in general (Slatkin and Barton 1989; Avise 1994; Dybdahl and Lively 1996). For example, in a host-parasite system, high parasite gene flow will tend to counteract local host adaptation (Slatkin 1987), expose parasites to a mosaic of selection (Thomson 1994), and restore variation that is lost by recurrent extinction of local populations in a metapopulation (Frank 1991, 1993). Because mainly rejecters reproduce successfully in parasitized populations and, therefore, are able to disperse to other populations, extensive gene flow between host populations may result in the establishment of defense genes against the parasite in a host population before it becomes parasitized (Soler and Møller 1990; Briskie et al. 1992; Lotem and Rothstein 1995). However, low migration by both parasite and host should lead to high degrees of local adaptation and perhaps host-race formation by the parasite (Dybdahl and Lively 1996; Gibbs et al. 1996, 1997).

Avian brood parasites lay their eggs in nests of other species (hosts), which incubate and raise the parasitic offspring. Moreover, brood parasites provoke a major reduction in the breeding success of their hosts, being nil in some cases (Rothstein 1990). In this scenario, host defense against brood parasitism is of selective advantage and hosts that recognize and reject parasitic eggs from their nests have genes that quickly spread in the host population (Rothstein 1975). However, the evolution of counter-defenses by brood parasites, such as egg mimicry, counteracts host defense, thereby increasing the re-

productive success of parasites (Rothstein 1990). The evolution of host defenses, especially the recognition and rejection of parasitic eggs, has been intensely studied in recent years using experimental and theoretical approaches (Kelly 1987; Soler and Møller 1990; Briskie et al. 1992; Takasu et al. 1993). These studies emphasize several aspects of the host-parasite relationship that are important for understanding the evolution of host defenses and parasite counter-defenses: duration of sympatry, effect of parasitism on host reproductive success, host and parasite population density, and parasitism rate. A few experimental studies have shown that responses against parasitism differ among populations of the same host species depending on the duration of sympatry between host and parasite (Soler and Møller 1990; Briskie et al. 1992) and that populations not currently parasitized show rejection behavior against parasitic eggs (Davies and Brooke 1989; Briskie et al. 1992). The persistence of rejection behavior in unparasitized host populations, and the rapid increase of rejection rate in parasitized populations have sometimes been explained as the result of gene flow of rejecter genes from sympatric to allopatric populations. Thus, recently parasitized host populations may hold rejecter genes before brood parasites start to exploit this population (rejecter-gene flow hypothesis; Soler and Møller 1990; Briskie et al. 1992; Lotem and Rothstein 1995).

The level of host defense (egg recognition and rejection) in sympatry with a brood parasite is higher than the level of host defense in allopatry. Davies and Brooke (1989) pointed

out that meadow pipits (*Anthus pratensis*) and white wagtails (*Motacilla alba*) in Iceland, where they are geographically isolated from European cuckoos (*Cuculus canorus*), show much less rejection of dissimilar eggs than do the parasitized populations of these species in Britain. Soler and Møller (1990) showed that a magpie (*Pica pica*) population in ancient sympatry with its brood parasite, the great spotted cuckoo (*Clamator glandarius*), had a higher egg recognition and rejection rate than in a magpie population recently colonized by the great spotted cuckoo, and that both sympatric magpie populations showed a higher level of defense than an allopatric population. Finally, Briskie et al. (1992) reported that populations of American robins (*Turdus migratorius*) and yellow warblers (*Dendroica petechia*) in sympatry with brownheaded cowbirds (*Molothrus ater*) presented higher levels of defense than populations of these species in allopatry. Davies and Brooke (1989) and Briskie et al. (1992) found host defense in areas of allopatry with a brood parasite that could be explained by gene flow between host populations. Although Soler and Møller (1990) did not detect any rejection behavior in the very distant allopatric Uppsala magpie population, it appeared in a recently parasitized magpie population; instead these experimental results were suggested to arise from gene flow between host populations.

However, although gene flow between host populations of a brood parasite has been invoked to explain host rejection behavior and its rapid increase, when host populations are in sympatry with the brood parasite (see above), no tests of the rejecter-gene flow hypothesis have been made until now. Using a wide range of host populations, both in sympatry and allopatry with a brood parasite, we assess host rejection behavior to test predictions from the hypothesis that gene flow is responsible for the occurrence of egg rejection in host populations in allopatry (rejecter-gene flow hypothesis, hypothesis 1). If gene flow occurs, as is the case for magpie populations in this study (Martínez et al. 1999), we should expect that genetically and geographically nearby magpie populations would show a more similar rejection rate than genetically and geographically separated magpie populations.

The ability of hosts to recognize and reject cuckoo eggs is generally accepted to have a genetic basis (Rothstein 1990), and all models of host–brood parasite coevolution are based in this assumption (e.g., Kelly 1987; Takasu et al. 1993; Haraguchi and Seno 1995). However, recent studies have revealed variability in rejection behavior of the same individual host due to age (Lotem et al. 1992, 1995; Lotem 1993) or ecological factors (Alvarez 1996), thereby suggesting a sort of imprinting process during the first breeding attempt or adjustment of the response to experimental cuckoo eggs to ecological factors such as the presence of cuckoos in the area (Alvarez 1996). However, a continuous learning process (i.e., not only during the first breeding attempt) has been suggested to explain the rapid increase in rejection rate in a host population of the great spotted cuckoo (Soler et al. 1994) and in two European cuckoo hosts, the azure-winged magpie (*Cyanopica cyanea*; Nakamura 1990) and the reed warbler (*Acrocephalus scirpaceus*; Brooke et al. 1998). If learning occurs, recognition ability will increase between years independently of the generation time of the host species. If the ability to recognize foreign eggs and rejection of such eggs

by the host are genetically determined, that is, not based on learning of the appearance of the host's own eggs (hypothesis 2), we expect that only genetic distance would explain differences in rejection rate between different host populations, whereas geographic distances would not explain additional variance.

If a learning process is needed to recognize and reject foreign eggs by the host (hypothesis 3), we should expect that only hosts in sympatry with brood parasites would be able to recognize and reject model cuckoo eggs. However, migration of adult hosts from sympatric to allopatric areas would change the prediction to an expected positive relationship between differences in rejection rate and geographic distance of host populations, after controlling for genetic distances.

We tested these hypotheses and predictions by studying the rejection behavior of mimetic and nonmimetic model eggs in relation to genetic and geographic distances in 15 European magpie populations (Fig. 1), the main host of the great spotted cuckoo in Europe. Nine of the studied magpie populations were sympatric with the cuckoo and six were allopatric. We also discuss the hypothesis that in addition to a genetic basis a learning process is necessary for the recognition of mimetic eggs, thereby explaining previously found differences in rejection rates of mimetic and nonmimetic model eggs (e.g., Davies and Brooke 1989; Soler and Møller 1990; Soler 1990; Soler et al. 1994; Soler et al. 1998a).

