

Change in host rejection behavior mediated by the predatory behavior of its brood parasite

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Passerine hosts of parasitic cuckoos usually vary in their ability to discriminate and reject cuckoo eggs. Costs of discrimination and rejection errors have been invoked to explain the maintenance of this within-population variability. Recently, enforcement of acceptance by parasites has been identified as a rejection cost in the magpie (*Pica pica*) and its brood parasite, the great spotted cuckoo (*Clamator glandarius*). Previous experimental work has shown that rejecter magpies suffer from increased nest predation by the great spotted cuckoo. Cuckoo predatory behavior is supposed to confer a selective advantage to the parasite because magpies experiencing a reproductive failure may provide a second opportunity for the cuckoo to parasitize a replacement clutch. This hypothesis implicitly assumes that magpies modulate their propensity to reject parasite eggs as a function of previous experience. We tested this hypothesis in a magpie population breeding in study plots varying in parasitism rate. Magpie pairs that were experimentally parasitized and had their nests depredated, after their rejection behavior had been assessed, changed their behavior from rejection to acceptance. The change in host behavior was prominent in study plots with high levels of parasitism, but not in plots with rare or no cuckoo parasitism. We discuss three possible explanations for these differences, concluding that in study plots with a high density of cuckoos, the probability for a rejecter magpie nest of being revisited and depredated by a cuckoo is high, particularly for replacement clutches, and, therefore, the cost for magpies of rejecting a cuckoo egg in a replacement clutch is increased. Moreover, in areas with high levels of host defense (low parasitism rate), the probability of parasitism and predation of rejecter-magpie nests by the cuckoo is reduced in both first and replacement clutches. Therefore, rejecter magpies in such areas should not change their rejection behavior in replacement clutches. *Key words*: brood parasitism, *Clamator glandarius*, cuckoos, evolution, host defense, magpies, mafia behavior, *Pica pica*. [*Behav Ecol* 10:275–280 (1999)]

Brood parasites, such as cuckoos and cowbirds, lay their eggs in the nests of another species (the host), which incubates and rears their offspring (Rothstein, 1990). This reproductive strategy can be extremely costly for foster parents, because the reproductive success of parasitized hosts is dramatically reduced, and in most cases (depending on parasite and host species) is nil (Rothstein, 1990). Therefore, brood parasites exert strong selection pressures on their hosts. As a consequence of these selection pressures, some passerine species that are parasitized by brood parasites have evolved defense mechanisms such as egg recognition and rejection (Davies and Brooke, 1989a,b; Moksnes et al., 1991). The appearance of host discrimination toward alien eggs has subsequently selected for the evolution of host-egg mimicry by the brood parasite (Brooke and Davies, 1988; Gibbs et al., 1996), which may give rise to an evolutionary arms race between the two species (Dawkins and Krebs, 1979).

Given that brood parasites dramatically reduce host reproductive success, why do hosts still accept cuckoo eggs and nestlings? At least two possible answers to this question exist. First, the maintenance of a polymorphism among hosts with respect to rejection of parasitic eggs can be explained if hosts have not yet evolved the ability to discriminate against parasitic eggs (the evolutionary lag hypothesis; Brooke and Davies, 1988). Second, a within-population polymorphism in rejection behavior could be maintained if ejector hosts suffer costs of rejection. For instance, discriminating hosts may make mistakes and instead of ejecting the parasite egg, eject their own eggs (Davies et al., 1996; Lotem et al., 1995; Marchetti, 1992; Pal-

omino et al., 1998). Parasites may themselves impose a cost on ejector hosts. Zahavi (1979) suggested that brood parasites could act as nest predators against hosts that reject parasitism (a “mafia” hypothesis). In this case the advantage for discriminating hosts is reduced or disappears completely because the reproductive success of acceptors eventually may exceed that of ejectors (Soler et al., 1995). This nest predatory behavior could thus prevent the fixation of rejection behavior in a host population. Moreover, predator cuckoos could directly benefit from their behavior because (1) ejector hosts that failed to breed later would lay a replacement clutch and thus offer a second opportunity to the brood parasite (Arcese et al., 1996), and (2) ejector hosts may learn that it is not beneficial to remove cuckoo eggs from their nests during the first breeding attempt, and they may subsequently change their response to cuckoo eggs in replacement clutches and become acceptors (Soler et al., 1995), thereby increasing the probability of success of cuckoo eggs.

