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LIFE HISTORY OF MAGPIE POPULATIONS SYMPATRIC OR ALLOPATRIC WITH THE BROOD PARASITIC GREAT SPOTTED CUCKOO

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Abstract. Parasites can have dramatic effects on life-history decisions of hosts such as timing of reproduction, clutch size, and investment in individual offspring, depending on the timing of parasite effects on host fitness. Moreover, parasites may influence the optimum values of important life-history traits such as clutch size and brood size by having different fitness effects for large and for small values. Here, by analyzing data from a Magpie (*Pica pica*) population sympatric with the Great Spotted Cuckoo (*Clamator glandarius*), we demonstrated that Magpies laying a large clutch suffer less from parasitism than do those laying a small clutch, because the first have a higher probability of successfully raising some of their own offspring. Therefore, we predicted that (1) Magpie hosts in sympatry with Great Spotted Cuckoos should produce more eggs, and (2) eggs should be smaller than those in areas of allopatry. We also predicted that (3) this change in life history should be directly related to selection pressures by cuckoos, as evidenced from current levels of parasitism and Magpie rejection of cuckoo model eggs. We tested these predictions by comparing the life-history parameters of 15 European host populations that are either sympatric or allopatric with the parasite. In accordance with predictions, we found an increase in clutch size and a decrease in egg volume of Magpies in populations sympatric with the Great Spotted Cuckoo, as compared to allopatric populations, even when statistically controlling for laying date and latitude. By using parasitism rate and experimentally testing the ability of Magpies to recognize and reject mimetic and nonmimetic model eggs, we were able to test prediction 3 in the 15 Magpie populations. Clutch size was positively related to the rejection rate of nonmimetic model eggs, whereas mean egg volume was significantly negatively related to the rejection rate of mimetic model eggs. These findings provide evidence of a strong influence of the parasitic Great Spotted Cuckoo on the life history of its Magpie host.

Key words: brood parasitism; Clamator glandarius; *clutch size; egg size; Great Spotted Cuckoo; laying date; life history; Magpie; parental effort;* Pica pica.

INTRODUCTION

Parasites consistently reduce the reproductive success of their hosts through their direct or indirect effects on host condition or resource availability for host reproduction (e.g., Rothstein 1990, Lehmann 1993, Møller 1997, Payne 1997). Parasites may severely affect the reproductive success of hosts by imposing costs at different stages of the host's life cycle. For example, parasites can affect the survival prospects of hosts and, hence, the evolution of time of first reproduction. Alternatively, parasites may influence the reproductive success of hosts at later stages of their life, either as a direct cause of offspring mortality or through a reduction in the reproductive value of offspring in the presence of parasites. In theory, parental effort should be adjusted to the reproductive value of offspring (Schaffer 1974, Pianka and Parker 1975, Forbes 1993); thus, parasitism may reduce the amount of parental effort allocated to currently parasitized offspring.

On the other hand, host condition may directly affect the risk of parasitism, if parasites are better able to exploit hosts in good rather than poor condition, because such hosts can cope with parasitism without increasing their parental effort considerably. For example, malaria appears to perform better (larger multiplication rate) in pregnant human hosts, who can be considered to be in prime body condition (McGregor 1988). A second example concerns the parasitic Great Spotted Cuckoo *Clamator glandarius*, which parasitizes Magpie *Pica pica* hosts in prime condition more often than expected by chance, because such hosts are better able to raise a cuckoo nestling (Soler et al. 1995). Parasitism may be less costly for hosts in good condition, although parasitism, by definition, will still tend to depress reproductive output in a population of hosts over evolutionary time.

If parasites exploit the competitive edge that they have in reproducing hosts, such hosts may particularly suffer from the long-term costs of parasitism. Consis-

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tent with this prediction, ectoparasitism has been shown to increase the cost of reproduction in a brood size manipulation experiment on the Barn Swallow *Hirundo rustica* (Møller 1993). Subsequent studies have suggested that this cost of reproduction is mediated through the negative effects of parental effort on immune responsiveness (Deerenberg et al. 1996, Nordling et al. 1998; for a negative result in a small laboratory population, see Birkhead et al. 1998).

Given that parasites impose costs on their hosts both at short-term and long-term ecological scales, which are the opportunities for hosts to respond adaptively, in terms of life history, to parasitism? One possibility is phenotypic adjustments of reproductive effort to the risk of parasitism (Minchella 1985). This can be done either by enhancing fecundity (Minchella and LoVerde 1981) or by reducing age at maturity in response to the actual presence or the risk of parasitism (Lafferty 1993). Increased investment in reproduction in the presence of signs of parasitism, as in snails that are intermediate hosts of schistozomes (Minchella and LoVerde 1981), indicates that hosts are able to adaptively increase their reproduction when the risk of future infection is high. Similarly, reductions in reproductive effort, as in parasitized pea aphids that drop to the ground to reduce the possibility of transmission of hymenopteran parasites to close kin (McAllister and Roitberg 1987), indicate that hosts are able to respond adaptively in their parental effort to perceived risks of parasitism.

The alternative time scale of adaptation is in terms of microevolutionary changes in life history in response to selection pressures imposed by parasites in the recent and more distant past (Hochberg et al. 1992). The optimal host response, in terms of life-history adaptations to parasitism, depends strongly on the timing of parasitism during the life cycle of the host and on the kinds of costs imposed by parasites on their hosts. Parasites that impose fitness costs early during the life of the host, before start of reproduction, may select for advanced start of reproduction. Conversely, parasites that exploit their hosts at a later stage of the life cycle may cause a microevolutionary change in other life-history variables, such as the optimal clutch size and the optimal size of offspring (e.g., Lyon 1998), which, in this case, are more likely to be shaped by the selection pressures imposed by parasites. In other words, parasites may influence the optimum values of important life-history traits such as clutch size and brood size by having different fitness effects for large and small trait values (Richner and Heeb 1995). For instance, an increase in clutch size will be favored in a host population if fitness of a parasitized individual host is greater when laying a large than when laying a small clutch.