MATERIALS AND METHODS

The study was conducted during 1992–1995 in 15 populations throughout the range of the magpie in Europe. The experimental recognition tests were made in approximately 30 magpie nests, but predation before recording the response of the magpie decreased the number of experimental nests in some areas (see Table 1 for number of experimental magpie nests in each study area). To perform genetic analyses of magpie populations, in every successful nest a drop of blood was taken from only the heaviest chick and kept in ethanol until molecular analysis.

Recognition Tests

For the recognition experiments we used two kinds of model eggs, mimetic and nonmimetic. Mimetic eggs were made by filling molds of great spotted cuckoo eggs with plaster of Paris. Once dry, the model egg was painted with a color similar to the background color of great spotted cuckoo eggs. Subsequently, we added brown spots with distribution and size resembling those of real cuckoo eggs. Finally, the model egg was covered with a thin layer of lacquer, which simulates the sheen of real cuckoo eggs. Also, the mass of model eggs was similar to the mass of real cuckoo eggs (see Soler and Møller 1990). For nonmimetic eggs we used quail (*Coturnix coturnix*) eggs painted using acrylic red paint, differing from the magpie and great spotted cuckoo eggs in size (mean volume of magpie eggs = $3.16 \text{ cm}^3 \pm 0.02$ [SE], $n = 201$; mean volume of mimetic model eggs = $2.94 \text{ cm}^3 \pm 0.06$, $n = 14$; mean volume of quail egg = $4.22 \text{ cm}^3 \pm 0.11$, $n = 16$; data from Les Camargues), background color, and spot size and distribution. Each model egg was used only once. The results
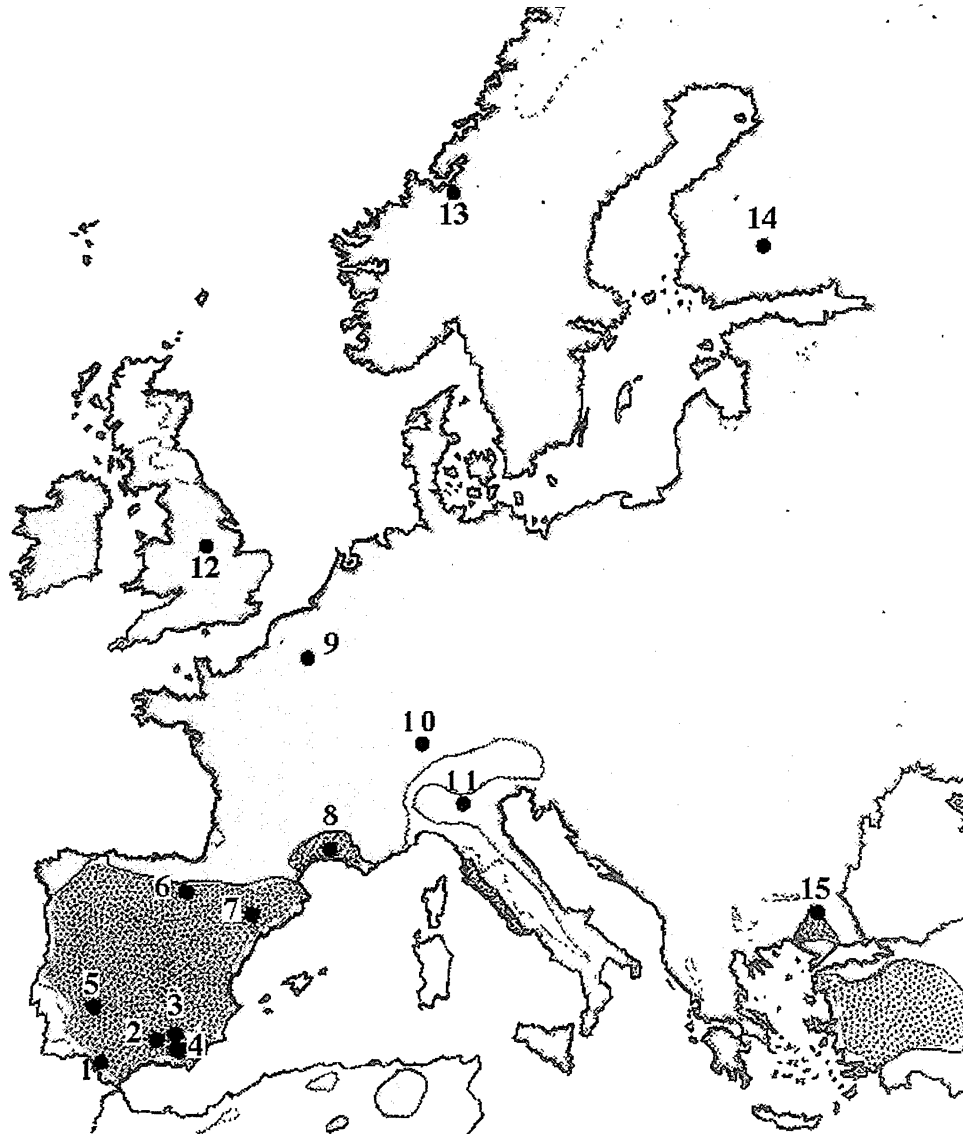
FIG. 1. Magpie populations included in this study: Doñana (1), Santa Fe (2), Guadix (3), Laujar (4), Badajoz (5), Calahorra (6), Torres del Segre (7), Les Camargues (8), Freneusse (9), Bern (10), Milano (11), Sheffield (12), Trondheim (13), Jyväskylä (14), and Eljovo (15). The gray area corresponds to the distribution range of the magpie, and the dotted area to the distribution range of the great spotted cuckoo.

of one experiment carried out in a magpie population in southern Spain indicated that magpies responded identically to nonmimetic model eggs made of plaster and quail eggs, both painted red (eggs made with plaster, rejection rate = 91.7%, $n = 12$; red quail egg, rejection rate 90.0%, $n = 10$; Fisher exact test, $P = 1$; Soler et al. 1998b).

We introduced the model eggs in the host nests during the egg-laying period of the magpie. Between four and seven days later (which is sufficient to detect the response of magpies to cuckoo eggs; Soler and Møller 1990) we revisited experimental magpie nests and scored the magpies as "acceptors" if the experimental model egg was still in the nest, "ejecters" if the model egg was no longer present, or "deserters" if the eggs were abandoned in the nest. Although both ejection and abandoning a cuckoo egg in the nest are supposed to be related to cuckoo-egg recognition by the host,

and are thus defined as egg rejection behavior (e.g., see Johnsgard 1997), nest desertion could also be related to selection pressures other than that imposed by brood parasites. Perhaps magpies were more likely to abandon the eggs if disturbed during the study and more likely to eject the cuckoo model egg if undisturbed. If this was the case, nest predation and nest parasitism would be confounded. However, predation rate was not significantly related to abandoning rate in experiments with nonmimetic model eggs ($r = 0.17$, $t = 0.63$, $n = 15$ populations, $P = 0.54$) or experiments with mimetic model eggs ($r = 0.38$, $t = 1.49$, $n = 15$, $P = 0.16$). Moreover, the frequency of nest desertion was very low (3.1%, $n = 483$) and was not significantly related to rejection rate of mimetic model eggs ($r = -0.22$, $t = 0.82$, $n = 15$, $P = 0.43$) or to that of nonmimetic model eggs ($r = -0.29$, $t = 1.11$, $n = 15$, $P = 0.29$). Thus, because we investigated variation

TABLE 1. Location, parasitism rates, and rejection rates of mimetic and nonmimetic model eggs of magpie populations sympatric or allopatric with the great spotted cuckoo. Mean (SD) genetic variability for each of the studied magpie populations are also shown.