Apart from anecdotal reports of brood parasites acting as nest predators (Alvarez, 1994; Bibby and Thomas, 1985; Davies and Brooke, 1988; Palomino et al., 1998; Vincent, 1933; Wyllie, 1981), only one study has experimentally shown that cuckoos may be responsible for a significant amount of nest predation on hosts. Soler et al. (1995) studied the relationship between the great spotted cuckoo (*Clamator glandarius*) and its magpie (*Pica pica*) host in southern Spain, where ejector magpies suffered from considerably higher levels of nest predation by cuckoos than acceptors. Because most host pairs that failed in their first reproductive attempt laid a replacement clutch, cuckoos could benefit from this second attempt if such hosts learned from their previous experience and therefore were more prone to accept the cuckoo egg during a subsequent breeding attempt.

In this study we experimentally tested whether the rejection

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behavior of individual hosts changed within a breeding season depending on nest predation after rejection of a cuckoo egg. However, any change in rejection behavior of hosts may not only depend on nest predation after ejection of the cuckoo egg from the nest (which can be experimentally manipulated), but also on the selection pressures exerted by the brood parasite on the host population (parasitism rate). Therefore, we repeated the cuckoo egg rejection experiment in different plots of the same magpie population: one with a low parasitism rate (level of parasitism < 10%) and others suffering from intense parasitism (>50%) during the last 4 years.

MATERIALS AND METHODS

The study was conducted during April–May 1996–1997 in the high altitude plateau Hoya de Guadix (37°18' N, 3°11' W), southern Spain. During 1996 we made the experiment in the Calahorra plot, where no magpie nest checked during that breeding season was parasitized. In this plot, parasitism rate has decreased from around 55% in 1992 to 0% in 1996 (Soler et al., 1998b). During 1997 we performed the experiment in five other plots (Fuente Alamo, Huéneja, Carretera, Ferreira, and Dólar) where great spotted cuckoos are common and parasitism rate during the last 4 years has exceeded 50%. Distances from Calahorra to the other plots varied between 5 and 15 km. A detailed description of the study plots and their levels of parasitism during the last 10 years can be found in Soler et al. (1998a).

Species characteristics

Magpies lay one clutch during the breeding season, but in the case of predation during laying or the incubation period, magpies are able to lay a replacement clutch (Birkhead, 1991). However, when a replacement clutch is depredated during the incubation period, the probability of laying a new replacement clutch is almost nil, but depends on date and magpie quality (Birkhead, 1991). On the other hand, great spotted cuckoos parasitize magpies by laying one or more eggs in a magpie nest. Moreover, predatory behavior has been detected in the great spotted cuckoo, and when magpies recognize and reject cuckoo egg from the nest, the probability of having their nest depredated greatly increases (Soler et al., 1995). Therefore, if a magpie ejects a cuckoo egg during the first breeding attempt and suffers depredation from the great spotted cuckoo, it has the opportunity to lay a replacement clutch which might not be parasitized. But when a magpie has a parasitized replacement clutch, which implies no further opportunity to lay additional replacement clutches in the case of depredation, it is predicted by the mafia hypothesis that the magpie should not eject a cuckoo egg (even in the case of recognition) and should try to rear some of its offspring together with the cuckoo chicks (Soler et al., 1995). This is the reason why recognizer magpies should eject cuckoo eggs from a first clutch, but not from the replacement clutch (Soler et al., 1995).