Here, we investigate the impact of brood parasitism on life history (i.e., clutch size and egg size) in a host, the Magpie, facing parasitism by the Great Spotted Cuckoo. Great Spotted Cuckoos cause a considerable reduction in the reproductive success of their hosts, mainly through the effects of adult cuckoos destroying Magpie eggs, but also through the effects of cuckoo nestlings on the survival and growth of host offspring (Soler et al. 1996). A second potential cost of parasitism for Magpies that has so far not been quantified is that cuckoo young require a more extended period of parental care by Magpie hosts than do Magpie offspring (Soler et al. 1998*a*). Such extended parental care is likely to delay the annual molt in the host, resulting in a reduction in survival.

The main cost for Magpies parasitized by the Great Spotted Cuckoo arises from the cuckoo behavior of destroying Magpie eggs when laying, or in subsequent visits to the Magpie nest (Soler et al. 1996). Magpies could reduce the cost of parasitism by laying a large clutch, because a larger number of undamaged eggs would then be left after parasitism. Thus, the breeding success of parasitized Magpies should be positively related to clutch size. Another possibility to reduce the cost of parasitism for Magpies is to increase egg volume, because chicks hatching from large eggs are heavier and structurally larger than those from smaller eggs (Clarkson 1984, Birkhead 1991). Such large Magpie chicks would have a higher probability of survival when competing for food with the Great Spotted Cuckoo chick(s). If that were the case, we should predict a positive relationship between egg size and breeding success in parasitized Magpies. However, these two possibilities for reducing the effect of parasitism are mutually exclusive because a trade-off between clutch size and egg size is likely (Clarkson 1984, Birkhead 1991). Thus, the relationship between clutch size and breeding success of parasitized Magpies is the key to predictions concerning the relationship between brood parasitism and optimal clutch size and egg size in Magpies. If a negative relationship exists, parasitism would select for Magpies to lay small clutches with large eggs. However, if clutch size and breeding success of parasitized Magpies are positively related, brood parasitism would select for Magpies to lay large clutches with small eggs. Finally, if no relationship between clutch size and breeding success in parasitized Magpies exists, selection pressures from parasitism should not affect clutch size or egg size in Magpies.

Therefore, predictions concerning how brood parasitism affects clutch size and egg size in Magpies will depend on the relationship between clutch size and breeding success of parasitized Magpies. We determined these relationships empirically using a large sample of parasitized Magpie nests from one study population in Spain.

Given that we found a positive relationship between clutch size and breeding success in parasitized Magpies, we predicted that (1) Magpie hosts in sympatry with Great Spotted Cuckoos should produce more, but (2) smaller eggs than those in areas of allopatry. (3)

This change in life history should be directly related to selection pressures by cuckoos, as evidenced from current levels of parasitism and Magpie rejection of cuckoo model eggs. We tested these predictions by using information on timing of reproduction, clutch size, and egg size in a number of European Magpie populations that were either sympatric or allopatric with the cuckoo. Furthermore, we used host responses to experimental parasitism by model eggs as a measure of past impact of parasites on hosts. The reason for this is that gene flow among host populations will give rise to the presence of resistance genes, even in allopatric host populations (Lotem and Rothstein 1995, Soler et al. 1999*a*), and that recent intense selection pressures by parasites are supposed to have caused an evolutionary increase in the frequency of rejector genes in the host population (Soler et al. 1999*a*).

METHODS

Study species

We have described the coevolutionary interactions between the Great Spotted Cuckoo and the Magpie in detail elsewhere (Soler 1990, Soler et al. 1994*b*, 1998*b*, 1999*a*, *b*). Presence of Great Spotted Cuckoos close to the nest of the host does not increase the probability that Magpies will reject cuckoo eggs (Soler et al. 2000). Magpies are single-brooded corvids that occur throughout a large part of the Holarctic region. They are territorial, sedentary, and relatively long-lived for passerine birds, with a well-described biology (extensively reviewed in Birkhead 1991). A single clutch is laid in spring from March to May in their Western European range, with a clutch size range of 3–10 eggs (Birkhead 1991). Laying date was advanced by experimental food provisioning by 3.5–8 d in different studies compared to control pairs (Högstedt 1981, Hochachka and Boag 1987, Knight 1988, Dhindsa and Boag 1990). In these same experiments, clutch size was not significantly influenced by experimental food provisioning. However, experimental food provisioning caused egg size to increase significantly by 2.7–7.7% in three different studies (Högstedt 1981, Clarkson 1984, Hochachka 1988). In case of nest failure early during the reproductive cycle, Magpies will lay a replacement clutch, with the frequency of replacement clutches decreasing as the season progresses (Birkhead 1991). When size of the first and replacement clutches of the same Magpie pairs was compared, those with smaller clutch size in the repeat clutch laid larger eggs than those in the original, but pairs that retained the same clutch size between attempts reduced the size of their eggs (Clarkson 1984, Birkhead 1991). This result is consistent with a trade-off between clutch size and egg size. Clutch size is positively, but not significantly, related to laying date across populations ($r = 0.36$, df = 14, NS; Birkhead 1991). Birkhead (1991) discussed the weak positive correlation coefficient in comparison with the strong relationship detected in other passerine species (see Perrins and Birkhead 1983), and he argued that this appeared because of the relatively large clutch size of Magpies breeding in southern Spain (an area with a high prevalence of brood parasitism).