Study area	Latitude	Longitude	Population	Parasitism (%) (N)	Rejection rates (%) (N)		Mean sample size per locus	Mean number of alleles per locus	Heterozygosity	
					Nonmimetic	Mimetic			Observed	Expected
Doñana	37°08'N	6°56'W	Sympatric	11.5 (52)	84.0 (25)	43.5 (23)	18.7	8.67 (2.08)	0.84 (0.11)	0.83 (0.06)
Santa Fe	37°11'N	3°43'W	Sympatric	85.7 (21)	100 (10)	33.3 (12)	6.0	4.67 (1.15)	0.78 (0.09)	0.77 (0.07)
Guadix	37°18'N	3°11'W	Sympatric	51.8 (85)	89.7 (39)	63.6 (44)	17.0	8.33 (2.15)	0.80 (0.07)	0.84 (0.05)
Laujar	37°00'N	2°52'W	Sympatric	80.0 (10)	66.7 (3)	33.3 (6)	6.0	6.00 (2.64)	0.77 (0.07)	0.85 (0.08)
Badajoz	38°52'N	6°56'W	Sympatric	0.0 (32)	78.6 (14)	43.8 (16)	22.0	10.00 (2.64)	0.92 (0.05)	0.86 (0.06)
Calahorra	42°18'N	2°02'W	Sympatric	0.0 (33)	69.2 (13)	62.5 (16)	12.3	9.00 (1.00)	0.78 (0.05)	0.87 (0.05)
Torres del Segre	41°32'N	0°31'E	Sympatric	2.3 (43)	71.4 (21)	38.1 (21)	6.3	6.33 (0.58)	0.74 (0.31)	0.87 (0.02)
Les Camargues	43°40'N	4°37'E	Allopatric	0.0 (32)	62.5 (16)	18.8 (16)	13.3	8.33 (2.31)	0.82 (0.08)	0.86 (0.06)
Milano	45°28'N	9°11'E	Allopatric	0.0 (33)	56.3 (16)	25.0 (16)	9.3	6.67 (2.08)	0.85 (0.13)	0.81 (0.03)
Bern	46°56'N	7°27'E	Allopatric	0.0 (49)	57.9 (19)	26.3 (19)	6.3	5.67 (0.58)	0.84 (0.02)	0.80 (0.07)
Freneusse	49°00'N	2°30'E	Allopatric	0.0 (38)	52.9 (17)	22.2 (18)	9.0	5.33 (0.58)	0.67 (0.39)	0.76 (0.06)
Sheffield	53°23'N	1°30'W	Allopatric	0.0 (28)	57.1 (14)	21.4 (14)	6.3	4.33 (2.08)	0.79 (0.18)	0.73 (0.17)
Eljovo	42°09'N	26°30'E	Sympatric*	0.0 (34)	25.0 (4)	11.1 (9)	6.0	6.33 (2.31)	0.78 (0.19)	0.80 (0.14)
Jyväskylä	62°15'N	26°10'E	Allopatric	0.0 (24)	87.5 (16)	7.1 (14)	7.7	6.00 (1.73)	0.70 (0.06)	0.75 (0.10)
Trondheim	63°24'N	10°18'E	Allopatric	0.0 (45)	100.0 (6)	16.7 (6)	11.3	4.67 (0.58)	0.77 (0.14)	0.76 (0.05)

* Although the Eljovo magpie population is within the limit of the distribution of the great spotted cuckoo, careful checking of the area and surroundings (more than 20 km) did not reveal any great spotted cuckoo adults or parasitized magpie nests (B. Milchev, pers. comm.). Therefore, although we considered this magpie population sympatric with the great spotted cuckoo, we also analyzed the data considering Eljovo an allopatric population.

in ability to recognize foreign eggs by different host populations, we lumped ejector and deserter individuals. The conclusions would not have changed if the analyses instead were based on ejection rates.

Differences in intraspecific nest parasitism between magpie populations also could potentially confound the analyses. However, intraspecific parasitism is rare in birds in general, with less than 3% of 165 bird species being studied with molecular techniques having any recorded cases (A. P. Møller, unpublished). Moreover, in a study of two magpie populations (in England and in Spain), no case of intraspecific nest parasitism was recorded (Parrot 1995).

Population Genetic Analyses

We calculated genetic distances between host populations using microsatellite loci as markers (Bruford and Wayne 1993; Jarne and Lagoda 1996). Three loci, *Ppi 1, Ppi 2,* and *Ppi 3* were isolated from magpies and primer sequences were 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.

DNA was extracted from blood following standard protocols (Bruford et al. 1992). A total of 173 magpies were genotyped (six to 22 from each population). For more details on genotyping procedures see Martínez et al. (1998). Information on sample sizes, number of alleles, and heterozygosity is given in Table 1. All loci were in Hardy-Weinberg equilibrium, showing non-significant deviations from equilibrium (Markov chain exact test, $P > 0.05$) for all combinations of populations and loci, except for the Freneusse population for loci *Ppi 3*, which showed significant heterozygote deficiency (Mann-Whitney U-test, $P = 0.03$; Rousset and Raymond 1995). However, a global exact test (Fisher test, Rousset and Raymond 1995) for all populations and loci was nonsignificant ($\chi^2 = 86.8$, df = 82, $P = 0.34$). We also tested the loci for linkage disequilibrium using a Fisher's test (Raymond and Rousset 1995) and found no evidence of linkage for all combinations of loci ($P > 0.05$). 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 (Mantel test, $r_S = 0.58$, $n = 105$, $P < 0.001$). 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 program GENEPOP (version 3.1, Raymond and Rousset 1995) and FSTAT (version 1.2, Goudet 1995). We estimated genetic distances between pairs of populations using the chord distance (Cavalli-Sforza and Edwards 1967), calculated with the computer program GENDIST (PHYLIP package, Felsenstein 1993). This and other traditional genetic distance measures are based on the infinite alleles model (IAM, Ohta and Kimura 1973) and assume that genetic drift is the main factor responsible for changes in genotype frequencies. However, microsatellites might evolve following a stepwise mutation process (SMM; Slatkin 1995), and new

statistics have been developed specifically to meet these assumptions (Goldstein et al. 1995; Shriver et al. 1995). Although the exact nature of the mutation process is still not clear (Deka et al. 1995), whatever mutation model is appropriate for microsatellites, IAM-based statistics such as Cavalli-Sforza and Edwards' (1967) chord distance or Nei's distance (Nei 1972) can be used in cases where the time scale of interest is sufficiently short for mutation to play a minor role (Slatkin 1995). Actually, Paetkau et al. (1997) have shown empirically that IAM-based genetic distances outperform statistics specifically designed for microsatellites such as Goldstein's $(\sigma\mu)^2$ (Goldstein et al. 1995), when applied to studies of fine-scale population structure. Several other population surveys in different species have shown a high efficiency of microsatellites in estimating population differentiation and genetic distances using IAM-based approaches (Bowcock et al. 1994; Estoup et al. 1996; Perez-Lezaun et al. 1997).