Experimental design

At the beginning of April we searched systematically for magpie nests. The location of each nest was indicated on an aerial photograph. We regularly revisited the nests, and when the nest contained at least one egg we added a mimetic cuckoo model egg. Previous experiments have shown that the rejection probability does not depend on the timing of model egg introduction during the egg-laying sequence (J. Soler et al., unpublished data). Model eggs were made by filling molds of great spotted cuckoo eggs with plaster of Paris. Once dry, the

model was removed from the mold and, using a water-based paint (Acualux, Industrias TITAN, S.A.), it was painted with a color similar to the background of great spotted cuckoo eggs. Subsequently, we added brown spots with a distribution and size resembling those of cuckoo eggs. Finally, the model egg was covered with a thin layer of lacquer (Sintex S-19, Quilosa, Industrias químicas Lowenberg, S.A.), which simulates the sheen of real cuckoo eggs. Moreover, the mass of model eggs was similar to the mass of real cuckoo eggs (see Soler and Møller, 1990). Between 3 and 5 days later (sufficient time to record all rejection; Soler and Møller, 1990), we revisited the nests and scored the magpies as “accepters” if the mimetic model was still in the nest, or as “rejecters” if the model egg was no longer present or if the eggs were abandoned in the nest (only one case in the present study).

After scoring the magpies as accepters or rejecters, we simulated cuckoo predation behavior in most of the magpie nests by breaking the eggs and leaving them in the nest (magpie eggs depredated by cuckoos are also left damaged in the nest). In areas with a high parasitism rate we mainly depredated nests without great spotted cuckoo eggs (3 parasitized nests out of 40 depredated nests), thereby attempting to avoid problems of interference between our experiments and real cuckoo parasitism; however, during the first breeding attempt we used parasitized and nonparasitized nests to test for magpie rejection behavior. Because the probability of making a replacement clutch decreases as the season progresses (Birkhead, 1991), we decided to depredate the last nests on 5 May, which is close to the mean laying date of magpies in the study area (Soler et al., 1995). A total of 61 and 20 experimental nests were depredated during 1996 and 1997, respectively. Moreover, during 1997, we found eight replacement clutches of nests that were naturally depredated during the first clutch; we knew the rejection behavior of magpies of five of those nests, and the replacement clutches were found, and a second recognition test of all these eight nests was performed.

About 1 week after depredating the nests, we started to look for replacement clutches. Although magpies were not individually marked, we could determine the owners of all replacement clutches because the new nests were always in the proximity of the first nests (maximum distance between first and repeat clutch nests = 80 m), and always at a shorter distance than the closest first-clutch nests (minimum distance between nearest neighboring first-clutch nests = 100 m; see also Birkhead, 1991; Soler et al., 1995). Studies of color-banded populations of magpies have demonstrated that replacement nests are built much closer to first-clutch nests than to neighboring nests (Birkhead, 1991). Moreover, some pairs used the same nest or built a new nest on the top of the previous one. As for the first clutches, we added a mimetic model egg in the replacement nests and scored the magpies as accepters or rejecters (no nest was scored as being abandoned).

To control for the possibility that rejection rate decreases during the season independently of cuckoo predation, we depredated 13 additional first-clutch nests without adding a model egg during 1996 and 11 during 1997. We also used rejection rate of magpie nests that were not depredated after recognition tests (reference nests). Figure 1 shows the experimental design and the number of nest used.

Statistical tests

Frequencies were compared using a chi-square test (when all frequencies in the contingency table were >5) and Fisher's Exact tests (when at least one frequency in the contingency table was <5), and significance tests of the change from rejection to acceptance were based on sign tests. All statistical tests were two-tailed at a significance level of 5%.