The Great Spotted Cuckoo is a migratory brood parasite that in Europe occurs commonly in the Iberian Peninsula, Southern France, and Bulgaria (Cramp 1985). One or more cuckoos may parasitize Magpie nests with one or more eggs (Martínez et al. 1998). Parasitism severely reduces host reproductive success because adult cuckoos destroy Magpie eggs when laying, or because of early hatching and effective competition for parental food delivery by cuckoo offspring (Soler 1990, Soler and Soler 1991, Soler et al. 1996, 1997). Great Spotted Cuckoos do not remove host eggs when parasitising (e.g., Soler 1990). Magpie hosts provide parental care for cuckoo chicks for an extended period of almost five weeks after fledging (Soler et al. 1994*a*), compared to the usual duration of parental care of three weeks for their own offspring (Husby and Slagsvold 1992, Soler et al. 1994*a*). Thus, it is likely that parasitism will severely delay the annual molt, hence imposing a mortality cost on adult hosts.

Sampling and study areas

The study was conducted during 1993–1995 in 15 Magpie populations throughout the species' range in Europe (Table 1; for the location of these populations, see Martínez et al. 1999). Nine of these populations were within the distributional range of the brood parasitic Great Spotted Cuckoo, whereas the remaining six were outside this range. We obtained information on laying date, assuming that a single egg was laid per day, and that the duration of the incubation period was 21–22 d (Birkhead 1991, Cramp 1994). The parasitism rate was nonzero in our samples of Magpie nests in only seven of the nine sympatric populations, and we thus used rejection rate of eggs during artificial nest parasitism experiments to assess the response of host populations to parasitism (Soler et al. 1999*a*).

In order to study the within-population relationship between clutch size and breeding success of parasitized Magpies (i.e., selection pressure of parasitism on clutch size of Magpie hosts), we use data from the Magpie population in Guadix, southern Spain, an area of sympatry where parasitism by the Great Spotted Cuckoo is common (for information on this Magpie population and variation in frequency of parasitism since 1983, see Soler et al. 1998*a*, *b*). We used information on laying date, clutch size, breeding success, and number of broken eggs of naturally parasitized nests during 1982–1999. No replacement clutches or experimental nests for other studies were included in the analyses.

Laying date, clutch size, hatching success, and brood size at a nestling age of ~18 d were estimated by regular (at least weekly) visits to all nests within our study areas. All eggs were measured to the nearest 0.1 mm

TABLE 1. Mean clutch size, egg volume, hatching success, brood size, and laying date in unparasitized Magpie nests. Parasitism rate, rejection rate of mimetic and nonmimetic model eggs, and information on sympatry or allopatry of the 15 European Magpie populations are also shown.

Population	Status†	Clutch size	Egg volume (cm^3)	Hatching success (%)	Brood size
		$\bar{X}$ ± 1 SE (*N*)	$\bar{X}$ ± 1 SE (*N*)	$\bar{X}$ ± 1 SE (*N*)	$\bar{X}$ ± 1 SE (*N*)
Donaña	s	6.27 ± 0.14 (44)	9.63 ± 0.11 (44)	6.00 ± 0.23 (20)	4.66 ± 0.23 (38)
Santa Fe	s	7.00 ± 0.00 (3)	10.06 ± 0.46 (3)	7.00 ± 0.00 (1)	4.00 ± 0.00 (1)
Guadix	s	7.00 ± 0.15 (28)	9.54 ± 0.16 (24)	5.81 ± 0.32 (16)	3.59 ± 0.23 (17)
Laujar	s	7.50 ± 1.50 (2)	8.86 ± 0.28 (2)		
Badajoz	s	6.41 ± 0.16 (29)	9.71 ± 0.14 (27)	6.20 ± 0.33 (10)	4.65 ± 0.29 (20)
Calahorra	s	6.11 ± 0.19 (27)	9.33 ± 0.14 (26)	5.00 ± 0.68 (10)	3.72 ± 0.42 (18)
Torres del Segre	s	6.92 ± 0.18 (36)	9.30 ± 0.18 (36)	4.88 ± 0.77 (16)	4.08 ± 0.50 (25)
Les Camargues	s	6.52 ± 0.17 (31)	9.94 ± 0.13 (30)	5.50 ± 1.50 (2)	3.65 ± 0.34 (20)
Eljovo	s	6.42 ± 0.21 (19)	10.11 ± 0.25 (19)	5.50 ± 0.50 (2)	5.40 ± 0.24 (5)
Milano	a	6.23 ± 0.18 (31)	10.05 ± 0.11 (31)	5.00 ± 0.00 (2)	3.53 ± 0.34 (15)
Bern	a	6.44 ± 0.19 (34)	9.71 ± 0.16 (32)	6.00 ± 0.58 (3)	4.00 ± 0.62 (7)
Freneusse	a	5.88 ± 0.18 (33)	9.91 ± 0.19 (25)	6.10 ± 0.31 (10)	3.20 ± 0.49 (10)
Sheffield	a	5.58 ± 0.19 (26)	10.03 ± 0.11 (25)	4.00 ± 0.23 (13)	3.08 ± 0.33 (13)
Jyväskylä	a	7.00 ± 0.23 (27)	10.40 ± 0.18 (27)		3.57 ± 0.48 (7)
Trondheim	a	6.18 ± 0.23 (11)			3.00 ± 0.00 (2)

† Abbreviations: s, sympatric; a, allopatric.
‡ For laying data, 1 = 1 April.

with calipers. Egg volume was assumed to be ellipsoidal and was calculated as $(4/3)\pi a^2 b$, where a is the smallest radius and b is the largest radius of the egg. Replacement clutches, which are readily recognized from their late start of laying within a territory with a nest that had already previously contained eggs (Birkhead 1991), were not included in the study. We only used unparasitized Magpie nests (those with no cuckoo egg or broken host eggs) in the subsequent calculations (comparisons among different Magpie populations), because the estimates of life-history variables may have been influenced by parasitic cuckoos and by Magpies in response to parasitism (Soler et al. 1997). For example, parasitism often results in destruction of one or more host eggs that subsequently may be removed by the Magpie (Soler et al. 1997). Hence, there are good reasons to exclude parasitized host nests in order to obtain unbiased estimates of host life-history variables. The potential effect of host choice by the Great Spotted Cuckoo on these estimates will be considered in detail in the *Discussion*. Moreover, we did not use depredated or abandoned nests to estimate hatching success and brood size.