Statistical Analyses

We calculated rejection rates of mimetic and nonmimetic model eggs for each magpie population. Distances between populations were measured in kilometers on a map. We constructed a genetic distance matrix, a geographic distance matrix, and a matrix of differences in rejection rates of mimetic and nonmimetic model eggs between populations. To control for phylogenetic effects, we used autocorrelation analysis (Foster and Cameron 1996; for further information on the use of autocorrelation analysis to remove phylogenetic effects at the species level, see also Gittleman and Luh 1992; Edwards and Kot 1995, and references therein), because the use of population phylogenies is not recommended when gene flow between populations is high (Foster and Cameron 1996), as in our case (Martínez et al. 1999), and the Mantel test corrects for the nonindependence among elements in a pairwise matrix. To perform autocorrelation analysis we used the computer program "Le progiciel R" (Legendre and Vaudor 1991). Using the import-export section, we transformed the distance matrix into binary files (which are required by the computer program) and performed a multiple autoregression analysis using the Mantel section of the computer program. We chose the methodology of Smouse et al. (1986), which is the only methodology allowing calculation of partial correlation coefficients (Legendre and Vaudor 1991). This calculation is performed making a matrix with residuals (A') of the relationship between the dependent matrices (A) and one of the independents (B), and another matrix with 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. Here we report the Mantel statistic R, which is the correlation coefficient, and (ii) the standardization of R proposed by Hubert (1985), which varies between $+1$ and -1 and consists of a real value of R produced by the extreme values (maximum and minimum) obtained from the permutations (Legendre and Vaudor 1991). Probabilities of the correlation coefficients were calculated using 1000 permutations. By using partial autocorrelation coefficients, we were
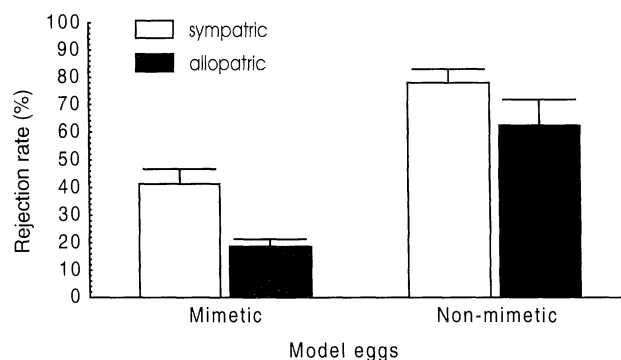

FIG. 2. Rejection rates of mimetic and nonmimetic model eggs in sympatric (white columns) and allopatric (black columns) magpie populations. Values are means, bars represent standard errors.

able to distinguish between genetic and geographic effects on differences in rejection rates of magpie populations.

RESULTS

Parasitism rates, rejection rates of mimetic and nonmimetic model eggs, and geographic locations of magpie populations are reported in Table 1, as well as information on whether magpie populations are in sympatry or allopatry with the great spotted cuckoo. Only three magpie populations located in southeastern Spain (Granada and Almería provinces) experienced high levels of parasitism from the great spotted cuckoo; except for these and the Doñana magpie population, all other sympatric populations had few parasitized nests (Table 1).

The rejection rates of mimetic model eggs were significantly higher in sympatric than in allopatric magpie populations when based on estimates of magpie population as datapoints (Fig. 2; Eljovo as sympatric magpie population: populations in sympatry, mean = 37.8, n = 9; populations in allopatry, mean = 19.8, n = 6, t = 2.34, df = 13, P = 0.04; Eljovo as allopatric magpie population: t = 3.49, df = 13, P = 0.004). A similar result was found when calculations were based on the rejection behavior of individual magpies (Eljovo as sympatric magpie population: sympatric magpies, rejection rate = 42.9%, n = 147; allopatric magpies, rejection rate = 27.2%, n = 103; χ^2 = 6.43, df = 1, P = 0.01; Eljovo as allopatric magpie population: sympatric magpies, rejection rate = 44.9%, n = 138; allopatric magpies, rejection rate = 25.9%, n = 112, χ^2 = 9.68, df = 1, P = 0.002). Rejection rates of nonmimetic model eggs were higher in sympatric than allopatric populations, but not significantly so (Fig. 2; Eljovo as sympatric magpie population: populations in sympatry, mean = 71.9, SE = 7.5, n = 9; populations in allopatry, mean = 68.6, SE = 8.9, n = 6; t = 0.30, df = 13, P = 0.77; Eljovo as allopatric magpie population: t = 1.55, df = 13, P = 0.14). When analyzing individual magpie rejection behavior as independent datapoints, we found significant differences (Eljovo as sympatric magpie population: sympatric magpies, rejection rate = 79.6%, n = 132; allopatric magpies, rejection rate = 65.4%, n = 101; χ^2 = 5.90, df = 1, P = 0.015; Eljovo as allopatric magpie population: sympatric magpies, rejection rate = 81.25%, n = 128; allopatric mag-

TABLE 2. Comparison between rejection rates of mimetic and nonmimetic model eggs of magpies from populations suffering a high, low, and no parasitism rate (see text for the magpie populations included in these three groups) from the great spotted cuckoo. We report results including or excluding the Eljovo population from the sympatric magpie group. Values reported are percentage of rejecter magpie nests; (1) and (2) refer to different magpie populations in the comparisons.

| | Rejection rates (%) (N) | | χ^2_1 | P |
	(1)	(2)		
Mimetic model eggs				
High (1) versus low (2) parasitism rate populations	51.8 (85)	37.2 (78)	3.50	0.06
(Eljovo as allopatric population)	51.8 (85)	40.6 (69)	1.91	0.17
High (1) versus no (2) parasitism rate populations	51.8 (85)	20.7 (87)	18.0	0.00002
(Eljovo as allopatric population)	51.8 (85)	19.8 (96)	20.3	0.00001
Low (1) versus no (2) parasitism rate populations	37.2 (78)	20.7 (87)	5.50	0.019
(Eljovo as allopatric population)	40.6 (69)	19.8 (96)	8.52	0.004
Nonmimetic model eggs				
High (1) versus low (2) parasitism rate populations	88.3 (77)	67.7 (68)	9.17	0.0025
(Eljovo as allopatric population)	88.3 (77)	70.3 (64)	7.11	0.008
High (1) versus no (2) parasitism rate populations	88.3 (77)	64.8 (88)	12.4	0.0004
(Eljovo as allopatric population)	88.3 (77)	63.3 (79)	13.2	0.0003
Low (1) versus no (2) parasitism rate populations	67.7 (68)	64.8 (88)	0.14	0.71
(Eljovo as allopatric population)	70.3 (64)	63.3 (79)	0.78	0.38

pies, rejection rate = 63.81%, n = 105, χ^2 = 8.98, df = 1, P = 0.003).