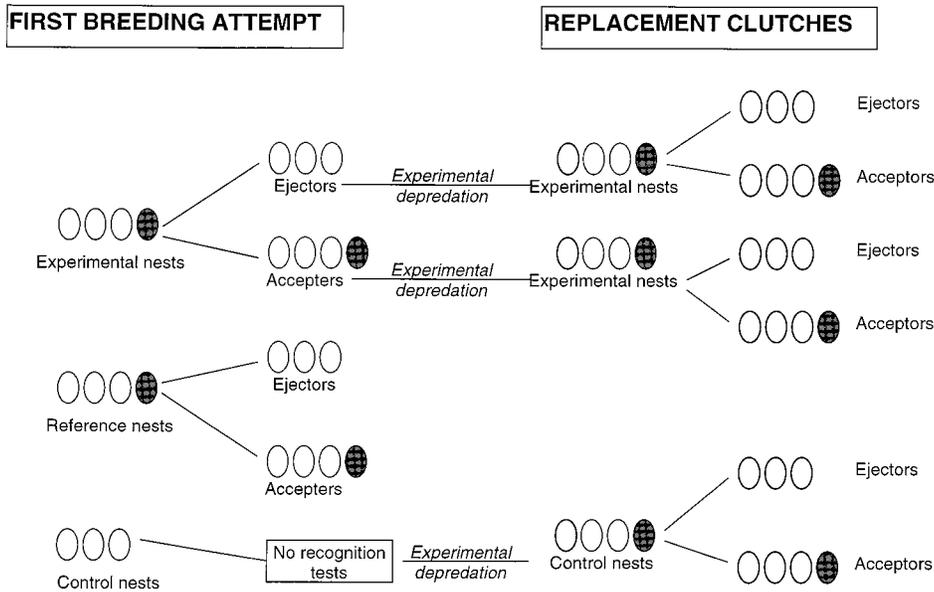


Figure 1
Experimental design of the study. Dark eggs represent experimental model eggs, and white eggs represent magpie eggs. The number of each kind of nest is also indicated.

RESULTS

Parasitism rates

The overall parasitism rate in the study area was 34.2% ($n = 295$), and there was no overall statistical differences between first and replacement clutches (Table 1; $\chi^2 = 0.15$, $df = 1$, $p = .70$). However, we did not observe any natural parasitism in the Calahorra plot during 1996. Parasitism rates were not significantly different among study plots in 1997 (Table 1; $\chi^2 = 4.48$, $df = 4$, $p = .35$), and we therefore pooled all data from 1997. Fifty-three percent of first clutches were parasitized ($n = 141$) in these plots. Some nests checked during 1997

suffered from natural or experimental predation, and magpies subsequently laid replacement clutches (see Table 1 for the number of replacement clutches found in different plots).

Rejection rates

We found that 46.0% ($n = 124$) of the magpie pairs rejected the model egg from the nest during first clutches. In the replacement clutches the rejection rate of control nests was 65.0% ($n = 20$), whereas it was 32.7% ($n = 52$) in experimental nests, with the difference between control and experimental nests reaching statistical significance (Figure 2; $\chi^2 =$

Table 1
Parasitism rate of parasitized and nonparasitized magpie nests in study plots during 1996–1997

Study plots	Year	Clutch	Parasitized nests (%)	Nonparasitized nests (%)	Total nests	Experimentally depredated nests ^a
Calahorra	1996	First	0 (0)	74 (100)	74	74 (43)
		Replacement	0 (0)	43 (100)	43	
		Total	0 (0)	117 (100)		
Fuente Alamo	1997	First	5 (33.3)	10 (66.7)	15	5 (5)
		Replacement	6 (85.7)	1 (14.3)	7	
		Total	11 (50.0)	11 (50.0)	22	
Huéneja	1997	First	15 (71.4)	6 (28.6)	21	3 (3)
		Replacement	5 (83.3)	1 (16.7)	6	
		Total	20 (74.1)	7 (25.9)	27	
Carretera	1997	First	26 (50.0)	26 (50.0)	52	15 (14)
		Replacement	10 (58.8)	7 (41.2)	17	
		Total	36 (52.2)	33 (47.8)	69	
Ferreira	1997	First	22 (59.5)	15 (40.5)	37	8 (4)
		Replacement	2 (50.0)	2 (50.0)	4	
		Total	24 (58.5)	17 (41.5)	41	
Dolar	1997	First	7 (43.8)	9 (56.2)	16	9 (3)
		Replacement	3 (100)	0 (0)	3	
		Total	10 (52.6)	9 (48.4)	19	
Total	1997	First	75 (53.2)	66 (46.8)	141	40 (29)
		Replacement	25 (69.4)	11 (30.6)	36	
		Total	100 (56.5)	77 (43.5)	177	

^a The number of experimentally depredated nests in each study plot is shown as well as the number of replacement clutches that were tested for egg rejection (in parentheses).