We tested Magpies for their ability to recognize and successfully reject mimetic and nonmimetic model eggs introduced into their nests during their laying period. We used both kinds of eggs because the rejection rate for nonmimetic model eggs has a strong genetic component, whereas the main component of rejection rates for mimetic model eggs is phenotypic rather than genetic (Soler et al. 1999*a*). Although differences in rates at which nonmimetic model eggs were rejected would provide information on genetic differences between populations in terms of the Magpies' ability to discriminate dissimilar eggs, differences in rates at which mimetic model eggs were rejected would be related to geographic distances and, thus, to adult migration rates from sympatric areas (Soler et al. 1999*a*). Rejection rates for nonmimetic model eggs would not be directly related to the current impact of brood parasitism on host populations; instead, they are likely to be related to gene flow among individuals from areas of sympatry or allopatry with the Great Spotted Cuckoo (Soler et al. 1999*a*). Conversely, the rejection rate for mimetic model eggs could be used as an index of recent selection pressure from brood parasitism because it is likely to be related to gene flow from recognizer individuals, mainly from populations sympatric with the brood parasite (Soler et al. 1999*a*). These estimates of selection pressure due to parasitism have the advantage of being more repeatable than estimates of parasitism rate based on a single study year. Although the rate of parasitism fluctuates greatly among years, rejection rates are relatively constant among years. They increase rapidly when cuckoos begin to colonize a host population, but remain quite stable once the asymptote has been reached (Soler et al. 1998*b*).

We made mimetic eggs by filling molds of Great Spotted Cuckoo eggs with plaster of Paris; once dry, these models were painted with a color similar to the background color of cuckoo eggs. In a second step, we added brown spots similar in distribution and size to those of real cuckoo eggs. Finally, we covered the model eggs with a thin layer of lacquer that simulates the sheen of real cuckoo eggs. These model eggs are similar in mass to real cuckoo eggs (Soler and Møller 1990). Quail (*Coturnix coturnix*) eggs covered with red acrylic paint were used as nonmimetic eggs in the Guadix area, since these differed from Magpie and cuckoo eggs in size, background color, and spot size and dis-

TABLE 1. Extended.

Laying date‡	Latitude (°N)	Rejection rate		
		Parasitism rate	Mimetic	Nonmimetic
$\bar{X}$ ± 1 SE (*N*)		% (*N*)	% (*N*)	% (*N*)
−1.69 ± 1.15 (39)	37.13	11.5 (52)	43.5 (23)	84.0 (25)
13.79 ± 3.26 (14)	37.18	85.7 (21)	33.3 (12)	100.0 (10)
18.38 ± 1.01 (37)	37.30	51.8 (85)	63.6 (44)	89.7 (39)
	37.00	80.0 (10)	33.3 (6)	66.7 (3)
9.96 ± 1.44 (24)	38.87	0.0 (32)	43.8 (16)	78.6 (14)
15.33 ± 2.40 (27)	42.30	0.0 (33)	62.5 (16)	69.2 (13)
19.54 ± 1.43 (37)	41.53	2.3 (43)	38.1 (21)	71.4 (21)
9.10 ± 1.73 (29)	43.67	0.0 (32)	18.8 (16)	62.5 (16)
14.67 ± 4.81 (3)	42.15	0.0 (34)	11.1 (9)	25.0 (4)
−5.64 ± 0.53 (14)	45.47	0.0 (33)	25.0 (16)	56.3 (16)
15.13 ± 2.00 (23)	46.93	0.0 (49)	26.3 (19)	57.9 (19)
7.91 ± 1.10 (32)	49.00	0.0 (38)	22.2 (18)	52.9 (17)
45.15 ± 3.18 (26)	53.38	0.0 (28)	21.4 (14)	57.1 (14)
19.83 ± 0.61 (18)	62.25	0.0 (24)	7.1 (14)	87.5 (16)
	63.40	0.0 (45)	16.7 (6)	100.0 (6)

tribution (see Soler et al. 1999*a*). An experiment in a Magpie population in southern Spain demonstrated that Magpies responded identically (Fisher exact test, $P = 1.00$; Soler et al. 1998*b*) to red-painted nonmimetic model eggs made from plaster of Paris (rejection rate 91.7%, $n = 12$ eggs) and to red-painted Quail eggs (rejection rate 90.0%, $n = 10$ eggs). Thus, we used plaster of Paris eggs in the remaining populations to avoid differences in egg mass arising from egg desiccation during transport to the study areas. Each model was used only once. Nests were revisited 4–7 d after introduction of the model egg, which is sufficient to record reliably the response of a Magpie to a parasitic egg (Soler and Møller 1990). Magpies were scored as ‘‘acceptors’’ if the model egg was still in the nest, ‘‘ejectors’’ if the model egg was no longer present, or ‘‘deserters’’ if the nest was abandoned with the eggs remaining in the nest. Deserted nests are relatively uncommon, comprising only 3.1% of the nests in all Magpie populations. Soler et al. (1999*a*) have provided evidence for why ejection and desertion can be considered an estimate of the ability of Magpies to recognize and discriminate against foreign eggs. We follow their procedure in the present study by classifying Magpies as acceptors or rejecters (ejectors and deserters combined). The conclusions of the present study do not change if the analyses instead are based on ejection rates. Estimates of rejection rates are given in Table 1.