When magpie populations were classified as (1) suffering from a high parasitism rate (Doñana, Santa Fe, Guadix, and Laujar); (2) a low parasitism rate (Badajoz, Calahorra, Torres del Segre, Les Camargues, and Eljovo); and (3) no parasitism (Milano, Bern, Freneusse, Sheffield, Jyväskylä, and Trondheim), comparisons revealed no significant differences in rejection rates of mimetic model eggs between frequently and rarely parasitized magpie populations (Table 2). Magpie populations in high and low parasitism areas (which were all sympatric with the great spotted cuckoo) rejected mimetic eggs significantly more frequently from their nests than magpies in areas with no parasitism (which were all allopatric with the great spotted cuckoo; Table 2). Magpies from populations suffering from a high parasitism rate rejected nonmimetic eggs more frequently than those from populations suffering a low parasitism rate or no parasitism (Table 2). No significant differences appeared when comparing magpies from rarely parasitized and unparasitized populations (Table

2). These results were independent of whether the Eljovo population was classified as a rarely parasitized population or an allopatric population (Table 2).

Differences in rejection rate of mimetic and nonmimetic eggs were significantly related among magpie populations (Mantel test, r = 0.33, r_{std} = 0.93, P = 0.003), even when controlling for phylogenetic effects (relationships between matrix of differences in rejection behavior of mimetic and nonmimetic model eggs controlled for genetic distances; Mantel's test, partial correlation coefficient r = 0.30, r_{std} = 0.73, P = 0.007). Therefore, although magpie rejection behavior appeared to be different for mimetic and nonmimetic eggs, the ability of magpies to recognize mimetic and nonmimetic model eggs covaried among areas.

The analysis of matrices of genetic and geographic distances (Table 3) in relation to the matrix of differences in rejection rates of mimetic and nonmimetic model eggs showed that differences in rejection of mimetic model eggs were significantly related to both genetic and geographic distances between populations (Mantel test, r = 0.25, r_{std} =

TABLE 3. Matrix of genetic and geographical distances between magpie populations. The values above the diagonal are geographic distances (km) and the values below the diagonal are genetic distances.

Populations	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
Doñana (1)	—	225	300	300	225	700	800	1200	1600	1575	1450	1850	2900	3550	3150
Santa Fe (2)	.138	—	60	75	310	580	615	1000	1450	1400	1400	1750	2600	3400	3000
Guadix (3)	.050	.117	—	25	385	560	575	950	1400	1375	1350	1750	2550	3350	3000
Laujar (4)	.083	.164	.081	—	415	585	590	975	1400	1400	1375	1775	2550	3375	3025
Badajoz (5)	.038	.117	.039	.071	—	565	700	1100	1500	1450	1325	1650	2850	3350	2900
Calahorra (6)	.057	.148	.072	.091	.046	—	225	550	950	900	775	1200	2325	2825	2400
Torres del Segre (7)	.107	.168	.099	.106	.079	.094	—	375	875	800	775	1250	2150	2775	2450
Les Camargues (8)	.063	.131	.073	.148	.071	.082	.101	—	400	450	625	1100	1750	2425	2175
Milano (9)	.152	.126	.136	.163	.125	.110	.173	.112	—	200	650	1125	1425	2100	1950
Bern (10)	.183	.137	.119	.170	.135	.110	.140	.117	.078	—	450	900	1575	2025	1800
Freneusse (11)	.190	.209	.156	.181	.160	.128	.134	.151	.159	.090	—	625	2025	2050	1650
Sheffield (12)	.200	.227	.174	.243	.217	.178	.211	.165	.174	.161	.161	—	2350	1825	1375
Eljovo (13)	.162	.204	.128	.215	.143	.126	.148	.131	.116	.098	.132	.139	—	2175	2500
Jyväskylä (14)	.195	.210	.178	.222	.168	.112	.144	.156	.152	.119	.143	.151	.108	—	800
Trondheim (15)	.193	.145	.157	.202	.142	.154	.124	.145	.175	.139	.159	.189	.187	.150	—

0.64, $P = 0.016$; and $r = 0.35$, $r_{std} = 0.998$, $P = 0.002$, respectively), but differences in rejection rate of nonmimetic model eggs were not significantly related to genetic and geographic distances, in accordance with hypothesis 1 (genetic distances matrix: Mantel test, $r = 0.17$, $r_{std} = 0.45$, $P = 0.077$; geographic distances matrix: $r = -0.04$, $r_{std} = -0.11$, $P = 0.36$, respectively). However, genetic and geographic distances covaried (Mantel test, $r = 0.47$, $r_{std} = 1$, $P = 0.001$), and a multiple autocorrelation analysis allowed us to distinguish between the effects of genetic and geographic distances on the difference in rejection behavior of magpie populations. Differences in rejection rates of mimetic model eggs depended significantly on geographic distance, but not on genetic distance, in accordance with hypothesis 3 (Mantel test, partial correlation coefficient of genetic distances $r = 0.11$, $r_{std} = 0.33$, $P = 0.18$; partial correlation coefficient of geographic distances $r = 0.27$, $r_{std} = 0.91$, $P = 0.007$). Opposite results were obtained for differences in rejection rates of nonmimetic model eggs in accordance with hypothesis 2 (Mantel test, partial correlation coefficient of genetic distances $r = 0.21$, $r_{std} = 0.54$, $P = 0.043$; partial correlation coefficient of geographic distances $r = -0.13$, $r_{std} = -0.35$, $P = 0.38$). In conclusion, rejection rates of mimetic model eggs had a strong geographic component, whereas the main component of rejection rates of nonmimetic model eggs was genetic.

Genetics, geography and ecology could be confounded in the analyses of matrices of genetic and geographic distances in relation to matrices of differences in rejection rates. Distant populations are likely to include sympatric and allopatric comparisons, as well as to be genetically the most distinct. Trying to solve this potential problem, we reanalyzed the data by only including sympatric populations ($n = 9$). In accordance with previous results, differences in rejection rates of mimetic model eggs were significantly related to geographic distances (Mantel test, $r = 0.61$, $r_{std} = 0.87$, $P = 0.008$), but not to genetic distances (Mantel test, $r = -0.13$, $r_{std} = -0.47$, $P = 0.25$). Moreover, when only using sympatric populations, differences in rejection rate of nonmimetic model eggs became significantly related to geographic distances (Mantel test, $r = 0.77$, $r_{std} = 0.96$, $P = 0.016$), but not to genetic distances (Mantel test, $r = 0.03$, $r_{std} = 0.07$, $P = 0.35$). Because gene flow is greater in sympatric than in allopatric populations (Martínez et al. 1999), in these analyses genetic variation is greatly reduced compared to geographic variation. Therefore, we did not find a significant relationship between genetic and geographic distances (Mantel test, $r = -0.12$, $r_{std} = -0.69$, $P = 0.26$).