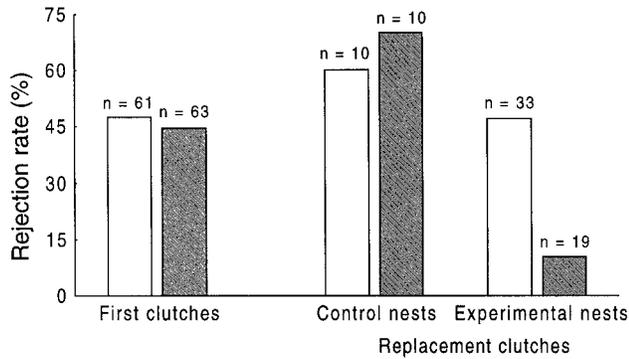


Figure 2

Rejection rate of first and replacement magpie clutches (control, nests where we did not introduce a model cuckoo egg before predation; experimental, nests where we added a model cuckoo egg before predation) in study plots with a low (open bars) and a high parasitism rate (shaded bars).

6.20, $df = 1$, $p = .013$). Differences in rejection rate between first and replacement clutches (only control nests) were not significant (Figure 2, $\chi^2 = 2.50$, $df = 1$, $p = .11$), indicating that the rejection rate did not decrease during the season. Moreover, among 28 rejecter-magpie pairs in the first clutch, 12 changed to become accepters in the replacement clutch, whereas among 25 acceptor-magpie pairs in the first clutch, only 1 changed to become a rejecter in the replacement clutch. Thus, the change from ejection to acceptance was statistically significant in replacement clutches (sign test, number of changes = 13, percentage of change from rejection to acceptance = 92.3%, $z = 2.77$, $p = .005$). These results, which are in accordance to the mafia hypothesis (Soler et al., 1995), indicate that rejecter magpies learn to accept cuckoo eggs in replacement clutches when the first clutch has been depredated after rejection of a cuckoo egg and when there is not another opportunity to breed in the season.

However, when comparing plots with a low parasitism rate (Calahorra; Table 1) with other plots with a high parasitism rate (the remaining plots in the area; Table 1), the results of the experiment were quite different. In Calahorra, where magpies did not suffer from parasitism, the rejection rate in first clutches was 47.5% ($n = 61$; Figure 2). We found 43 replacement clutches, and the rejection rate of magpie pairs that did not encounter the model egg in the first clutch (control nests) was 60% ($n = 10$; Figure 2), not statistically different from the rejection rate during the first attempt (Fisher's Exact test, $p = .51$). Of the pairs that were tested for rejection behavior in their first clutches (experimental nests), 90.9% ($n = 33$) expressed the same behavior in the replacement clutches. All pairs that accepted the model egg in the first clutch also accepted it in the replacement attempt ($n = 15$), and only 3 of 18 pairs that ejected the model egg in the first attempt accepted it in the replacement clutch, with the difference in change from rejection to acceptance not being statistically significant (sign test, number of changes = 3, percentage of change from rejection to acceptance = 100%, $z = 1.15$, $p = .25$).

In plots with a high parasitism rate (> 50%), the rejection rate of first clutches was 44.4% ($n = 63$), and we found no significant difference between the rejection rate of experimental (depredated) and nonexperimental magpie nests (experimentally depredated: rejection rate = 50%, $n = 20$; not experimentally depredated: rejection rate = 41.9%, $n = 43$; $\chi^2 = 0.37$, $df = 1$, $p = .55$). We located 29 replacement clutches (control nests = 10; experimental nests = 19), and the rejection rate in replacement clutches of those pairs that did

not encounter the model egg in the first clutch (control nests) was 70% ($n = 10$; Figure 2), which was not statistically different from the rejection rate of the first attempt (Fisher's Exact test, $p = .49$). However, when analyzing experimental magpie nests, the rejection rate in replacement clutches decreased significantly (Fisher's Exact test, $p = .0012$; Figure 2). Moreover, the difference between control and experimental nests was also significant (Fisher's Exact test, $p = .002$; Figure 2), with a lower rejection rate among magpie pairs experimentally parasitized in the first clutch with a model cuckoo egg (Figure 2). Nine of the ten rejecter magpie pairs in the first breeding attempt changed their behavior during their replacement clutch, whereas only one of the nine acceptor magpies changed to reject in the replacement clutches (sign test, number of changes = 10, percentage of change from rejection to acceptance = 90%, $z = 2.21$, $p = .027$).