Statistical methods

We tested whether mean values of the reproductive variables of Magpies were normally distributed. As this was the case for clutch size and egg volume (Kolmogorov-Smirnov tests), transformations of variables were not required.

Sample sizes differ among Magpie reproductive variables because of loss caused by predation or because irregular visits to the study area did not allow us to estimate some variable for all nests (i.e., laying date or hatching success). Furthermore, we experienced a few cases of inconsistency in data collection by the many different field assistants involved in this project. Egg volume was not measured in Trondheim, and laying date, hatching success, and brood size at fledging could not be estimated in some populations because of irregular visits to the study areas (see Table 1). Hence, we did not obtain all kinds of information for all nests in all populations. However, it seems unlikely that this would cause any consistent bias in the database.

We investigated the relationship between reproductive variables of Magpies and parasitism by the Great Spotted Cuckoo using two different methods. First, we used nested analyses of covariance, with Magpie reproductive traits as dependent variables and sympatry or allopatry of Magpie and cuckoo populations as an independent factor. In these analyses, we were unable to use latitude as a covariate because variation within populations does not exist. However, laying date is related to latitude in Magpies (weighted regression analysis, $r = 0.45$, $F = 79.17$, df = 1, 321, $P < 0.0000001$; Soler et al. 1999*b*). Thus, we used laying date instead of latitude as a covariate in the analyses. Moreover, because reproductive traits in Magpies are negatively related to laying date within a population (Birkhead 1991), the use of laying date as a covariate has the advantage of controlling for variation within populations. In these analyses, we used each observation of a Magpie pair nested within populations as an independent data point. These analyses provide appropriate weighting of the estimates for each population by the number of observations.

Second, we used spatial autocorrelation analyses to calculate correlations of Magpie life-history variables with the rate of cuckoo parasitism and with the rate of rejection of experimental cuckoo eggs, respectively. Because we used mean population values, we only used populations for which we collected information for more than 10 nests (see Table 1 for sample sizes of the different populations and different variables). Geographical distances between populations were measured in terms of degrees of latitude because avian clutch size generally increases with increasing latitude (e.g., Lack 1966, Perrins and Birkhead 1983, Birkhead 1991). In a previous study, we calculated genetic distances between the 15 European Magpie populations based on frequencies of alleles at three microsatellite loci (Martínez et al. 1999). We constructed a genetic distance matrix (Martínez et al. 1999), a latitudinal distance matrix, a matrix of differences in parasitism rate between populations, a matrix of differences in rejection rate of mimetic and nonmimetic model eggs between populations, and a matrix of differences in clutch size and egg volume, respectively, between populations. We controlled for phylogenetic effects by autocorrelation analyses (Gittleman and Luh 1992, Edwards and Kot 1995, Foster and Cameron 1996), because the use of population phylogenies is not recommended for comparative analyses when gene flow is high among populations (Foster and Cameron 1996), as is the case for the Magpie (Martínez et al. 1999). Spatial autocorrelation analyses were made with the computer program ‘‘Le Progiciel R’’ (Legendre and Vaudor 1991). The import–export section was used to transform the distance matrix into binary files, which were used for multiple autocorrelation analysis using the Mantel section of the program. Partial correlation coefficients were calculated as suggested by Smouse et al. (1986) by 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). The Mantel test (Mantel 1967) was subsequently performed for the two residual matrices (A' and B'), with the estimated ‘‘r’’ being the partial correlation coefficient between A and B while controlling for the effect of matrix C. We report (1) the Mantel statistic R, which is the correlation coefficient, and (2) 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 extremes (maximum and minimum) obtained from the permutations (Legendre and Vaudor 1991). We tested the statistical significance of the autocorrelation coefficients using permutation tests with 1000 permutations. By using partial autocorrelation analyses, we were able to distinguish between genetic and purely geographic effects on differences in clutch size and egg volume in different Magpie populations.

RESULTS

Relationship between clutch size and breeding success in parasitized Magpies in an area at high risk for parasitism

Clutch size was positively related to breeding success in parasitized Magpies. When depredated nests were included, multiple $r = 0.29$, $F = 9.86$, df = 2, 216, $P = 0.00008$; for laying date, partial $r = -0.086$, $P = 0.208$; for clutch size, partial $r = 0.24$, $P = 0.0004$. When depredated nests were excluded, multiple $r = 0.31$, $F = 8.70$, df = 2, 161, $P < 0.00026$; for laying date, partial $r = -0.10$, $P = 0.204$; for clutch size, partial $r = 0.27$, $P < 0.001$. Moreover, parasitized Magpie pairs that successfully reared some Magpie chicks laid a larger clutch than those parasitized Magpies that were able to rear only cuckoo chick(s) (including depredated nests: ANCOVA, laying date as covariate, $F = 14.26$, df = 1, 227, $P = 0.0002$; excluding depredated nests: ANCOVA, laying date as covariate, $F = 15.16$, df = 1, 171, $P = 0.00014$; Fig. 1). Therefore, because parasitism has different fitness effects for large and small host clutch sizes, it should influence the optimum clutch size in Magpie populations that differ in the degree of parasitism. Moreover, because the correlation coefficient is positive, parasitism should select for larger clutch size and, hence, smaller eggs.