DISCUSSION

Magpie populations from areas of allopatry with the great spotted cuckoo rejected models of brood parasite eggs placed in their nests. This host defense in the absence of selection pressures from brood parasites has been proposed to be related to gene flow from host populations in sympatry with the brood parasite to allopatric host populations (Davies and Brooke 1989; Soler and Møller 1990; Briskie et al. 1992). Using the magpie populations in the present study, Martínez et al. (1999) showed that nearby populations are genetically more similar than magpie populations far from each other, but that the amount of gene flow between populations is high.

Magpie populations suffering strongly from parasitism showed higher rejection rates than populations with low parasitism, and rarely parasitized magpie populations rejected experimental model eggs more frequently than allopatric magpie populations. This finding is in agreement with the previous results by Soler and Møller (1990). However, whereas in the present study we detected rejection behavior in magpie populations in allopatry with the great spotted cuckoo, Soler and Møller (1990) did not find rejection behavior in a Swedish allopatric population, although the 95% confidence intervals range from 0% to 29.1% (data from Soler and Møller 1990; see Sokal and Rohlf 1981, p. 158). The difference with our present results were more apparent for nonmimetic eggs.

One possibile explanation for the resulting rejection rate of model eggs in allopatric populations is that the great spotted cuckoo may have had a more extensive distribution in the recent past, and host populations considered allopatric in the present study once may have been sympatric with the great spotted cuckoo. However, it is known that during the middle Pleistocene the great spotted cuckoo was distributed in Israel and Judea, but was not recorded in Spain during the entire Holocene period (Tyrberg 1998). Control information for the European cuckoo showed that during the Pleistocene this species was distributed widely in Europe (Germany, Czechoslovakia, France, Austria, Hungary, Italy, and Spain; Tyrberg 1998). Therefore, the current distribution of the great spotted cuckoo in the Palearctic is almost certainly more extensive than in the past. Moreover, it is known that the great spotted cuckoo recently has extended its range northward in France, Italy, and Bulgaria (Cramp 1985), indicating that the distribution of the parasite is currently increasing. Thus, the rejection rate of model cuckoo eggs in currently allopatric populations does not seem to be related to a more extensive distribution of the parasite in the recent past.

In accordance with the rejecter-gene flow hypothesis (hypothesis 1), which predicts that population differences in rejection rate could be explained by genetic and/or geographic distances, we found that population differences in rejection rate of mimetic model eggs were mainly explained by geographic distance among populations, whereas differences for nonmimetic eggs were significantly related to genetic distances but not geographic distances. Moreover, because genetics, geography, and ecology are potentially confounded in the previous analyses relating to sympatry/allopatry, we restricted the analyses to sympatric populations. In this case, geographic distances explained differences in rejection rate of both mimetic and nonmimetic model eggs. However, when only using sympatric populations, genetic variation is differentially reduced in relation to geographic variation because gene flow is greater among sympatric as compared to allopatric host populations (Martínez et al. 1999). Therefore, because sympatric magpie populations are genetically more homogeneous than allopatric populations, analyses of sympatric populations partially control for genetic effects and only geographic effects thus appear to explain differences in rejection rates.

Although statistical tests including sympatric and allopat-

ric populations are potentially confounded because distant populations are likely to include sympatric and allopatric comparisons, as well as to be genetically the most distinct, it is difficult to imagine how allopatry can differentially affect the relative importance of genetic and geographic distances. In a multiple autocorrelation analysis genetic, distances mainly explained differences in rejection rates of nonmimetic model eggs, whereas geographic distances mainly explained differences in rejection of mimetic eggs. These differences are likely to be related to differences in gene flow between allopatric and sympatric populations. The different influence of geography and genetics on rejection of mimetic and nonmimetic eggs could be related to different processes involved in recognition of these two kinds of model eggs. Previous studies have shown that host rejection behavior depends on the appearance of eggs, with nonmimetic eggs more frequently being rejected than mimetic ones (Fig. 2).

Two different nonexclusive processes have been proposed for egg recognition of hosts: (1) a genetic process (Rothstein 1990) for which mutations allow egg recognition to appear and quickly spread in a host population; and (2) a learning process (defined as learning the appearance of the host's own eggs, in relation to those of the cuckoo), that is, explains the rapid increase in rejection rate in recently parasitized host populations (Nakamura 1990; Soler et al. 1994; Brooke et al. 1998). However, another possibility is that the egg recognition ability of hosts is genetically based, but requires a learning process for the development of a fine tuned recognition ability.

In accordance with the first possibility, significant differences in rejection rates of nonmimetic model eggs as a function of genetic distances among populations (after controlling for geographical distances) suggests that only a genetic component can explain the results; thus, no other process would be involved in the recognition ability of nonmimetic eggs (hypothesis 2). However, differences in rejection rates of mimetic model eggs were significantly related to geographic distances (after controlling for genetic distances), as predicted by hypothesis 3. Although geographic and genetic distances were significantly correlated, the fact that geographic distances better explained rejection rates of mimetic model eggs suggests that a fine tuned recognition ability by hosts would require an additional process depending on geographic distance (e.g., learning).

If a learning process is required for foreign egg recognition by hosts, even with gene flow, it would be difficult to explain host recognition in areas not suffering from brood parasitism because magpies are unable to encounter cuckoo eggs in allopatry. One possibility is that adult hosts with the ability of learning the appearance of their own eggs in relation to those of the cuckoo migrate to areas of allopatry. Although magpies are remarkably sedentary, long-distance movements sometimes occur in response to adverse environmental conditions (e.g., cold weather, Birkhead 1991) as in other bird species (Berthold 1993). In magpies, both breeding and natal dispersal occurs, with dispersal distances of juveniles (mean = 7.9 km, SD = 18.2 km; Paradis et al. 1998) being larger than those of adults (mean = 2.1 km, SD = 7.5 km; Paradis et al. 1998). Brood parasitism, which greatly reduces the reproductive success of magpies in southeastern Spain (Soler

et al. 1996), where the highest rejection rates are found, could give rise to increasing adult magpie dispersal to areas with superior conditions (allopatric areas). However, the high rejection rate of nonmimetic model eggs found in the present study, even in areas of allopatry, is difficult to explain only on the basis of dispersal.

The third possibility is that recognition ability of foreign eggs is genetically based, but perfection of recognition requires a learning process; that is, all hosts with recognizer genes will be able to recognize foreign eggs clearly different from their own, but only those with learning experience will be able to detect and reject mimetic eggs. That could explain the difference in rejection rate of mimetic and nonmimetic eggs in this and others studies (Davies and Brooke 1989; Soler 1990; Soler and Møller 1990; Soler et al. 1994, 1998a).