Finally, we investigated differences in rejection rate between plots suffering and not suffering from brood parasitism and found a nonsignificant difference in the rejection behavior during the first breeding attempt between rarely and intensely parasitized study plots ($\chi^2 = 0.12$, $df = 1$, $p = .73$, Figure 2). When analyzing the rejection behavior in the replacement clutches, we found no significant differences between control nests in plots suffering from parasitism and control nests from the area with no parasitism (Fisher's Exact test, $p = .50$; Figure 2). However, when considering experimental nests, rejection rate in replacement clutches was significantly lower in plots with a high parasitism rate than in the plot not suffering from parasitism (Fisher's Exact test, $p = .014$; Figure 2). Moreover, whereas only 3 of the 18 ejector magpie pairs changed to accept the model egg in areas not suffering from parasitism, 90% of the pairs changed their behavior in areas with a high parasitism rate (Fisher's Exact test, $p = .0003$). Therefore, the change in magpie rejection behavior related to the experimental manipulation was dramatic in areas suffering from a high rate of natural parasitism.

Naturally occurring mafia behavior by cuckoos during 1997

We found eight depredated magpie nests with eggs, possibly by the great spotted cuckoo, as corvid nest predators always remove eggs and nestlings from depredated nests. Five of the eight nests were tested for rejection behavior before natural predation using model eggs, the ejection rate being 60% ($n = 5$). In three of these eight first clutches, we detected one or more cuckoo eggs (parasitism rate = 37.5%). During the replacement clutch, seven of the eight nests were parasitized and only one of those parasitized pairs removed both the cuckoo and the model eggs. This latter nest was again depredated, probably by the great spotted cuckoo. All these eight replacement clutches were tested for rejection behavior, and all three nests, where the owners ejected the cuckoo model egg during the first breeding attempt, subsequently became acceptors. The overall rejection rate was 0.13 ($n = 8$), not significantly different from the rejection behavior during the first breeding attempt (Fisher's Exact test, $p = .10$). Therefore, the results from our experiments were similar to these possible cases of natural cuckoo mafia behavior.

DISCUSSION

We found a significant change from rejection of model cuckoo eggs in first clutches that were subsequently depredated to acceptance in replacement clutches in our study of the magpie, the main host of the great spotted cuckoo. Moreover, magpie pairs that were not experimentally parasitized, but still had their first-clutch nest depredated (control nests), showed a rejection rate similar to that of the overall population during

the first breeding attempt. These results show a direct benefit for cuckoos that act as predators against magpies that reject cuckoo eggs. Because a great spotted cuckoo female can lay eggs for a period of approximately 44 days (in our study area; Martínez et al., 1998) or more (10 weeks; Payne, 1973, 1974), individual cuckoos will benefit from their own predatory behavior. As the mafia model assumes (Soler et al., 1995), many magpie pairs that had their first-clutch nests depredated laid a replacement clutch, thereby increasing the availability of host nests for cuckoos and, more importantly, rejecter magpies during their first breeding attempt subsequently became accepters in replacement clutches. A rejecter magpie during the replacement clutch will probably suffer from predation by cuckoos, and there will be no further opportunity to lay additional replacement clutches. Therefore, as predicted by the mafia hypothesis, magpies should not eject a cuckoo egg from replacement clutches (even in the case of recognition) and should try to rear some of their offspring together with the cuckoo chicks (Soler et al., 1995).

We found differences in parasitism rate among plots due to the difference between Calahorra and the remaining plots. When we analyzed the effect of experimental nest predation in these two different kinds of plots, we found that rejecter magpies in the first breeding attempt changed more frequently to acceptance in the replacement clutch in plots with a high parasitism rate. At least three not mutually exclusive explanations may account for why the change from rejection to acceptance mainly occurred in plots with a high parasitism rate:

1. A change in rejection behavior of magpies may depend on the presence of cuckoos. Rejecter magpies may require auditory or visual cues of great spotted cuckoos close to their nests before changing their behavior to acceptance of cuckoo eggs in replacement clutches. However, we can partially reject this possibility because in study plots with a high parasitism rate the rejection rate of replacement clutches of pairs that had their first clutch depredated without presentation of a model egg did not differ from the overall rejection rate in first clutches (see Results). However, the presence of both a model cuckoo egg in a magpie nest and a cuckoo around the nest may be required to provoke a change in the behavior of magpies from rejection to acceptance.
2. The cost of cuckoo mafia behavior for a rejecter magpie depends on the probability that a magpie nest is revisited, which may depend on the structure of cuckoo populations. In study plots where the great spotted cuckoo is abundant, parasitism rate is high, magpie nests often contain several cuckoo eggs laid by different females, and several cuckoos may be reared in a single host nest (Martínez et al., 1998; Soler, 1990; Soler et al., 1994; Zuñiga and Redondo, 1991). If more than one cuckoo female parasitizes the same nest, the probability that the nest of a rejecter magpie pair is revisited and depredated by a cuckoo after ejection is increased. Therefore, the cost of mafia behavior by cuckoos is higher in areas with a high parasitism rate than in areas with a low rate, and this difference could account for the different responses of magpies to the mafia experiment. Mafia behavior is also costly for cuckoos that are forced to repeatedly revisit all parasitized host nests (Soler et al., 1995) because this activity requires time and energy. However, the small number of replacement clutches compared to first clutches reduces this cost considerably for the cuckoo. Therefore, the probability that the nest of a rejecter magpie is revisited and depredated by a cuckoo is considerably greater for replacement clutches than for first clutches, and this may enforce magpies to accept the cuckoo egg in a replacement clutch. If the probability of a rejecter magpie being depredated by the cuckoo is high for the nest (as is presumably the case for replacement clutches), a magpie would maximize its own reproductive success by accepting the cuckoo egg in replacement clutches because in the case of depredation magpies are unable to lay an additional replacement clutch (Soler et al., 1995).
3. Magpies confronted with a “mafia” cuckoo may pay a cost of recognizing and ejecting cuckoo eggs because of possible recognition errors (Davies et al., 1996; Marchetti, 1992) and depredation of their nests (Soler et al., 1995). However, the probability of magpies suffering from these costs depends on the level of individual defense mechanisms, such as egg rejection, the distance to the nearest neighboring nests, and the degree of laying synchrony with other magpies. A magpie nest in a high-density plot with a laying date similar to that of most nests in the area has a reduced risk of being parasitized by the great spotted cuckoo (Martínez et al., 1996) and, therefore, also of being depredated due to the mafia mechanism. Even parasitized nests may have a reduced risk of suffering from nest predation by cuckoos in a synchronously breeding magpie population because the same defense mechanisms that prevent cuckoos from parasitizing magpie nests will also efficiently prevent cuckoos from revisiting an already parasitized magpie nest. In other words, the cost for magpies of cuckoo mafia behavior is smaller in plots with a high level of defense (low parasitism rate) than in plots with low density and asynchronously breeding magpie populations. Calahorra is the study plot with the highest level of defense (a high density of magpie nests and a high degree of laying synchrony; Martínez et al., 1996), and the costs of cuckoo mafia behavior are thus minimal. Therefore, magpies breeding in this plot should generally not change their ejection behavior in replacement clutches, as observed.

Alternatively, other ecological factors such as habitat quality and food availability may interact with host behavior in determining rejection rates. However, the most apparent difference between Calahorra and the other study plots was the parasitism rate (and cuckoo density). Thus, we believe that differences in parasitism rate are the most likely explanation for differences in rejection rate of model cuckoo eggs added to replacement clutches in Calahorra and the other study plots.

Learning processes are important determinants of animal behavior. It has been suggested that, although rejection behavior is assumed to be innate, it can be modulated by learning, which minimizes the risk of making mistakes (e.g., Lotem, 1993; Lotem et al., 1991). Our results clearly show that the egg recognition ability of magpies can be modulated by a learning process in plots with a high parasitism rate. Moreover, magpies should assess risk of parasitism every season, and this learning should be temporary. As far as we know, this is the first experimental study demonstrating that host rejection behavior, mediated by mafia cuckoo behavior, can change during the same breeding season from ejection to acceptance, as predicted by Soler et al. (1995).

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