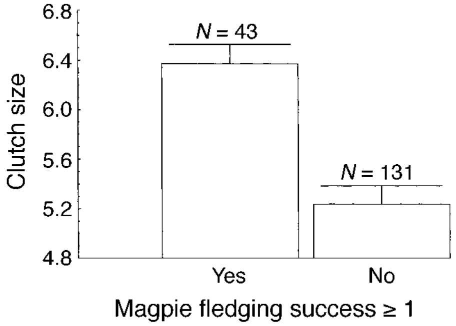

FIG. 1. Clutch size for parasitized and nondepredated Magpie nests that successfully raised at least one Magpie chick, and for those that did not raise a Magpie chick but raised one or more cuckoo chicks. Values are means + 1 SE. Sample size is also shown.

Clutch size, brood size, and parasitism

Laying date differed significantly between sympatric and allopatric Magpie populations in a nested ANCOVA (Table 2). Laying in the more southern, sympatric populations started, on average, 5 d earlier than in the northern, allopatric populations (Table 2). Subsequent analyses of reproductive variables were performed by including laying date as a covariate to reflect this difference in timing. This procedure also controlled for any association between clutch size and laying date within populations, because a decline in clutch size with progressing season has been reported in at least five different Magpie populations (Birkhead 1991). However, the conclusions of the subsequent analyses remained unchanged when the analyses were performed without statistical control for laying date. Hence, in the following, we only report the analyses using laying date as a covariate.

Clutch size of unparasitized hosts differed significantly between sympatric and allopatric Magpie pop-

TABLE 2. Nested ANCOVAs (nested ANOVA for laying date) with reproductive variables of Magpies as dependent variables, laying date as a covariate, and individual nests nested within areas.

Variable	MS	df	F	P	Sympatric ($\bar{X} \pm 1$ SE)	Allopatric ($\bar{X} \pm 1$ SE)
Laying date						
Cuckoo presence	905.18	1	11.22	0.00092	11.88 ± 0.84	16.48 ± 1.79
Error	80.67	281				
Clutch size						
Cuckoo presence	9.10	1	10.39	0.0014	6.74 ± 0.07	6.13 ± 0.10
Error	0.876	280				
Hatching success						
Cuckoo presence	0.449	1	0.15	0.703	5.73 ± 0.24	5.05 ± 0.29
Error	3.064	80				
Brood size at fledging						
Cuckoo presence	6.54	1	2.81	0.096	4.32 ± 0.15	3.33 ± 0.18
Error	2.33	152				
Egg volume (cm^3)						
Cuckoo presence	7.37	1	10.53	0.0013	9.59 ± 0.06	10.00 ± 0.08
Error	0.700	262				

Note: For laying date, 1 = 1 April.

ulations when we controlled statistically for laying date in a nested ANCOVA (Table 2). The mean clutch size of sympatric populations was 10% larger than that of allopatric populations (Table 2). Birds often show a latitudinal increase in clutch size, presumably associated with a more marked seasonal peak in food abundance at higher than at lower latitudes (e.g., Lack 1966). The difference in mean clutch size between sympatric and allopatric Magpie populations was not caused by a latitudinal cline in clutch size, as this relationship was weakly negative and statistically significant (linear regression: $F = 9.54$, df = 1, 379, $r^2 = 0.025$, $P = 0.0021$, slope ±1 SE = −0.157 ± 0.051).

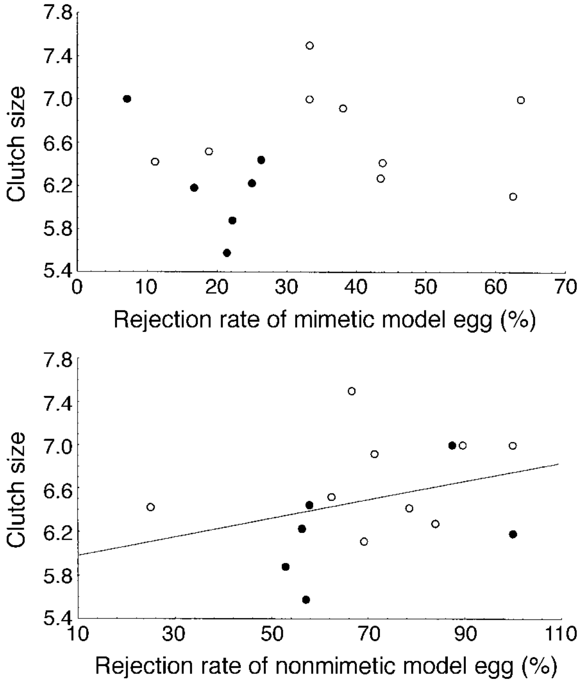

FIG. 2. Mean clutch size in Magpie populations in relation to rejection rate of mimetic and nonmimetic model eggs. Each observation represents the mean value for a population. Open and solid circles represent Magpie populations in sympatry and allopatry, respectively, with the Great Spotted Cuckoo. The regression line for nonmimetic eggs has the equation $y = 5.7 + 0.011x$.

The relationship between clutch size of Magpies and the prevalence of parasitism was highly significant in a spatial autocorrelation analysis while we controlled for differences in latitude (Mantel's test, $r = 0.38$, $r_{\mathrm{std}} = 0.83$, $P = 0.002$), or for genetic distances among populations (Mantel's test, $r = 0.44$, $r_{\mathrm{std}} = 1.00$, $P = 0.001$).