If a learning process is needed for host recognition of mimetic eggs, this is more likely to occur in sympatric magpie populations. Thus, dispersal by adult magpies would account for the current results because immigration of recognizer magpies to allopatric areas is more likely to occur close to sympatric areas. Costs of recognition of foreign eggs include accidental rejection of a pair's own eggs (Davies and Brooke 1988; Marchetti 1992). Therefore, in allopatric areas without brood parasitism this recognition ability will disappear (Cruz and Wiley 1989). Likewise, if recognition of mimetic eggs is based on a learning process, the ability to recognize mimetic eggs will quickly disappear in allopatry and for the most part dispersal of rejecters individuals from other areas will maintain rejection of mimetic model eggs. Moreover, the rejecter genotypes, if they require a learning process to reject mimetic model eggs, would become effectively nonrejectors in allopatric populations and, therefore, would not pay the cost of rejecting own eggs. As a result, rejecter genotypes would disappear less quickly in allopatry if associated with a learning "switch" because such genotypes would not be selected against.

An alternative hypothesis explaining differences in rejection rates of mimetic and nonmimetic model eggs is that recognition ability is only genetically determined, but more than one gene is involved in the process. An individual host with all recognizer alleles is able to recognize mimetic eggs and the recognition ability is related to the number of recognizer alleles. Due to the differential cost of rejecting mimetic and nonmimetic eggs (see above), selection pressures will favor loss of some recognizer alleles in allopatry to a point where recognition of nonmimetic eggs is uncostly and only dispersal of young rejecters from other areas maintains rejection. However, in this case genetic distance should be a better predictor of differences in rejection rates among magpie populations and an additional mechanism mainly related to geographic distance, such as immigration, is needed. Therefore, our results suggest that a learning process is involved in the recognition ability of mimetic eggs in different magpie populations.

In conclusion, our findings support the recognizer-gene flow hypothesis because differences in rejection of mimetic model eggs were related to both genetic and geographic distances between magpie populations. Furthermore, they suggest that a learning process is necessary for a fine-tuned recognition ability of the eggs of the great spotted cuckoo

by the magpie because differences in rejection rate of mimetic model eggs between populations have a strong geographic component, whereas the main component of rejection rate of nonmimetic model eggs is genetic.

LITERATURE CITED

ALVAREZ, F. 1996. Model cuckoo *Cuculus canorus* eggs accepted by Rufous Bush Chats *Cercotrichas galactotes* during the parasite's absence from breeding area. Ibis 138:340–342.

AVISE, J. C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, London.

BENNETT, A. T. D., I. C. CUTHILL, AND K. J. NORRIS. 1994. Sexual selection and the mismeasure of color. Am. Nat. 144:848–860.

BERTHOLD, P. 1993. Bird migration. A general survey. Oxford Ornithology Series. Oxford Univ. Press, Oxford.

BIRKHEAD, T. R. 1991. The magpies. The ecology and behaviour of black-billed and yellow-billed magpies. T. & A. D. Poyser, London.

BOWCOCK, A. M., A. RUIZ-LINARES, J. TOMFOHRDE, E. MINCH, J. R. KIDD, AND L. L. CAVALLI-SFORZA. 1994. High resolution of human evolutionary trees with polymorphic microsatellites. Nature 368:455–457.

BRISKIE, J. V., S. G. SEALY, AND K. A. HOBSON. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution 46:334–340.

BROOKE, M. DE L., N. B. DAVIES, AND D. G. NOBLE. 1998. Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. Proc. R. Soc. Lond. B Biol. Sci. 256:1277–1282.

BRUFORD, M. W., AND R. K. WAYNE. 1993. Microsatellites and their application to population genetic studies. Curr. Opin. Genet. Develop. 3:939–943.

BRUFORD, M. W., O. HANOTTE, J. F. Y. BROOKFIELD, AND T. BURKE. 1992. Single-locus and multilocus DNA fingerprinting. Pp. 225–268 in Molecular genetic analysis of populations, A. R. Hoelzel, ed. Oxford Univ. Press, Oxford.

CAVALLI-SFORZA, L., AND A. W. F. EDWARDS. 1967. Phylogenetic analysis: models and estimation procedures. Am. J. Hum. Genet. 19:233–257.

CRAMP, S. 1985. The birds of the Western Palearctic. Vol. IV. Oxford Univ. Press, Oxford.

CRUZ, A., AND J. W. WILEY. 1989. The decline of an adaptation in the absence of a presumed selection pressure. Evolution 43:55–62.

DAVIES, N. B., AND M. DE L. BROOKE. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. Anim. Behav. 36:262–284.

———. 1989. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J. Anim. Ecol. 58:207–224.

DEKA, R., L. JIN, M. D. SHRIVER, L. M. YU, S. DECROO, J. HUN-

DRIESER, C. H. BUNKER, R. E. FERRELL, AND R. CHAKRABORTY. 1995. Population genetics of dinucleotide (dC-dA)n-(dG-dT)n polymorphisms in world populations. Am. J. Hum. Genet. 56:461–474.

DYBDAHL, M. F., AND C. M. LIVELY. 1996. The geography of coevolution: comparative population structures for a snail and its trematode parasite. Evolution 50:2264–2275.

EDWARDS, S. V., AND M. KOT. 1995. Comparative methods at the species level: geographic variation in morphology and group size in Gray-crowed Babblers (*Pomatostomus temporalis*). Evolution 49:1134–1146.

ESTOUP, M., J. M. SOLIGNAC, J. CORNUET, A. GOUDET, AND A. SCHOLL. 1996. Genetic differentiation of continental and island populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. Mol. Ecol. 5:19–31.

FELSENSTEIN, J. 1993. PHYLIP (Phylogeny Inference Package) version 3.5c. Distributed by the author. Department of Genetics, Univ. of Washington, Seattle, WA.

FOSTER, S. A., AND S. A. CAMERON. 1996. Geographic variation in behavior: a phylogenetic framework for comparative studies. Pp. 138–165 in E. P. Martin, ed. Phylogenies and the comparative method in animal behavior. Oxford Univ. Press, Oxford.

FRANK, S. A. 1991. Ecological and genetic models of host-pathogen coevolution. Heredity 67:73–83.

———. 1993. Coevolutionary genetics of plants and pathogens. Evol. Ecol. 7:45–75.

GIBBS, H. L., M. DE L. BROOKE, AND N. B. DAVIES. 1996. Analysis of genetic differentiation of host races of the common cuckoo *Cuculus canorus* using mitochondrial and microsatellite DNA variation. Proc. R. Soc. Lond. B Biol. Sci. 263:89–96.

GIBBS, H. L., P. MILLER, G. ANDERSON, AND S. G. SEALY. 1997. Genetic analysis of brown-headed cowbirds *Molothrus ater* raised by different hosts: data from mtDNA and microsatellite DNA markers. Mol. Ecol. 6:189–193.

GITTLEMAN, J. L., AND H. K. LUH. 1992. On comparing comparative methods. Annu. Rev. Ecol. Syst. 23:383–404.

GOLDSTEIN, D. B., A. RUIZ-LINARES, L. L. CAVALLI-SFORZA, AND M. W. FELDMAN. 1995. Genetic absolute dating based on microsatellites and the origin of modern humans. Proc. Natl. Acad. Sci. USA 92:6723–6727.

GOUDET, J. 1995. Fstat version 1.2: a computer program to calculate *F*-statistics. J. Hered. 86:485–486.