Although parasitism rates in sympatric populations may vary among years (Soler et al. 1998*b*), and thus would not reflect long-term selection pressures on the host imposed by the brood parasite, rejection rates for experimental mimetic cuckoo eggs would be a more appropriate estimate of selection pressures imposed by the cuckoo during the recent past (Soler et al. 1999*a*). On the other hand, rejection rates of nonmimetic cuckoo eggs could be used as an index of genetic similarity because of their association with genetic distances, but not as an index of selection pressures imposed by cuckoos (see *Methods*). For mimetic experimental eggs, we found no significant relationship between clutch size and rejection rate while we controlled for differences in latitude (Fig. 2; Mantel's test, $r = 0.05$, $r_{\mathrm{std}} = 0.10$, $P = 0.37$), or for genetic distances among populations (Mantel's test, $r = 0.18$, $r_{\mathrm{std}} = 0.48$, $P = 0.08$). However, an analysis of rejection of nonmimetic eggs revealed a strongly positive relationship between clutch size and the percentage of eggs rejected while we controlled for differences in latitude (Fig. 2; Mantel's test,

r = 0.40, r_{std} = 0.84, P = 0.003), as well as while controlling for genetic distances among populations (Mantel's test, r = 0.33, r_{std} = 0.79, P = 0.014).

Hatching success of Magpie eggs in unparasitized nests did not differ significantly between sympatric and allopatric populations, when we controlled for laying date, although the average success was slightly higher in sympatric populations (Table 2).

Brood size of unparasitized nests at last nest check was not significantly larger in sympatric than in allopatric Magpie populations when laying date was controlled (Table 2). This result implies that sympatric Magpies do not experience a larger breeding success (i.e., hatching success, brood size) than do allopatric Magpies, although sympatric Magpies lay larger clutches.

Egg volume and parasitism

Mean egg volume per clutch of unparasitized nests varied significantly with cuckoo presence; sympatric populations of Magpies had egg volumes that were, on average, 4% smaller than those of allopatric populations, when we statistically controlled for laying date (Table 2).

The difference in mean egg volume between sympatric and allopatric Magpie populations could have been caused by a latitudinal cline in egg volume, because this relationship was strongly positive and statistically significant (Mantel's test, r = 0.70, r_{std} = 1.00, P = 0.001). Therefore, the relationship between egg volume and parasitism was investigated in a multiple autocorrelation analysis with latitude as the other independent variable; this relationship was nonsignificant (Mantel's test, r = −0.11, r_{std} = −0.23, P = 0.22). A second autocorrelation analysis between egg volume and parasitism rate, while controlling for genetic distances among populations, showed a significant negative correlation (Mantel's test, r = −0.38, r_{std} = −1.00, P = 0.001).

Mean egg volume was significantly negatively related to rejection rate for mimetic model eggs when we controlled for differences in latitude (Fig. 3; Mantel's test, r = −0.71, r_{std} = −1.00, P = 0.001), as well as controlling for genetic distances among populations (Mantel's test, r = −0.84, r_{std} = −1.00, P = 0.001). For nonmimetic model eggs, the relationship between mean egg volume and rejection rate also showed a negative relationship while controlling for differences in latitude among populations (Fig. 3; Mantel's test, r = −0.38, r_{std} = −0.56, P = 0.048). A second autocorrelation analysis between egg volume and rate of rejection for nonmimetic eggs while controlling for genetic distances among populations was also negative (Mantel's test, r = −0.30, r_{std} = −0.62, P = 0.07).

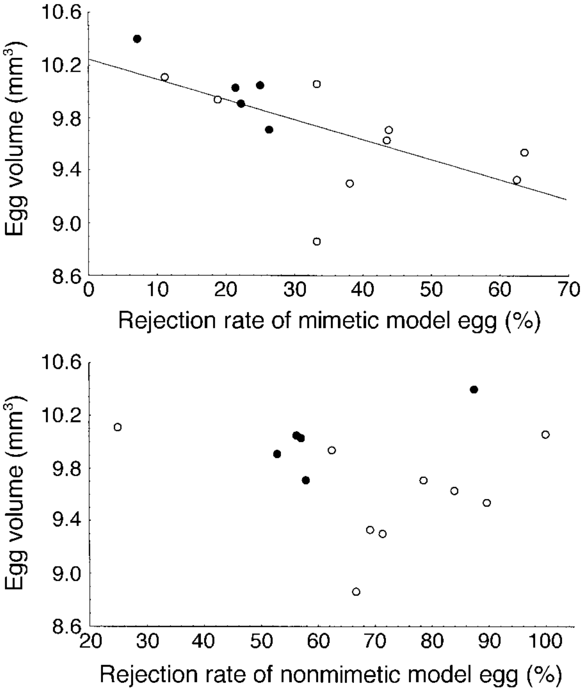

FIG. 3. Mean egg volume (mm^3) in Magpie populations in relation to rejection rate of mimetic and nonmimetic model eggs. Each observation represents the mean value for a population. Open and solid circles represent Magpie populations in sympatry and allopatry, respectively, with the Great Spotted Cuckoo. The regression line for mimetic model eggs has the equation $y = 10.25 - 0.016x$.

DISCUSSION

The analysis of clutch size and breeding success of parasitized Magpies revealed a positive relationship between these two variables; Magpies laying large clutches thus suffer less from parasitism than those with small clutches. Soler and colleagues (Soler 1990, Soler et al. 1996, 1997, 1998*a*) detected that the main damage caused by cuckoos was egg destruction during egg laying (in parasitized nests, 1.3 Magpie eggs hatched, in unparasitized nests, 5.0 Magpie eggs hatched; Soler et al. 1996), rather than competition with the cuckoo chick (in parasitized nests, 0.7 Magpie chicks died; in unparasitized nests, 1.5 chicks died; Soler et al. 1996). Thus, Magpies could reduce the negative effects of parasitism by increasing clutch size. That would be the case if clutch size did not affect the number of Magpie eggs destroyed by the adult cuckoo when laying, as demonstrated by data from parasitized Magpies (1982–1999, the Guadix population, r = 0.09, N = 288, P = 0.14). Therefore, based on the hypothesis that brood parasitism affects host life history, we can make clear predictions that clutch size will increase in areas sympatric with the Great Spotted Cuckoo. Moreover, a trade-off between clutch size and egg size in Magpies (Clarkson 1984, Birkhead 1991), predicts a reduction in egg volume in Magpie populations sympatric with the Great Spotted Cuckoo.

Supporting the hypothesis, analyses of the relationship between Great Spotted Cuckoo parasitism and life-history characters of its Magpie host revealed adjustments in clutch size and egg size in areas of sympatry. Sympatric Magpie populations had significantly larger clutch sizes (Prediction 1) and smaller eggs (Prediction 2) than did allopatric populations (Table 2). These patterns were repeated in analyses of the relationship between the degree of cuckoo parasitism and Magpie clutch size and egg volume, respectively (Prediction 3). A correlational analysis such as the present one cannot be used to make inferences about causation. However, because the Magpie has a Holarctic distribution, with its main range in the temperate zone of Eurasia (Birkhead 1991), it seems likely that it has come into contact with the Great Spotted Cuckoo only relatively recently. This interpretation is also supported by fossil records of 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 (see Soler et al. 1999*a*). Hence, it seems likely that Magpie populations sympatric with the Great Spotted Cuckoo have adapted their life-history and reproductive parameters to the selection pressures imposed by the brood parasite. It seems less likely that the cuckoo has been restricted to exploiting Magpie populations with particular reproductive characteristics.

The phenotypic correlations between reproductive parameters of Magpies and parasitism by the Great Spotted Cuckoo could be of entirely phenotypic or genetic origin. We will discuss these two possibilities in turn. Laying date, clutch size, and egg size are all known to have a quantitative genetic basis in birds (reviewed in Boag and van Noordwijk 1987). Given the strong selection pressures imposed by Great Spotted Cuckoos on their hosts, these reproductive parameters should be able to change rapidly. Obviously, the simplest interpretation is that the correlations have an entirely phenotypic basis. The only way in which we can distinguish between genetic and environmental effects is through the lack of concordance of the effects of geographical and genetic distances between Magpie populations in spatial autocorrelations (Soler et al. 1999*a*). A spatial autocorrelation analysis that controls for differences in latitude will remove many of the environmental factors that cause phenotypic differences, whereas a spatial autocorrelation analysis that controls for genetic distances between host populations will remove genetic effects.

Although the parasitism rate and the rejection rate for mimetic eggs probably reflect the effects of current selection pressures, the rejection rate for nonmimetic eggs does not (Soler et al. 1999*a*). This interpretation is supported by a strongly positive autocorrelation between the rejection rate for nonmimetic eggs (but not mimetic eggs) and genetic distance; the opposite pattern was found for geographic distance (Soler et al. 1999*a*). The spatial autocorrelation between the rejection rate for mimetic and nonmimetic model eggs was significant and weakly positive at $r = 0.33$ (Soler et al. 1999*a*), as was the spatial autocorrelation between the rates of parasitism and rejection of mimetic eggs ($r = 0.28$). However, the correlation was much stronger for parasitism and rejection of nonmimetic eggs ($r = 0.60$; J. J. Soler, J. G. Martínez, M. Soler, and A. P. Møller, *unpublished data*). We found statistically significant positive autocorrelations between Magpie clutch size and the rates of both parasitism and rejection of nonmimetic model eggs. The similarity of the sign and magnitude of these correlations suggests that both environmental and genetic factors contribute equally to the response of Magpies to parasitism by the Great Spotted Cuckoo.

Results of the autocorrelation analyses were different for egg volume. There was a significant negative relationship between egg volume and rate of parasitism only in the analysis controlling for genetic distance, not in the analysis controlling for latitudinal differences. Analyses based on rejection rates for both mimetic and nonmimetic model eggs revealed consistent negative correlations for both. We interpret these results as implying that there is a phenotypic, but not an evolutionary, response in egg volume to current selection pressures imposed by the Great Spotted Cuckoo, as evidenced from correlations with the rate of parasitism. Furthermore, there is a phenotypic and evolutionary response in egg volume to past selection pressures imposed by the parasite, as evidenced from negative correlations with rejection rates for the two kinds of model eggs.

Analyses of Magpie life-history and reproductive variables in different populations were based on a sample of nests after excluding of cases of parasitism. This procedure could potentially cause a bias. However, Great Spotted Cuckoos are known to prefer Magpie hosts with large nests, and nest size of Magpies is related to laying date and clutch size (Soler et al. 1995, 2001). Thus, elimination of parasitized nests will result in the exclusion of early and large clutches of sympatric populations from the analyses. In other words, the significant differences in reproductive parameters between sympatric and allopatric populations of Magpies reported here are conservative because inclusion of early, large clutches (which are preferentially parasitized by the Great Spotted Cuckoo) would result in an even larger difference than that reported in Table 2. We found no indication that mean egg volume was significantly related to laying date in the present study, or in previous studies of Magpies in Guadix, southern Spain (J. J. Soler, M. Soler, and J. G. Martínez, *unpublished data*). However, even if such a relationship had existed, this would have been partially controlled by the nested ANCOVA with laying date as a covariate. Thus, the conclusions for egg volume could not be confounded by a bias caused by Great Spotted Cuckoos selecting early-breeding hosts with large nests.

In conclusion, the brood parasitic Great Spotted Cuckoo has affected the evolution of life-history characters of its Magpie host, as evidenced by differences between sympatric and allopatric populations. These differences are consistent with hypotheses concerning the effect of parasitism on optimal host life history.

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