HARAGUCHI, Y., AND H. SENO. 1995. A mathematical modelling on population dynamics for brood-parasitism: what is the benefit for host? J. Theor. Biol. 174:281–297.

HUBERT, L. H. 1985. Combinatorial data analysis: association and partial association. Psychometrica 50:449–467.

JARNE, P., AND P. J. L. LAGODA. 1996. Microsatellites, from molecules to populations and back. Trends Ecol. Evol. 11:424–429.

JOHNSGARD, P. A. 1997. The avian brood parasites. Deception at the nest. Oxford Univ. Press, Oxford.

KELLY, C. 1987. A model to explore the rate of spread of mimicry and rejection in hypothetical populations of cuckoos and their hosts. J. Theor. Biol. 125:283–299.

LEGENDRE, P., AND A. VAUDOR. 1991. Le Progiciel R—Analyse Multidimensionnelle, Analyse Spatiale. Département de Sciences Biologiques, Université de Montréal, Canada.

LOTEM, A. 1993. Learning to recognize nestlings is maladative for cuckoo *Cuculus canorus* hosts. Nature 362:743–645.

LOTEM, A., AND S. I. ROTHSTEIN. 1995. Cuckoo-host coevolution: from snapshots of an arms race to the documentation of microevolution. Trends Ecol. Evol. 10:436–437.

LOTEM, A., H. NAKAMURA, AND A. ZAHAVI. 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. Behav. Ecol. 3:126–132.

———. 1995. Constraints on egg discrimination and cuckoo-host co-evolution. Anim. Behav. 49:1185–1209.

MARCHETTI, K. 1992. Costs to host defense and the persistence of parasitic cuckoos. Proc. R. Soc. Lond. B Biol. Sci. 248:41–45.

MARTÍNEZ, J. G., T. BURKE, D. DAWSON, J. J. SOLER, M. SOLER, AND A. P. MØLLER. 1998. Microsatellite typing reveals mating patterns in the brood parasitic great spotted cuckoo (*Clamator glandarius*). Mol. Ecol. 7:289–297.

MARTÍNEZ, J. G., J. J. SOLER, M. SOLER, A. P. MØLLER, AND T. BURKE. 1999. Comparative population structure and gene flow of a brood parasite, the great spotted cuckoo (*Clamator glandarius*), and its primary host, the magpie (*Pica pica*). Evolution 53:269–278.

NAKAMURA, H. 1990. Brood parasitism by the cuckoo *Cuculus canorus* in Japan and the start of new parasitism on the azure-winged magpie *Cyanopica cyana*. Jpn. J. Ornithol. 39:1–8.

NEI, M. 1972. Genetic distance between populations. Am. Nat. 106:283–292.

OHTA, T., AND M. KIMURA. 1973. A model of mutation appropriate to estimate the number of electrophoretically detectable alleles in a finite population. Genet. Res. 22:201–204.

PAETKAU, D., L. P. WAITS, P. L. CLARKSON, L. CRAIGHEAD, AND C. STROBECK. 1997. An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae) populations. Genetics 147:1943–1957.

PARADIS, E., S. R. BAILLIE, W. J. SUTHERLAND, AND R. D. GREGORY. 1998. Patterns of natal and breeding dispersal in birds. J. Anim. Ecol. 67:518–536.

PARROT, D. 1995. Social organization and extra-pair behaviour in the European black-billed magpie *Pica pica*. Ph.D. diss., University of Sheffield, Sheffield, U.K.

PEREZ-LEZAUN, A., F. CALAFELL, E. MATEU, D. COMAS, R. RUIZ-PACHECO, AND J. BERTRANPETIT. 1997. Microsatellite variation and the differentiation of modern humans. Hum. Genet. 99:1–7.

RAYMOND, M., AND F. ROUSSET. 1995. GENEPOP (version 1.2)—population genetics software for exact tests and ecumenicism. J. Hered. 86:248–249.

ROTHSTEIN, S. I. 1975. Evolutionary rates and host defenses against avian brood parasitism. Am. Nat. 109:161–176.

———. 1990. A model system for coevolution: avian brood parasitism. Annu. Rev. Ecol. Syst. 21:481–508.

ROUSSET, F., AND M. RAYMOND. 1995. Testing heterozygote excess and deficiency. Genetics 140:1413–1419.

SHRIVER, M., L. J. E. BOERWINKLE, R. DEKA, R. E. FERRELL, AND R. CHAKRABORTY. 1995. A novel measure of genetic distance for highly polymorphic tandem repeat loci. Mol. Biol. Evol. 12:914–920.

SLATKIN, M. 1987. Gene flow and the geographic structure of natural populations. Science 236:787–792.

———. 1995. A measure of population subdivision based on microsatellite allele frequencies. Genetics 139:457–462.

SLATKIN, M., AND N. H. BARTON. 1989. A comparison of three indirect methods for estimating average levels of gene flow. Evolution 43:1349–1368.

SMOUSE, P. E., J. C. LONG, AND R. R. SOKAL. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Syst. Zool. 35:627–632.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2d ed. Freeman, San Francisco, CA.

SOLER, M. 1990. Relationships between the great spotted cuckoo *Clamator glandarius* and its magpie host in a recently colonized area. Ornis Scand. 21:212–223.

SOLER, M., AND A. P. MØLLER. 1990. Duration of sympatry and coevolution between great spotted cuckoo and its magpie host. Nature 343:748–750.

SOLER, M., J. J. SOLER, J. G. MARTÍNEZ, AND A. P. MØLLER. 1994. Micro-evolutionary change in host response to a brood parasite. Behav. Ecol. Sociobiol. 35:295–301.

SOLER, M., J. G. MARTÍNEZ, AND J. J. SOLER. 1996. Effects of brood parasitism by the great spotted cuckoo on the breeding success of the magpie host: an experimetal study. Ardeola 43:87–96.

SOLER, M., J. J. SOLER, AND J. G. MARTÍNEZ. 1998a. Duration of sympatry and coevolution between the great spotted cuckoo *Clamator glandarius* and its primary host, the magpie *Pica pica*. Pp. 113–128 *in* S. I. Rothstein and S. K. Robinson, eds. Parasitic birds and their hosts. Oxford Univ. Press, Oxford.

SOLER, M., J. J. SOLER, J. G. MARTINEZ, T. PEREZ-CONTRERAS, AND A. P. MØLLER. 1998b. Micro-evolutionary change and population dynamic of a brood parasite and its primary host: the intermittent arms race hypothesis. Oecologia 117:381–390.

TAKASU, F., K. KAWASAKI, H. NAKAMURA, J. E. COHEN, AND N. SHIGESADA. 1993. Modeling the population dynamics of a cuckoo-host association and the evolution of host defenses. Am. Nat. 142:819–839.

THOMSON, J. N. 1994. The Coevolutionary Process. Univ. of Chicago Press, Chicago.

TYRBERG, T. 1998. Pleistocene birds of the Palearctic: a catalogue. Nuttall Ornithological Club, Museum of Comparative Zoology, Harvard University, Cambridge, MA.

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